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Suspended sediment and its effects on the behavior and physiology of coral reef fishes

Thesis submitted by
Amelia Scher Wenger
(BA, GDipResMeth)
in July 2013

For the degree of Doctor of Philosophy
in the School of Marine and Tropical Biology
James Cook University

STATEMENT OF CONTRIBUTION OF OTHERS

This work is the result of collaborations with my supervisors Prof. Geoffrey Jones, Prof. Mark McCormick, and Dr. Frederieke Kroon, who provided intellectual and editorial guidance throughout the project. In addition, Geoff Endo and Ian McLeod provided assistance with experimental setup and trials in Chapters 2 and 6. Dr. Jacob Johansen provided assistance with experimental setup and trials in Chapters 3 and 5. Research funding was provided the Australian Research Council, James Cook University, the ARC Centre of Excellence, the Australian Coral Reef Society, and the Great Barrier Reef Marine Park Authority. I received a stipend through the Postgraduate Research Scholarship from James Cook University and a CSIRO Flagship Scholarship.

DECLARATION OF ETHICS

This research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council (NHMRC) Australian Code of Practice for the Care and Use of Animals for Scientific Purposes, 7th Edition, 2004 and the Qld Animal Care and Protection Act, 2001. The proposed research study received animal ethics approval from the JCU Animal Ethics Committee Approval Numbers 1452, 1523, 1619, and 1713.

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GENERAL ABSTRACT

Urbanization and increased agricultural activities are causing long-term changes to many of the key physical characteristics in coastal aquatic environments through increased sediment and nutrient loading, elevated turbidity and reduced light penetration. Inshore coral reef habitats and their associated species are vulnerable to sediment loading, which has been responsible for habitat degradation and a reduction in biodiversity of corals. Many coral reef fish species depend on live coral for habitat at some stage of their life history and declines in the abundance and diversity of coral reef fishes have been linked to an indirect effect of habitat loss. Direct effects of suspended sediment on coral reef fishes may compound the indirect effects of habitat loss, leading to further changes in population dynamics. Importantly, early life history stages of coral reef fishes may be particularly vulnerable as the small scale ecological processes during early growth and development happen on short time scales. A quantitative evaluation of the direct interaction between sediment and coral reef fishes is crucial to increase our understanding of how changing water quality directly affects coral reef fishes. The overall aim of this project was to provide a comprehensive assessment of the direct effects of suspended sediment on early life history stages of coral reef fishes. This research was conducted experimentally in aquaria, using a suite of planktivorous coral reef damselfish species and one predator species, all commonly found associated with live coral, including in areas that are exposed to riverine flood plumes with sediment. All suspended sediment concentrations used have been consistently recorded on near-shore reefs.

The first critical stage of development post-hatching is larval development, during which time foraging efficiency and rapid growth are key factors in survivorship. Correlative studies suggest that suspended sediment may affect coral reef fishes, however, whether it could alter

recruitment patterns in areas prone to high suspended by impacting larval development is unknown. Chapter two investigated the effects of suspended sediment on larval development of *Amphiprion percula*. The fish in the no-sediment control experienced a median pelagic larval duration of 11 days, compared to 12 days for the sediment treatments. Fish in suspended sediment showed increased variation in time to metamorphosis, with 76% of the fish in the control settling by day 11, compared to only 40-46% in the sediment treatments, with some individuals extending their larval phase by 100%. Length and weight of fish in the low sediment treatment were significantly larger compared to the control, medium and high sediment treatments at settlement, suggesting an effect of sediment on foraging ability. The altered developmental patterns caused by suspended sediment on coral reef fish larvae may be one of the key mechanisms behind distribution patterns seen across tropical continental shelves, from inner to outer reefs.

Another potential driver of fish distributions from inner to outer reefs could be an impairment in the ability to successfully choose optimal habitat, which would reduce successful recruitment and survivorship. Chapter three tested the hypothesis that sediment-enriched water impairs the ability of *Pomacentrus amboinensis* and *Pomacentrus moluccensis* to find suitable settlement sites. In a clear water environment (no suspended sediment), pre-settlement individuals exhibited a strong preference for live coral over partially dead and dead coral, choosing live coral 70 and 80% of the time, respectively. However, when exposed to suspended sediment, no habitat choice was observed, with each habitat type being selected in equal frequency. An examination of chemosensory discrimination in sediment-enriched water showed that sediment also disrupts the ability of *P. moluccensis* to respond to chemical cues from

different substrata. A reduction in settlement success in conjunction with altered developmental patterns could reduce cohort strength during turbid conditions.

Chapter four expanded on chapter three by investigating the sediment thresholds for the behavioral changes that were observed in *P. moluccensis*. This chapter also examined post-settlement migration and home range movement in different concentrations of suspended sediment. The results elucidated that a clear threshold for habitat selection and home range movement existed, beyond which the fish were settling to, and remaining on sub-optimal habitat. A review of the literature highlighted that *P. moluccensis* could experience sub-optimal conditions between 8 and 53% of the time on inshore areas of the Great Barrier Reef. This chapter emphasizes that the sediment threshold for behavioral changes is already reached relatively frequently, and that the restricted movement due to a loss of visual cues will compound the increasing habitat loss occurring on coral reefs. Additionally, the results of the literature review underscore the importance of studying coral reefs vulnerable to sediment loading, as little information currently exists about these reefs.

Chapter five examined the influence of suspended sediment on the fitness-associated traits of individuals persisting in turbid environments. Here, I tested the hypothesis that suspended sediment can negatively affect foraging efficiency, nutritional state and survival in *Acanthochromis polyacanthus*, a damselfish commonly occurring on inshore, turbid reefs. Fish took longer to find food and consumed less of the food provided with increasing sediment. The decline in food acquisition was associated with a significant reduction in juvenile growth and body condition. Fish held in the medium and high sediment treatments had half the density of hepatocyte vacuoles (a proxy for condition) than the fish held in the control and low sediment treatments. Suspended sediment also caused a significant increase in mortality of the juvenile

fish in the high sediment treatment. Mortality reached almost 50% in the high sediment treatment, in contrast to the low and medium sediment treatments, which had less than 10%, and the control, which had no mortality. A reduction in growth and condition will have major implications for survivorship and reproductive success, which could change population demographics on reefs increasingly subjected to suspended sediment.

Although suspended sediment reduces visual cues necessary for vital processes in the development of planktivorous fishes, it may protect them from predation as predators often require a larger visual field to spot their prey. Chapter six examined whether suspended sediment could change predation patterns between *Chromis atripectoralis* and a ubiquitous predator, *Pseudochromis fuscus*, whose diet largely consists of damselfish. Increased turbidity led to a nonlinear response in predation patterns. The prey had about 50% survivorship in the control and low sediment levels. However, in the medium sediment level, survivorship declined to less than 30%, contradicting the hypothesis that the prey would be protected in higher turbidity. Interestingly, in the high sediment level, survivorship increased to resemble predation rates in the control. This non-linear predation pattern exposes different tolerance levels to suspended sediment, whereby the prey was more sensitive to suspended sediment initially, allowing the predator to capitalize on their reduced visual acuity. This study demonstrates that coral reef fishes from different families and functional groups are susceptible to increased turbidity. Changing predation patterns due to suspended sediment could lead to an imbalance in trophodynamics on coral reefs.

This research provides important evidence that coral reef fishes are directly affected by suspended sediment and that clear trigger values exist for behavioral changes. This work underscores the need to reduce suspended sediment inputs into coral reef environments due to its

potential effect on larval development, settlement success and habitat use, foraging, and survival of coral reef fishes. Changes in these fundamental processes that regulate fish assemblages may have long-term effects on the persistence of populations, particularly as habitat loss on coral reefs increases.

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CHAPTER 1: GENERAL INTRODUCTION

Global ecosystem degradation

One of the predominant goals in ecology is to determine how ecosystems function (Margalef, 1963). The interactions among species and with their physical environment dictate habitat selection, growth and development, competitive and predator- prey interactions, food acquisition, and reproduction, and it is widely accepted that these small scale ecological processes are central to ecosystem health and population persistence (Delcourt and Delcourt, 1988; Cornell and Lawton, 1992; Peterson et al., 1998). Abiotic fluctuations and disturbances are also essential to ecosystem functioning. Punctuated disturbances can restructure systems through differential mortality or by creating ideal conditions for rapid growth (Smetacek, 1986; Rogers, 1993; Molino and Sabatier, 2001). Although previously, the work of ecologists was an exercise in better understanding how pristine environments work, more recently, focus has shifted to understanding how ecosystems can continue to function in the face of degradation and increased disturbance (Peterson et al., 1998; Folke et al., 2004; Hughes et al., 2005). Ecosystem degradation is happening on a global scale and has already devastated a variety of terrestrial and marine environments (Vitousek et al., 1997; Tilman et al., 2001; Foley et al., 2005). Some causes of ecosystem degradation involve events that shape the ecosystem from within through changing how an ecosystem functions. For instance, the removal of apex predators or the invasion of a species may cause massive shifts in the trophic balance and can lead to an overabundance of certain species and a rapid decline of others (Mooney and Cleland, 2001; Myers et al., 2007). The overfishing of large shark species caused a boom in meso-predators, which in turn collapsed the Bay Scallop fishery in the Atlantic Ocean (Myers et al., 2007). Alternatively, other causes of

ecosystem degradation come from structural changes to the ecosystem, such as habitat destruction (Brooks et al., 2002; Foley et al., 2005), climate change (Malhi et al., 2008; Hoegh-Guldberg and Bruno, 2010), or pollution (Diaz and Rosenberg, 2008; Woodward et al., 2012). These threats have resulted in a loss of over 50% of the world's tropical forests (Pimm et al., 2001) and hypoxic 'dead zones' in over 400 marine systems, affecting a total area of more than 245,000 km² (Diaz and Rosenberg, 2008).

Threats to coral reef biodiversity

These threats to biodiversity are felt no more strongly than on coral reefs. Overexploitation of species has driven populations of fishes and invertebrates to dangerously low numbers, resulting in major ecological consequences for coral reefs (Jackson et al., 2001). For instance, the loss of herbivorous fishes to overexploitation and the subsequent loss, to disease, of *Diadema antillarum*, a sea urchin species that was the remaining herbivore in the Caribbean, led to an explosion of macro-algae growth, which caused massive coral mortality (Hughes, 1994). Additionally, dynamite fishing and other destructive fishing practices are causing massive mortality of both fishes and corals (Roberts, 1995). Marine protected areas have become the primary conservation tool used to protect coral reefs, with varying degrees of success (Jones et al., 2004; Russ et al., 2008), but their ability to protect coral reefs from external stressors may be minimal (Hughes et al., 2003; Halpern et al., 2013).

More recently, attention has shifted to the effects of climate change on coral reefs. Increasing temperatures are already causing major mortality events from bleaching, and have the potential to fundamentally change the development of coral reefs in the future (Hughes et al., 2003; Hoegh-Guldberg and Bruno, 2010). Evidence has recently emerged that coral reef fishes

are susceptible to increasing temperatures and ocean acidification (Munday et al., 2008, 2009), but may be able to acclimate gradually over generations (Donelson et al., 2012; Miller et al., 2012). Although overexploitation of fisheries and the predicted global effects of climate change on temperature and sea level are receiving a lot of attention, many shallow coastal and inshore coral reefs have already been severely modified from pollution, and yet, there is relatively little information on this topic compared to other stressors, creating a large knowledge gap in quantifying and managing threats to coral reefs.

The effect of pollutants on coral reefs is an especially important topic due to the large proximity of coral reefs to coastal zones. Coral reefs within easy distance from the shore have always been important for the coastal communities, which have depended on them for food and livelihood. In fact, 275 million people worldwide reside within 30 km from coral reefs (Burke et al., 2011). However, as agriculture and coastal development have increased, at least 25% of coral reefs globally are now threatened by coastal development and watershed-based pollution (Burke et al., 2011). This is of particular concern because coastal development is expected to increase substantially over the next fifty years, predominantly in areas like the coral triangle, which is a biodiversity hotspot. As a result, terrestrial derived pollution has been listed as a significant cause of concern to coral reefs by the National Oceanic and Atmospheric Administration (NOAA), the Coral Triangle Initiative, and the Great Barrier Reef Marine Park Authority. The sources of coastal pollution are diverse, including agriculture and deforestation, coastal and port development, dredging, and mining and the types of pollutants that are delivered into coral reefs include herbicides and pesticides, fertilizers, sewage, heavy metals, anti-foulants, and sediment (Burke et al., 2011; Brodie et al., 2012). Importantly, while assessments of the effectiveness of marine protected areas or predicting the effects of climate change have focused on both corals

and fishes (Munday et al., 2008; Hoegh-Guldberg and Bruno, 2010; McCook et al., 2010), research on the effects of pollutants has focused almost exclusively on corals (Fabricius, 2011).

Terrestrial and coastal pollutants and the impact on coral

Pollutants of terrestrial and coastal origin can have serious consequences for corals. Nutrient enrichment from fertilizers and sewage can augment organisms that compete with corals, such as macro-algae (Fabricius, 2005), and has also been linked to reduced coral calcification (Loya, 2004) and declining coral cover (Shimoda et al., 1998). Additionally, in the Great Barrier Reef coral cover loss has been mainly driven by *Acanthaster planci*, the Crown of Thorns sea-star (De'ath et al., 2012), whose outbreaks have been linked to nutrient enrichment (Brodie et al., 2005; Fabricius et al., 2010). Herbicides from agricultural run-off have been shown to cause bleaching and reduced photosynthetic ability in corals (Negri et al., 2005; Markey et al., 2007). Terrestrial run-off has also been linked to increased coral disease in the Great Barrier Reef (Haapkylä et al., 2011). Finally, heavy metals, including those commonly found in anti-foulants, can result in acute or chronic toxicity causing lethal effects or long-term impacts to key biological processes of corals, such as fertilization and metamorphosis (Negri and Heyward, 2001; Negri et al., 2002).

Sediment and coral reefs

Unlike other pollutants that are human derived, such as herbicides or anti-foulants, sediment loading onto coral reefs from terrestrial run-off is an important natural process that links terrestrial and marine systems and shapes inshore to offshore distributions (Perry and Smithers, 2010). It can either be suspended in the water column, causing higher turbidity, or it can be settled out of suspension as sedimentation (Larcombe et al., 2001). Re-suspension events

are often pulse occurrences and can fluctuate quite rapidly, depending on wind and tidal forcing (Larcombe et al., 2001; Wolanski et al., 2008). Though it is a natural process, it has increased worldwide and is now a major cause of concern on many inshore coral reefs (Bellwood et al., 2004; Fabricius, 2005; Maina et al., 2013). As a consequence, experimental research has focused on determining the effects of sediment on corals. Elevated turbidity has been 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).

Since coral reef fishes are closely associated with live coral, it stands to reason that any stressor that affects corals will indirectly affect coral reef fishes. Jones et al. (2004) demonstrated that as live coral declines, so do coral reef fishes, even species that do not use live coral habitat as adults. Therefore, it makes sense that if sediment causes declines in live coral, then coral reef fishes would show a comparable decline. Indeed, several studies have 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 (Letourneur et al., 1998; Fabricius et al., 2005; 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. This is a huge knowledge gap in the literature as it is important to understand all drivers of change, particularly as corals and coral reef fishes may be differentially susceptible to sediment. Furthermore, since coral reef fishes will be vulnerable to sediment-induced habitat loss, it is crucial to determine if they will experience additional, direct pressure from suspended sediment that could further threaten population persistence.

Sediment and fishes

There is substantial literature on freshwater and estuarine systems that demonstrate that fishes can be directly affected by sediment. A number of freshwater studies found that suspended sediment inhibited the foraging of planktivorous and drift feeding juveniles and adults by reducing the distance at which food could be detected (Gardner, 1981; Barrett et al., 1992; Asaeda et al., 2002; Sweka and Hartman, 2003; Zamor and Grossman, 2007). Sweka and Hartman (2001) showed that for brook trout, *Salvelinus fontinalis*, even though individuals foraging in high sediment did not experience a reduction in food consumption, specific growth rates decreased as suspended sediment increased, due to an increase in energy used to forage. Additionally, Hazelton and Grossman (2009) found a shift in the foraging strategy of both *Clinostomus funduloides* and *Notropis lutippinis* in higher turbidity. Mild turbidity in freshwater lakes and subtropical estuaries can also enhance the contrast of planktonic prey against its background, making it easier for planktivores to see them (e.g., Gregory and Northcote 1993; Utne 1997; Rowe and Dean 1998; Utne-Palm, 1999). However, at higher levels of turbidity, foraging success declines, generating a non-linear relationship between foraging success and turbidity (Utne-Palm, 2002). 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 of light 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 der 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, not all fish species are vulnerable to sediment. Granqvist and Matilla (2004) found no effect of suspended sediment or reduced light on foraging by *Perca fluviatilis* (Linnaeus, 1758), a species that may be adapted to the turbid conditions of the Baltic Sea. Similarly, Blaber et al., (1995) found that several species of fish in inshore and estuarine environments were positively correlated with turbidity. Gregory and Levings (1996) found that turbidity had no effect on predation of juvenile salmonids by *Oncorhynchus clarkii*, a cutthroat trout species, so that prey species were unable to use turbid areas as shelter. Isono et al. (1998) found that there was 50% mortality at 1000 mg l⁻¹ of suspended sediment for *Pagrus major* larvae, whereas, Partridge and Michael (2010) showed that *Pagrus auratus* larvae experienced 50% mortality at 157 mg l⁻¹. The differential responses of fishes to suspended sediment highlights first of all that direct effects of suspended sediment on coral reef fishes is likely, and secondly, that it is crucial to examine how sediment may affect them as even species within the same genus (as described above) respond very differently to sediment, meaning that results found in other aquatic environments cannot necessarily be applied to coral reef fishes. There have only been two published studies on the effects of sediment on coral reef fishes prior to the work from this thesis. Au et al. (2004) showed increased mortality and gill damage in *Epinephelus coioides* when exposed to sediment. Leahy et al. (2011) found that *A. polyacanthus* reduced their level of boldness when exposed to a chemical alarm cue while in turbid water, thereby affecting their assessment of predation threat.

Anticipated ways sediment will affect coral reef fish (Small scale ecological processes)

Although the work in other systems cannot be directly applied to coral reef fishes, it does provide a foundation on which to hypothesize about how sediment may affect coral reef fishes. Since the effects of suspended sediment have most often been studied in relation to how it

obscures the visual environment, it is important to consider how suspended sediment may be detrimental to important activities that use visual cues. If we consider the life cycle and the small scale ecological processes that the majority of coral reef fishes undergo, we can begin to make predictions on when they will most likely be affected. The majority of coral reef fishes have a pelagic larval stage. During this time, fast growth and developmental rates are important for successful survival and recruitment. If high turbidity reduces visual acuity, then larvae could experience lower feeding efficiency. This could reduce growth, and body condition (Sweka and Hartman, 2001) may be expected to decline, while larval duration could increase as development slows (e.g. Green and McCormick, 1999). If the larvae survive until settlement then they will need to detect visual and chemical cues from their preferred habitat. If one or more of the environmental cues is weak or not properly detected, settlement choices may not accurately reflect the habitat suitability for the species, which could lead to reduced fitness and increased mortality (Jones, 1991; Munday, 2001; McCormick, 2009; Munday et al., 2009). Though many coral reef fishes tend to be closely associated with a particular habitat once they have settled, a fish's home range will often include a broad array of habitat patches in order to exploit more resources and visual cues may be important for this movement (Lewis, 1997). Part of the movement around a home range is driven by foraging. Coral reefs have a high diversity of planktivorous fishes that acquire planktonic prey primarily through visual detection (Hobson, 1991; Rowland, 1999; Williams and Hatcher, 1983). Any reduction in the visual field due to suspended sediment has the potential to affect prey intake and growth in planktivorous fishes. Finally, piscivores tend to detect prey from farther away and may have a harder time seeing the prey due to light reduction and contrast degradation created by suspended sediment (Fiksen et al., 2002). In this way, suspended sediment may actually shelter prey species from predation

(Utne-Palm, 2002). Coral reef fishes must undergo all of these processes to reach adulthood and to successfully reproduce. What is important about each of these processes is that they happen on relatively short time scales. Since turbidity events are often pulsed and short-lived, these early life history processes are more vulnerable to suspended sediment because they happen on short time scales so the risks are higher if they are coincident with a turbidity event.

Research aims and thesis structure

The overarching aim of this thesis is to examine the effects of suspended sediment on early life history stages of coral reef fishes, with the intent of addressing a large knowledge gap that exists in understanding how coral reefs worldwide are affected by increasing sediment loading. This thesis represents the first comprehensive investigation of the effects of suspended sediment on coral reef fishes and will provide important insight on the topic. Although all the data chapters are related in this overarching goal, each data chapter addresses a different life history stage or process, and are written as stand-alone publications. Damsel-fishes (Pomacentridae) were chosen as the focal family for this research because they are ubiquitous and are found on both inshore and outer reefs (Williams, 1982). They exhibit widespread use of branching live coral as habitat and settlement sites, and have exhibited declines in abundance associated with live coral loss (Syms and Jones, 2000; Bellwood et al., 2006; Pratchett et al., 2008), meaning that they have the potential to be both indirectly and directly affected by suspended sediment. An array of damselfishes from different genera was used in order to examine the effects of suspended sediment on a more broad scale. Insights gained from this thesis will provide a framework on which to further address the effects of suspended sediment on coral reef fishes, as there is currently little information on the subject. The specific aims of this thesis are to:

1. *Examine the effects of suspended sediment on larval development and pelagic larval duration.*
2. *Test the effects of suspended sediment on visual and chemical cues used during settlement.*
3. *Determine the threshold at which suspended sediment impairs habitat choice and home range movement.*
4. *Assess the effects of suspended sediment on foraging, growth, and body condition.*
5. *Investigate the effects of suspended sediment on predator-prey interactions of two coral reef fishes.*

In Chapter 2, I focus on the effects of suspended sediment on larval development of the anemone-fish, *Amphiprion percula*. I used a range of suspended sediment concentrations that have been recorded during the wet season in Australia, which coincides with a high level of coral reef fish spawning and recruitment. I hypothesize that larvae in the low concentration of suspended sediment would have a foraging advantage over individuals in all other treatments due to the increased contrast between the prey and the background, and that this would result in a shorter developmental stage. I also hypothesize that the fish in the higher concentrations of sediment would have reduced foraging efficiency, so that it would take them longer to reach the size and condition necessary to undergo metamorphosis.

Chapter 3 examines different ways in which suspended sediment can affect settlement patterns of coral reef fishes. In this two-part experiment, I first test the effects of reduced visual cues from suspended sediment on habitat choice in two coral reef fishes, *Pomacentrus amboinensis* and *P. moluccensis*. I then test whether suspended sediment impairs chemical cues associated with live coral that *Pomacentrus moluccensis* use during settlement. I hypothesize that

sediment reduces the visual cues necessary for habitat choice and masks the chemical cues that live coral emits.

Chapter 4 builds on Chapter 3 by determining the threshold at which suspended sediment concentrations begin to impair habitat choice. I also examine how suspended sediment affects post-settlement migration and home range movement. I hypothesize that there will be a clear threshold where suspended sediment impairs habitat choice, and post-settlement movement. This chapter uses *Pomacentrus moluccensis* because it is found in areas that experience high suspended sediment concentrations. I then compare the concentrations of suspended sediment that elicit a response to observed patterns of suspended sediment recorded on reefs in the Great Barrier Reef where *P. moluccensis* lives to examine the frequency that *P. moluccensis* would be likely to experience sub-optimal concentrations of suspended sediment.

Chapter 5 continues to focus on key early life history processes by examining how foraging behavior changes in increasing suspended sediment. I hypothesize that as suspended sediment will reduce foraging efficiency by impairing visual acuity. I also hypothesize that this reduction in foraging ability will lead to reduction body condition and growth rate. I use *Acanthochromis polyacanthus*, a widespread damselfish found on turbid reefs.

Chapter 6 uses the foundational work from other aquatic ecosystems to test predator prey interactions between *Pseudochromis fuscus*, a ubiquitous predator species that forages on damselfish (Feeney et al., 2012), and *Chromis atripectoralis*, a common damselfish. Based on previous literature, I hypothesize that *C. atripectoralis* will have an advantage over *P. fuscus*, so that their survivorship will increase as suspended sediment concentrations increase.

CHAPTER 2: SUSPENDED SEDIMENT PROLONGS LARVAL DEVELOPMENT IN A CORAL REEF FISH

2.1 ABSTRACT

Increasing sediment input into coastal environments is having a profound influence on shallow marine habitats and associated species. Coral reef ecosystems appear to be particularly sensitive, with increased sediment deposition and re-suspension being associated with declines in the abundance and diversity of coral reef fishes. While recent research has demonstrated that suspended sediment can have negative impacts on post-settlement coral reef fishes, its effect on larval development has not been investigated. In this study, we tested the effects of different levels of suspended sediment on larval growth and development time in *Amphiprion percula*, a coral reef damselfish. Larvae were subjected to four experimental concentrations of suspended sediment spanning the range found around coastal coral reefs (0-45 mg L⁻¹). Larval duration was significantly longer in all sediment treatments (12d) compared to the average larval duration in the control treatment (11d). Approximately three quarters of the fish in the control had settled by day 11, compared to only 40-46% among the sediment treatments. In the highest sediment treatment, some individuals had a larval duration twice that of the median duration in the control treatment. Unexpectedly, in the low sediment treatment, fish at settlement were significantly longer and heavier compared to the other treatments, suggesting delayed development was independent of individual condition. A sediment-induced extension of the pelagic larval stage could significantly reduce numbers of larvae competent to settle, and in turn, have major effects on adult population dynamics.

2.2 INTRODUCTION

Development and modification of coastal zones around the globe have led to a reduction in the water quality of inshore marine ecosystems (Cloern 2001; Tilman et al., 2001; Boesch, 2002; Duarte 2002). Among these, coral reefs are especially susceptible to increases in nutrient levels, sediment loads and pollutants from land-based sources (Sebens 1994; Fabricius, 2011; Kroon et al., 2012). Exposure to reduced water quality has been linked to declines in abundance of coral reef organisms and shifts in species composition (Letourneur et al., 1998; Mallela et al., 2007; De'ath and Fabricius, 2010; Brodie et al., 2012). While most research has focused on the impacts of sediment on coral, recent research has shown that reef-associated fishes are also very sensitive to changes in water characteristics. Suspended sediment appears to negatively impact on critical ecological processes, including habitat selection at settlement (Wenger et al., 2011), foraging (Wenger et al., 2012), and predator/prey interactions (Wenger et al., 2013). The effects of declining water quality are likely to be magnified during early life history stages because there are naturally higher mortality rates during this time. Despite the risk that the larval period may coincide with a high turbidity event created by increased suspended sediment, the effects of increasingly turbid environments on development during the pelagic larval phase have never been investigated.

Terrestrial run-off has the potential to affect the development and survival of fish larvae in a number of ways. River plumes may promote higher growth of marine fish larvae because of a positive effect on phytoplankton and zooplankton production (Grimes & Kingsford, 1996; Carassou et al., 2010). Indeed, fish larvae sampled from nutrient enriched river plumes have been reported to exhibit higher growth rates compared to larvae that are not in flood plumes (Lang et al., 1994; Allman & Grimes, 1998). Increased suspended sediment may also improve feeding

success by aiding the discrimination of food particles (Boehlert and Morgan, 1985; Miner and Stein, 1993; Utne-Palm, 2004). Grimes and Kingsford (1996) predicted that these higher growth rates within flood plumes may reduce the time in the pelagic larval stage, which could enhance survivorship to settlement and increase recruitment

On the other hand, there is the potential for numerous negative effects of increased suspended sediment. Too much turbidity can hinder visual cues, which is expected to affect an individual's ability to forage (Fiksen et al., 2002; Wenger et al., 2012; Johansen and Jones 2013). If high turbidity does ultimately reduce feeding efficiency in coral reef fish larvae, then growth and body condition would be expected to decline with increasing sediment, while pelagic larval duration (PLD) should increase as development slows (e.g. Green and McCormick, 1999). Previous research has shown that periods of low fish recruitment coincide with turbid water conditions associated with the summer monsoon in Papua New Guinea (Srinivasan and Jones, 2006). If suspended sediment causes a reduction in the number of individuals available to settle, then coral reefs that are frequently exposed to high levels of suspended sediment may be more prone to recruitment failure.

Terrestrial run-off and associated increases in suspended sediment concentrations and turbidity are considered one of the major stressors to coral reefs (Burke et al., 2011), and it is crucial to understand the interplay between reduced water quality and coral reef fish development and recruitment patterns. In this study, we tested the hypothesis that increasing concentrations of suspended sediment would increase developmental time in the coral reef damselfish *Amphiprion percula* (Lacapède, 1802) due to a reduction in foraging ability. To test this, we manipulated concentrations of suspended sediment under controlled aquarium conditions and measured effects on larval duration, size at settlement and mortality. The range of

levels of suspended sediment employed in the experiment were set to reflect those recorded both in river plumes around coral reefs (Devlin et al., 2012) and on coral reefs during re-suspension events (Ogston et al., 2004; Browne et al., 2013).

2.3 METHODS

2.3.1 Study species and brood stock maintenance

Five breeding pairs of *Amphiprion percula* (Pomacentridae) were captured from reefs from around the Cairns region of the northern Great Barrier Reef and transported to the Marine and Aquaculture Research Facilities Unit (MARFU) at James Cook University, Townsville, Australia. This species was used because they are easy to breed in captivity, have high survivorship as larvae and have relatively short pelagic larval durations. Breeding pairs were maintained in 60L outdoor aquaria with a flow-through of filtered water (28.5° C) and fed twice per day with 0.075g per pair of INVE Aquaculture Nutrition 12/20 pellets (Proaqua Pty Ltd, Queensland Australia). Each breeding pair was provided with half a terracotta pot on the bottom of their aquarium for shelter and to serve as a structure for egg deposition. The pots were inspected each morning for the presence of eggs.

2.3.2 Larval rearing conditions

The experiments were conducted between January-April 2012 at MARFU, which corresponds with the natural breeding time of this species. On the afternoon when hatching was predicted (6-8 days after eggs were laid), the pot containing the eggs was transferred to another 60L aquarium inside a temperature-controlled (28.5° C) experimental lab, where hatching occurred within a few hours after darkness.

Larvae were reared in the 60L aquarium (28.5° C) for five days in a semi-closed system; static during the day, then slowly flushed with filtered seawater each morning prior to light. Green *Nannochloropsis* spp. paste (Reed Mariculture, California, USA) was added to the water each morning after flushing until the bottom of the aquarium could not be seen, equating to approximately 4 million cells mL⁻¹ (Moorhead and Zeng, 2011). This was done to both dissipate light and maintain the nutritional value of the rotifers (*Brachionus* sp.) that were fed to the larvae at a density of 10 rotifers per mL each morning for the first three days. After the 3rd day, the diet of the larvae was increasingly enriched with newly hatched *Artemia* sp. nauplii (INVE technologies, Thailand LTD; GSL0) and the amount of rotifers they received decreased proportionally (G. Miller, pers. comm.).

2.3.3 Experimental apparatus and sediment suspension method

The sediment exposure trials were carried out in 24 2L polyethylene terephthalate (PET) bottles used as tanks. These readily available containers were chosen because of their food-safe characteristics and a shape that aided in the movement of suspended sediments. Each tank was fitted with a 1 mm plastic mesh screen that was used as a physical barrier to prevent larval loss from the tank, and shaded with black polyurethane sheeting to minimize light exposure. Each tank was also fitted with a partial plastic lid that reduced light glare and allowed for larval rearing without the addition of Green *Nannochloropsis* spp. paste (B. Green, pers. comm.). Each sediment treatment was delivered to individual tanks via a submersible pump (1,200 L h⁻¹) placed in an external 100L aerated sump. An airline was positioned directly in front of the suction inlet of this pump, which created consistent dissolved oxygen levels (>90%) to each larval rearing tank for the duration of each trial. Each sump contained 3 disturbance pumps (1,000 L h⁻¹) to create uniform turbidity (Fig. 2.1a). Water inlet lines were arranged to allow for

supply of clear (control) water as well as one of the three treatments. Water was delivered to each tank through low pressure, low flow inlet lines that were sufficient to maintain consistent sediment levels without disturbing the larvae (determined in a pilot study, A.S. Wenger, unpublished data). Measurements using a WP88 Turbidity Meter (Thermofisher Scientific, Queensland, Australia) during a pilot study showed that the constant supply of water with sediment in suspension from the inlet lines [187 ± 19 (SE) s L^{-1}] ensured that sediment concentrations remained constant in each tank throughout the experiment. A power-assisted drain line was incorporated to mitigate sediment deposition within the tanks and plumbing. A dual draining standpipe manifold was used to ameliorate sediment movement and to equilibrate water levels amongst all tanks. The design allowed for randomization of tanks between trials and treatments (Fig. 2.1b). Tanks and sumps were arbitrarily assigned a sediment treatment between trials to eliminate any location bias within the experimental laboratory.

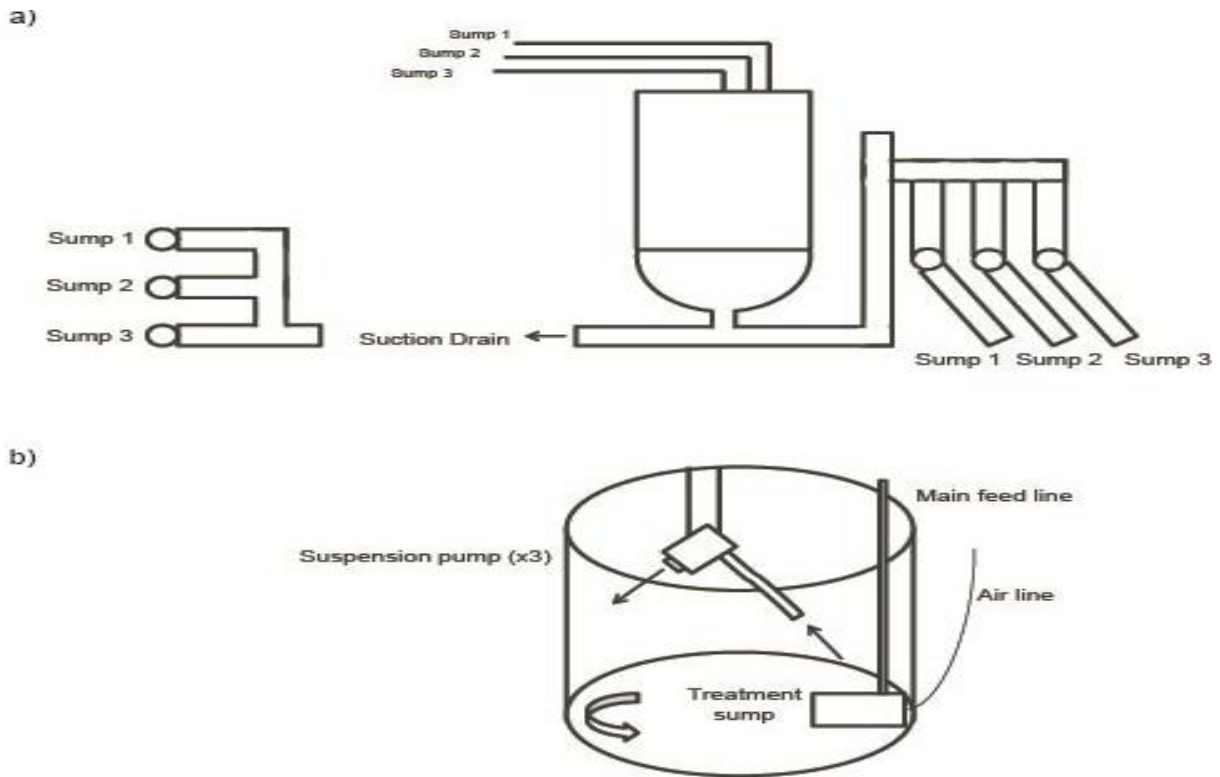


Figure 2.1 The sediment suspension method. (a) Each tank was fed low-flow water from the designated treatment sump. A suction drain ensured continuous flow of the water, allowing for constant sediment suspension, and returned the water to the correct sump. A standpipe maintained a constant water level in each tank and drained to the correct sump. (b) Each sump was equipped with three disturbance pumps to suspend the sediment. These pumps were attached to adjustable brackets so they could be held outside the water, so as to not heat up the water. Each sump also had a pump to deliver the water to the designated tanks.

2.3.4 Experimental design and measurements of larval development

Larval development was measured at four different suspended sediment concentrations: Control (0 mg L^{-1} ; 0 NTU), low (15 mg L^{-1} ; $\sim 2.5 \text{ NTU}$), medium (30 mg L^{-1} ; $\sim 5 \text{ NTU}$) and high (45 mg L^{-1} ; $\sim 7.5 \text{ NTU}$). A total of 20 replicates were run (1 replicate = 1 tank) for each sediment treatment. The levels of suspended sediment for the 4 treatments were within the range of

suspended sediment levels recorded in river plumes around coral reefs and on coral reefs during re-suspension events (Table 2.1). The higher sediment treatments were at levels that have been shown to affect the behavior and foraging ability of adult pomacentrid species (Wenger et al., 2012; Wenger and McCormick, 2013). The suspended sediment concentrations were maintained throughout the experiment, except for one hour every three days when full water exchanges were conducted in order to remove wastes. These water exchanges were completed before the first feeding of the day. The sediment used for the experiment was Australian bentonite, a commercially available clay. Muddy sediments and clays are common constituents of sediment found on inshore coral reefs, such as in the Great Barrier Reef (GBR; Carter et al., 1993; McCulloch et al., 2003) and the particle size of bentonite is in the same size class as particles found in suspension in the GBR (Bainbridge et al., 2012; Wenger, unpublished data).

Table 2.1 Suspended sediment concentrations measured on different coral reefs

Location	Suspended Sediment Values (mg l ⁻¹)	Sediment Source	Reference
GBR, Australia	120	fringing reef	Hopley and Van Woesik, 1988
GBR, Australia	5-45	inshore reefs	Larcombe et al., 1995
GBR, Australia	39-670	flood plumes	Devlin et al., 2001
Hawaii	0-100	fringing reef	Ogston et al., 2004
GBR, Australia	300	coastal reefs	Wolanski et al., 2008
GBR, Australia	10-38	flood plumes	Devlin et al., 2012
GBR, Australia	0-300	inshore reefs	Browne et al., 2013

On the fifth morning post-hatch (before feeding) larvae that were visually in good condition (i.e. displaying normal swimming behavior and balance) were gently collected using a glass beaker and arbitrarily distributed among the experimental tanks until there were ten larvae in each tank. The decision to use 5-day old larvae in this study was based on a pilot study examining the interaction between the flow required to keep consistent levels of suspended

sediment and the swimming ability of the larvae at different ages (A. S. Wenger, unpublished data). During the pilot study, larvae were added at day 3 but could not cope with the flow in the tanks, resulting in 100% mortality within an hour. All larvae were fed once transfers were complete. Because the water was in constant motion and food was being removed from the tanks by the suction outlet, larvae from all treatments were fed the same food levels three times a day for the duration of the trial to ensure adequate feeding opportunity. Once all the larvae in the tanks displayed normal swimming behavior, sediment was slowly added to the treatment sumps.

Larvae were carefully checked for metamorphosis by torchlight each morning before they had an opportunity to feed. Larvae were considered as having undergone metamorphosis when their post-orbital stripe appeared, which coincided with a positive attraction to the sides of the rearing tanks consistent with settlement behavior and has been used as a diagnostic tool for metamorphosis and settlement in previous experiments using both *A. percula* (Dixson et al., 2008; McLeod et al., 2013) and a congeneric species *A. melanopus* (Green and McCormick, 1999). Once the larvae were considered settled they were removed from the tank and euthanized using an ice-saltwater slurry. Euthanized larvae were then immediately transferred to Bouin's solution for 24 hours and then transferred to 70% ethanol, at which point the following measurements were taken. Larvae were removed from the preservative, blotted dry, weighed (nearest 0.0001 g) and photographed in a lateral position on a 0.5mm plastic grid. Standard length (SL) to the nearest 0.01mm was estimated from each fish from the digital photograph using image analysis software (ImageJ ver. 1.45s, National Institutes of Health, USA). Survival was measured as the difference between the number of larvae added to each tank at the beginning of each trial and the number of fish that remained at the end of each trial.

2.3.5 Data analysis

Analyses were performed based on both chronological age and age at metamorphosis. Chronological age refers to individuals that underwent metamorphosis on the same day. Age at metamorphosis refers to their pelagic larval duration, meaning the age the fish were when they metamorphosed. When the text refers to measurements made at metamorphosis, this means the age at metamorphosis. The distinction was made to assess whether length and weight were dependent on chronological age or on developmental stage, i.e., metamorphosis. A Kruskal-Wallis analysis with a Tukey's HSD post-hoc analysis were run to assess if there were significant differences in: i) median pelagic larval duration (PLD), ii) median standard length and weight at metamorphosis, and iii) differences in mortality among treatments. A two-way ANOVA was performed with treatment and age as factors to examine differences in mean standard length and weight at actual age. Analyses on differences at chronological age were only performed on fish aged day 10-13, as there were fish from each treatment that settled on these days. Two-sample Kolmogorov Smirnov tests were run to compare the differences in the distributions of age of metamorphosis between the control and the sediment treatments. Body condition was calculated as the blotted weight at metamorphosis after controlling for standard length at metamorphosis using analysis of covariance and a Tukey's HSD post hoc analysis (ANCOVA). Prior to ANCOVA, data were tested for homogeneity of slopes among treatments.

2.4 RESULTS

2.4.1 Larval duration

The pelagic larval duration (PLD) was significantly longer in the sediment treatments compared to the control, with no significant differences among the sediment treatments (Kruskal-Wallis, $\chi^2 = 25.8$, $p < 0.0001$; Fig. 2.2). The median age of metamorphosis among sediment treatments was 12 days, compared to 11 days in the control treatment. Although there was a relatively small difference in median age at metamorphosis between the sediment and control treatments, the frequency distribution curves for age at metamorphosis under increased sediment were consistently different from the control group (Kolmogorov Smirnov test, $p < 0.0001$). Almost 75% of the fish in the control had undergone metamorphosis by day 11, compared to 46%, 40%, and 45% of the fish in the low, medium, and high sediment treatments, respectively. By day 13, all of the fish in the control treatment had undergone metamorphosis compared to 63%, 80%, and 70% of the fish in the low, medium, and high sediment treatments, respectively. Two individuals in the high sediment treatment had a PLD of 22 days, twice the median PLD in the control.

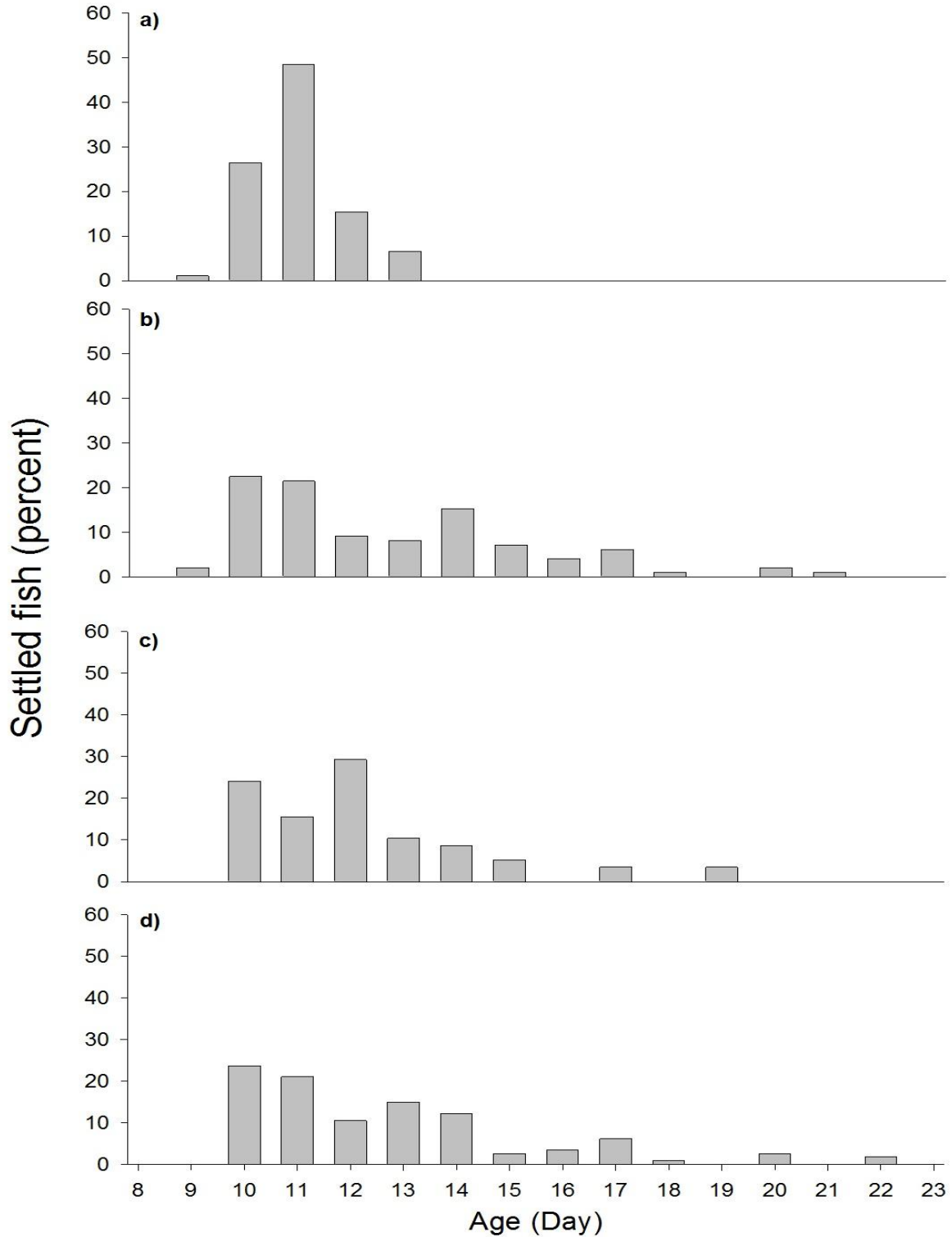


Figure 2.2 The proportion of larvae that settled on each day in the a) control (n= 89), b) low sediment (15 mg l⁻¹; n= 98), c) medium sediment (30 mg l⁻¹; n= 58), and d) high sediment (45 mg l⁻¹; n= 114) treatments.

2.4.2 Larval length and weight

Larvae in the low and high sediment treatments were significantly longer at metamorphosis than fish in the control (Kruskal-Wallis, $\chi^2 = 33.4$, $p < 0.0001$; Fig. 2.3a). Larvae in the low and high sediment treatments were also significantly heavier at metamorphosis than those in the control treatment, and those in the low sediment treatment were significantly heavier than fish from the medium and high sediment treatments (Kruskal-Wallis, $\chi^2 = 36.1$, $p < 0.0001$; Fig. 2.3b).

There was a significant difference in length and weight among treatments at the chronological, as opposed to the developmental age (two-way ANOVA, $F_{9, 256} = 13.6$, $p < 0.001$). For fish that settled on day 10, the fish in the low sediment treatment were significantly longer than the fish in the medium treatments, but were not significantly longer than the fish in the control and high sediment. Additionally, the fish in the low treatment were also significantly heavier than fish from all other treatments on days 10 and 11. The differences in sizes between the control and the sediment treatments at metamorphosis were driven in part by the continued growth of fish in the sediment treatments as they aged, resulting in fish that settled after or on day 14 being larger than fish that had settled earlier. Length at metamorphosis accounted for a significant amount of the variability in weight (ANCOVA, $F_{1, 347} = 411.8$, $p < 0.0001$). When comparing weight for a standardized length among treatments, larvae in the low sediment treatment were significantly heavier than those in the control, and high treatments (ANOVA, $F_{3, 347} = 9.0$, $p < 0.0001$; Fig. 2.3c). That is, at metamorphosis, regardless of age, the fish in the low sediment treatment had overall better body condition than the fish in the control and high treatments. The range of the weight of the fish in the medium treatment overlapped with all treatments.

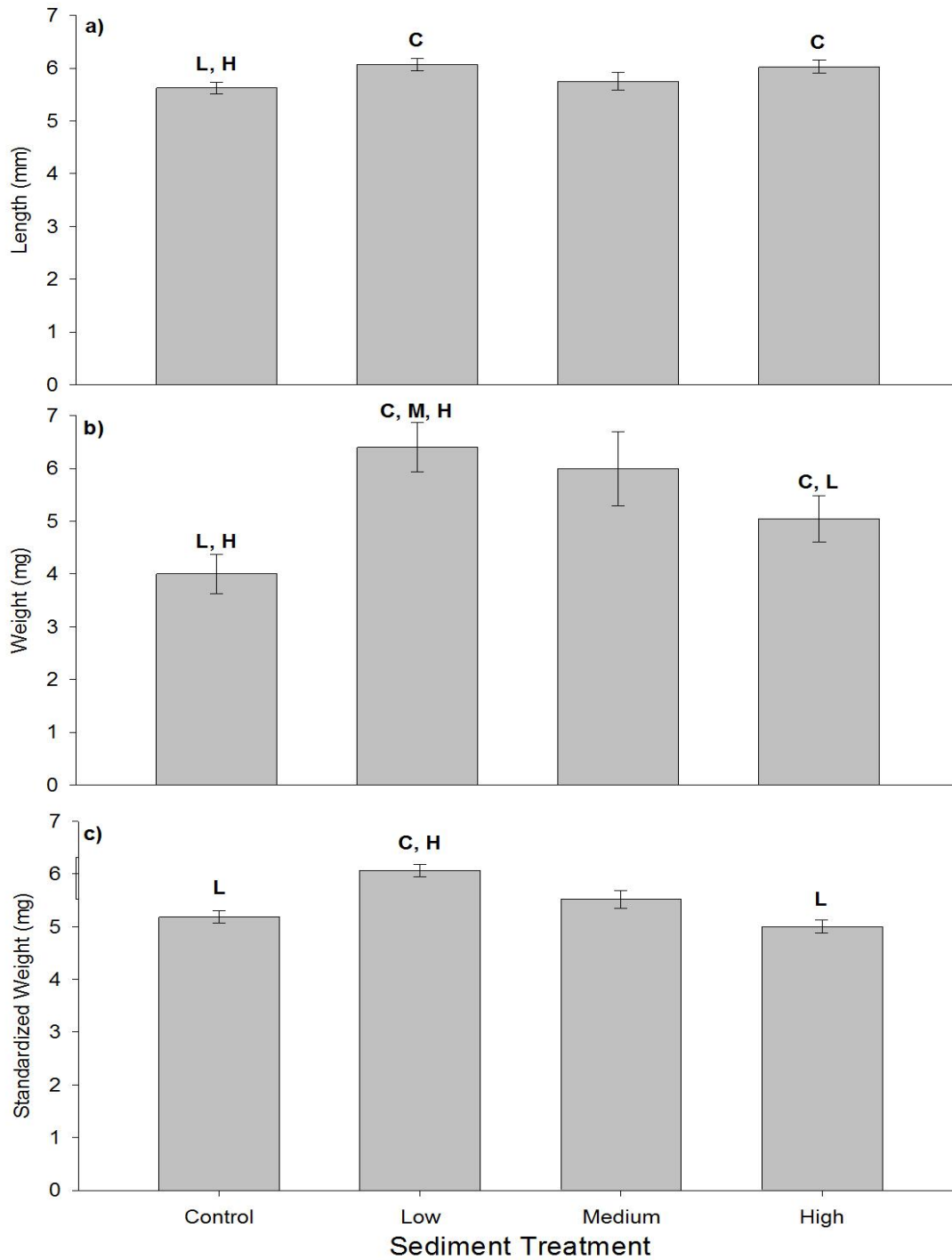


Figure 2.3 The median a) length (mm), b) weight (mg), and c) standardized weight (mg) (\pm 95% CI) of individuals at settlement in the different treatments. N= 88, 91, 55, 112 for the control, low, medium, and high treatments, respectively. The letters above each column indicate significant differences among the treatments. C= control, L = Low, M= medium, and H= high.

2.4.3 Larval survivorship

Mortality did not differ significantly among treatments (Kruskal-Wallis, $\chi^2 = 3.56$, $p = 0.31$; Fig. 2.4). Survivorship was, on average, 34.4 ± 3.32 (SE), 44.5 ± 5.45 , 32.6 ± 5.45 , and $42.6 \pm 4.64\%$ in the control, low, medium, and high sediment treatments, respectively.

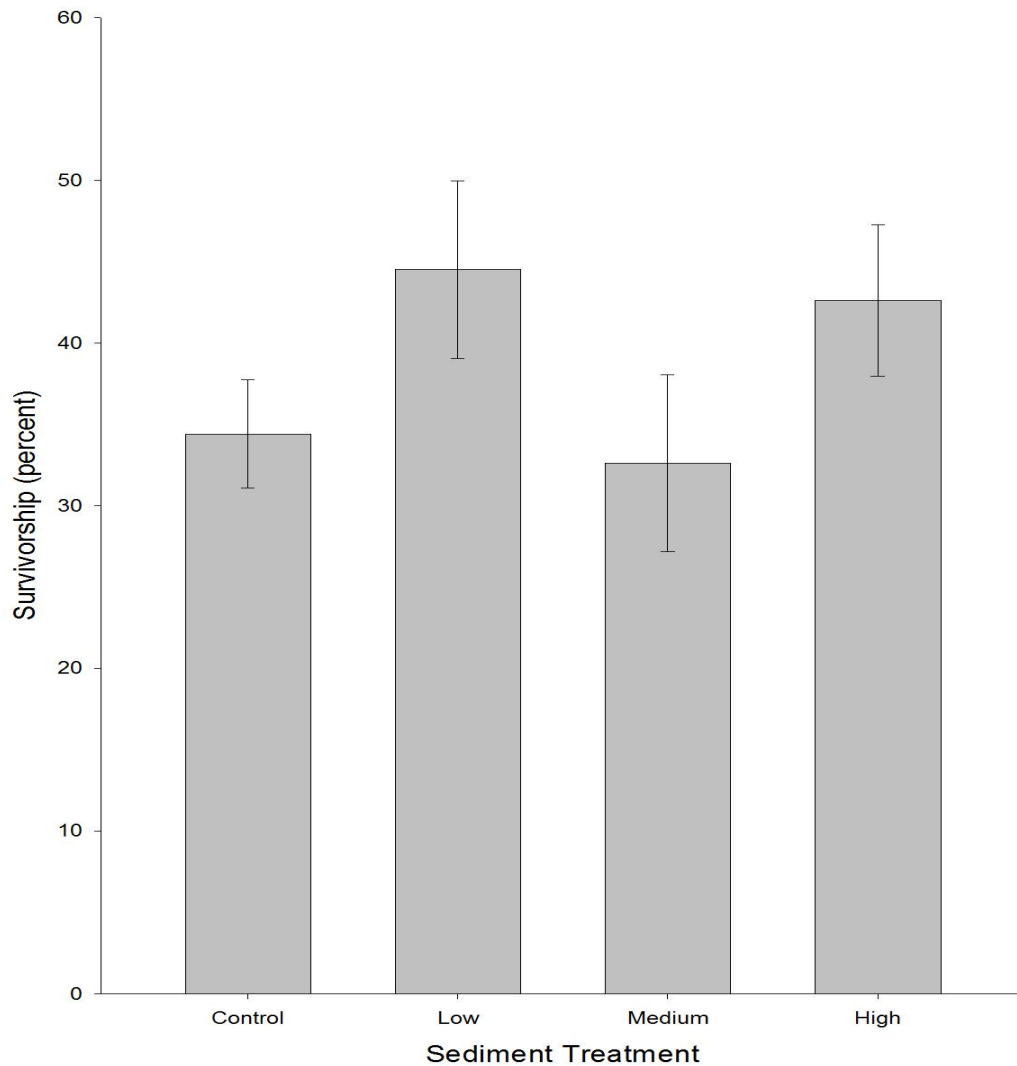


Figure 2.4 Average overall survivorship (\pm SE) in each of the treatments. Overall number of fish added to each treatment = 245, 220, 190, 270 for the control, low, medium, and high treatments, respectively.

2.5 DISCUSSION

The larval stages of marine fishes are likely to be susceptible to changes in water quality associated with increased sediment and nutrient loads. Much of the discussion in the literature has centered on the positive effects of increased nutrients driving increases in planktonic food (Lang et al., 1994; Grimes and Kingsford, 1996; Allman & Grimes, 1998). However, our study demonstrates that suspended sediment can cause a marked increase in the median and range in the pelagic larval duration (PLD) of a coral reef fish. Elevated sediment increased the median PLD by a day, and significantly increased the variation in PLD; in some cases PLD doubled from the normal 11 days to 22 days. Suspended sediment did not negatively affect length, weight, body condition at metamorphosis or survival to metamorphosis. Low levels of sediment led to increased size and enhanced body condition at metamorphosis, which may have been due to the increased ability to discriminate food particles. Sediment loading to coastal waters are likely to escalate with increasing coastal development (Tilman et al., 2001; Hamilton, 2010), creating higher levels of suspended sediment on coral reefs (Fabricius et al., 2013). This study provides evidence that suspended sediment levels currently reached in inshore areas could substantially change developmental patterns in a coral reef fish.

An increase in the PLD of marine organisms, even by a small amount, may have serious demographic consequences for a species due to extremely high mortality rates of larvae (Houde, 1987; Bertram and Leggett, 1994). All else being equal, this would be expected to reduce the number of larvae surviving to age at metamorphosis, and consequently, lower recruitment success (Leggett and DeBlois, 1994; Bergenius et al., 2002). On the other hand, being larger and with better body condition may confer advantages during the first few days after metamorphosis and settlement when mortality can also be extreme (Perez-Dominguez and Munch, 2010).

Longer PLDs could also lead to increased dispersal (Lester et al., 2007; Shanks, 2009). If so, increases in sediment may alter patterns of population connectivity on coastal reefs.

In our experiment, delayed metamorphosis and changes in growth and condition occurred at relatively low levels of suspended sediment. Exposure to such levels should be commonplace for communities on coastal reefs as peak fish recruitment overlaps with the wet season in both the Caribbean (Sponaugle and Cowen, 1996; Enfield and Alfaro, 1999) and the Great Barrier Reef (McCormick, 2003; Brodie et al., 2007). The effects of suspended sediment on coral reef fish larvae may be one of the driving mechanisms underlying distribution patterns seen across tropical continental shelves, from inner to outer reefs (Letourneur et al., 1998; Mallela et al., 2007). The increase in sediment loads is likely to affect both spatial and temporal patterns of coral reef fish distributions by reducing the number of coral reef fish larvae that can successfully settle on reefs experiencing elevated concentrations of suspended sediment (Wenger et al., 2011; Wenger and McCormick, 2013)

At this stage it is not known why larvae exposed to sediment have a longer development period. Therefore, what follows is a discussion on the potential mechanisms that could be driving the delay in reaching this developmental stage. Delays in metamorphosis have previously been described as a reduced growth rate once competency is reached, wherein the fish take the same amount of time to reach competency but then delay metamorphosis and continue to exist as larvae (Cowen 1991; McCormick 1999). Based on this definition of competency, it appears that the fish in the current study are delaying metamorphosis upon reaching competency. The fish in the sediment treatments were generally older, longer, and heavier at metamorphosis than the fish in the control, indicating that they have surpassed a critical threshold for competency according to the above guidelines.

Prolonged larval development can be associated with poor environmental conditions, such as reduced food or sub-optimal temperatures, so that it takes longer to reach a state where they are developmentally prepared for metamorphosis (e.g. McCormick and Molony 1992, 1995; Green and Fisher 2004; McLeod et al 2013). Sediment could have potentially affected larvae through an impairment of visual cues used for foraging, as was initially predicted as an outcome of this experiment. If increased sediment led to reduced foraging success then the results may be expected to more closely resemble the results of Green and McCormick (1999) who showed that for *A. melanopus*, reduced food led to longer PLDs and smaller size at metamorphosis than in well-fed larvae. However, in this study, PLD was positively correlated with weight and body condition at metamorphosis. If body condition is considered a proxy for foraging success, then the current study has demonstrated that sediment increased foraging success for fish in the low sediment treatment. The delay in metamorphosis is therefore not associated with slower larval growth or poorer body condition as a consequence of suspended sediment. Interestingly, the fish in the high sediment treatment were also significantly longer and heavier than the fish in the control at metamorphosis, which contradicts previous work that showed suspended sediment impaired foraging in a coral reef fish at this level (Wenger et al., 2012).

Although suspended sediment was not impairing foraging in this experiment, it was clearly affecting the larvae in other ways, resulting in extended PLDs. This result is particularly significant, as it highlights an important knowledge gap. Although river plumes can promote higher growth of marine fish larvae due to nutrient enrichment (Lang et al., 1994; Allman & Grimes, 1998), no studies have examined the PLD of these larvae that derive benefit from river plumes. It may be that even though nutrient enriched plumes provide more food, the effects of suspended sediment in the plume could still delay metamorphosis through mechanisms unrelated

to foraging efficiency. More research is necessary to examine the relationship between river plumes and the settlement success of larvae that are entrained in them. Competency to settle can be dictated by a complex interaction of developmental parameters and environmental cues, unrelated to growth and body condition. Suspended sediment could be interfering with developmental processes important for metamorphosis, not related to age or size, such as sensory development (Shand, 1997; Lara, 1999) or that a decoupling of physiological features has occurred, such that some developed more slowly than is typical (Spicer and Burggren, 2003). There are different mechanisms that trigger metamorphosis and settlement in the wild, particularly environmental cues that indicate suitable habitat (McCormick, 1999; Pechenik, 2006). Although it is unknown what is triggering fish metamorphosis in the laboratory, it is evident that suspended sediment is changing the ability of the fish in the sediment treatments to metamorphose within the typical time frame of 11 days (Almany et al., 2007).

Another explanation for delayed metamorphosis may be that increased suspended sediment induces a response to delay metamorphosis and settlement until better environmental conditions are encountered or external cues necessary to trigger metamorphosis are detected. Previous studies have shown that suspended sediment impairs habitat choice at settlement in certain coral reef species through a reduction in visual cues (Wenger et al., 2011; Wenger and McCormick, 2013). Therefore, there is the potential that if coral reef fishes cannot successfully perceive visual cues necessary for habitat choice, they may delay metamorphosis. Marine invertebrates have been shown to delay metamorphosis in the absence of chemical or physical cues (reviewed in Pechenik, 1990). McCormick (1999) experimentally demonstrated that a coral reef fish close to settlement can delay metamorphosis if kept away from suitable habitat or settlement sites (McCormick, 1999). It may be that if the larvae are in sub-optimal conditions,

such as reduced water quality, metamorphosis and settlement can be delayed. Delays in metamorphosis have previously been inferred through otolith analysis (e.g. Victor, 1986; Cowen, 1991). These studies have demonstrated, based on the variability in PLD and the size at settlement, that some species can be remarkably flexible in the timing of settlement. Plasticity in timing of metamorphosis may be favored in environments that frequently experience suspended sediment, due to the variability in environmental conditions, particularly if individuals will be larger at settlement (Sponaugle and Pinkard, 2004; Perez-Dominguez and Munch, 2010), however, as discussed above, the consequences of delaying metamorphosis may be great. Importantly, there was no significant difference in the time to metamorphosis among fish from the low, medium, and high sediment treatments, suggesting that the sediment threshold for behavioral changes may be close to conditions found relatively frequently in the natural environment (Table 2.1). More research is needed to determine the mechanism underpinning the delays in metamorphosis caused by suspended sediment and how a sediment-induced delay alters survivorship and recruitment patterns.

In conclusion, our study provides important evidence that suspended sediment can significantly alter a crucial life history stage of a coral reef fish. Even a relatively small increase in suspended sediment concentrations prolonged larval development of *A. percula* affected size at metamorphosis and body condition. Given the critical importance of this life history stage for recruitment and population viability, our study underscores the crucial role that suspended sediment may play in influencing reef fish population dynamics now and in the future.

CHAPTER 3: SUSPENDED SEDIMENT IMPAIRS HABITAT CHOICE AND CHEMOSENSORY DISCRIMINATION IN TWO CORAL REEF FISHES[†]

[†] Wenger AS, Johansen JL, Jones GP (2011) Suspended sediment impairs habitat choice and chemosensory discrimination in two coral reef fishes. *Coral Reefs* 30:879-887

3.1 ABSTRACT

Increasing sediment onto coral reefs has been identified as a major source of habitat degradation, and yet little is known about how it affects reef fishes. In this study, we tested the hypothesis that sediment-enriched water impairs the ability of larval damselfish to find suitable settlement sites. At three different experimental concentrations of suspended sediment (45, 90, and 180 mg l⁻¹), pre-settlement individuals of two species (*Pomacentrus amboinensis* and *P. moluccensis*) were not able to select their preferred habitat. In a clear water environment (no suspended sediment), both species exhibit a strong preference for live coral over partially dead and dead coral, choosing live coral 70% and 80% of the time, respectively. However, when exposed to suspended sediment, no habitat choice was observed, with individuals of both species settling on live coral, partially dead, and dead coral, at the same frequency. To determine a potential mechanism underlying these results, we tested chemosensory discrimination in sediment-enriched water. We demonstrated that sediment disrupts the ability of this species to respond to chemical cues from different substrata. That is, individuals of *P. moluccensis* prefer live coral to dead coral in clear water, but in sediment-enriched water, chemical cues from live and dead coral were not distinguished. These results suggest that increasing suspended sediment in coral reef environments may reduce settlement success or survival of coral reef fishes. A sediment-induced disruption of habitat choice may compound the effects of habitat loss on coral reefs.

3.2 INTRODUCTION

Increasing sediment input into coastal marine environments is having a profound influence on some shallow marine habitats and their constituent species (Airoidi, 2003; Syvitski et al., 2005; Orth et al., 2006). Coral reefs habitats, and corals in particular, appear to be particularly sensitive to sediment deposition and turbidity regimes (Rogers, 1990; Richmond, 1993; Fabricius, 2005; Ryan et al., 2008). Increased sediment deposited on coral reefs not only reduces coral cover by smothering live coral, it can also inhibit coral settlement and growth by covering suitable hard substrata (Rogers, 1983; Fabricius, 2005). In addition, an increase in suspended sediment concentrations leads to increased turbidity and light attenuation (Kleypas, 1996; Fabricius, 2005), resulting in reduced photosynthesis, decreased calcification rates and depth range of coral (Fabricius, 2005). However, while the impacts of sediment related factors on corals are becoming well known, the effects of these on other reef-associated organisms such as fishes have received little attention.

Large-scale gradients in the distribution and diversity of reef fishes, such as increasing diversity with distance from shore (Williams, 1982) or from river mouths (Fabricius et al., 2005; Mallela et al., 2007) suggest sediment levels may naturally influence them. Sediment may influence reef fishes either directly, through effects on growth or survivorship at different life history stages, or indirectly through effects on coral cover or topographic complexity. The close association between reef fish faunas and their underlying habitat (Jones and Syms, 1998; Jones et al., 2004; Wilson et al., 2006) suggests that any sediment-induced change to habitat structure will have major effects on coral-associated fishes. In terms of direct effects, reduced vision caused by turbidity may hinder the foraging ability of fish using visual cues (e.g., planktivorous fish), which could lead to a decrease in abundance or limit growth (Williams et al., 1986; Kingsford

and Hughes, 2005). However, apart from one study reporting gill damage in juvenile green grouper *Epinephelus coioides* after short-term exposure to suspended sediment (Au et al., 2004), direct links between coral reef fish and sediment are not well understood.

Because sediment loading onto coral reefs is increasing globally (Rogers, 1990; Fabricius, 2005), it is critical to understand exactly how sediment interacts with the ecology of fishes and reef organisms other than corals. To date, few studies have examined how sediment may influence vital population parameters such as recruitment and mortality. One of the challenges to isolating the direct links between sediment and reef fish is to distinguish them from indirect effects associated with habitat loss. For example, recruitment rates may be influenced not only by a decline in the availability of suitable settlement substrata (Jones et al., 2004), but also by impairing the ability of larval fishes to find suitable habitat. Experiments using sediment-enriched water provide the best means to distinguish between direct and indirect effects on larval settlement. Though reduced vision and gill damage provide indications that sediment can theoretically reduce the fitness of already established individuals (Au et al., 2004; Kingsford and Hughes, 2005), the effects of increased sediment on patterns of settlement have not been examined.

It is widely accepted that the composition of coral reef fish assemblages is governed initially by patterns of settlement of larval fishes to reef habitats (Williams, 1991; Booth and Wellington, 1998). Most species exhibit strong habitat selection at settlement (Öhman et al., 1998) and habitat choices made at settlement establish the initial distribution patterns of species (Jones, 1991). Many studies have also shown that an inappropriate choice of habitat can lead to reduced fitness and increased mortality (Jones, 1991; Munday, 2001; McCormick, 2009).

However, whether or not habitat choice is impaired in sediment-enriched water has not been investigated.

At settlement, fishes use a range of sensory modes to discriminate between habitats (Lecchini et al., 2005; McCormick et al., 2010). Chemosensory mechanisms, such as smell and taste, and visual stimuli are two of the primary sensory cues that fish use to find suitable habitat (Sweatman, 1983; Lecchini et al., 2005; Munday et al., 2009). Larvae often preferentially settle in habitat in response to strong chemical or visual cues (Sweatman, 1983; McCormick, 2009). If one or more of the environmental cues is weak or not properly detected, settlement choices may not accurately reflect the habitat suitability for the species (Munday et al., 2009). To date, no studies have investigated whether or not suspended sediment disrupts any of the sensory mechanisms associated with habitat choice.

The purpose of this study was to experimentally investigate whether suspended sediment affects settlement choice and disrupts a sensory mechanism used for habitat choice in two congeneric coral reef fishes, *Pomacentrus amboinensis* and *P. moluccensis* (Pomacentridae). In the first part of the study, the influence of suspended sediment on habitat choice in pre-settlement juveniles was experimentally tested. Settlement choices were examined under different suspended sediment regimes to see whether increasing levels of suspended sediment influenced habitat choice. A second experiment was conducted on *P. moluccensis* to test whether suspended sediment from coastal reefs impaired chemosensory responses derived from preferred habitats. We tested the prediction that suspended sediment would reduce the ability of juveniles to discriminate among different potential post-settlement habitats.

3.3 METHODS

3.3.1 Experiment 1: effects of suspended sediment on habitat choice at settlement

This experiment was conducted on Lizard Island on the northern Great Barrier Reef, Australia (14°40' S; 145°28' E) with the purpose of examining whether or not there would be any behavioral response to suspended sediment during settlement. Settlement stage larvae of *Pomacentrus amboinensis* and *P. moluccensis* were chosen as the study species due to their high abundance and their field distribution, with *P. moluccensis* commonly found on live coral and *P. amboinensis* dwelling in a broader type of habitats (Syms and Jones, 2000). To test whether increasing suspended sediment impairs the ability of reef fishes to find preferred habitat, settlement choice trials were run to determine the habitat preference of each species in increasing concentrations of suspended sediment.

The fishes were collected in February 2010 using light traps (Doherty, 1987). All fishes were held in featureless plastic tanks with filtered aerated seawater prior to experiments, to ensure that they would remain naïve to any habitat. *Pocillopora damicornis*, a complex branching coral used by many coral-dwelling fish for habitat (e.g., Feary et al., 2007b) was chosen for this habitat choice experiment. Three habitat types were used: live coral, partially dead coral (~25% coral cover), and dead coral, all of which were structurally intact (Feary et al., 2007b). Fourteen colonies of each habitat type were collected from the Lizard Island lagoon using a hammer and chisel. All colonies were between 15 and 20 cm in diameter. The habitat choice of each test species was recorded in four levels of suspended sediment: control (0 mg l⁻¹), 45 mg l⁻¹, 90 mg l⁻¹, and 180 mg l⁻¹. Ten individuals of each species were tested in ten independent trials for each level of suspended sediment. The sediment levels encompassed the range of sediment levels that have been recorded on coral reefs (e.g., Larcombe et al., 1995;

Wolanski et al., 2008). To test general behavioral responses of coral reef fishes settling in suspended sediment, bentonite, commercially available clay used in previous turbidity experiments, (e.g., Van de Meutter et al., 2005) was used as the sediment. Bentonite was chosen over natural sediment to specifically isolate the effect of different levels of suspended particles alone in impairing habitat choice and to control for variation in potential reef cues in natural sediment. Using bentonite as a standard ensured that different responses to test substrata were the result of the effects of suspended sediment on visual and chemosensory responses. Additionally, because of the particle size, this type of clay is representative of the type of sediment commonly found in the water column around coral reefs (Kleypas, 1996). Before each trial, the water was turned off in the experimental tanks so that no sediment could leave the tanks during the trials. Then, the sediment was manually dissolved into the tanks to avoid clumping. Once the water was uniformly turbid, one fish was placed into the center of each tank using a large (20 x 10 cm frame) dip net with the handle bent up so that there was a 90° angle between the handle and the frame. It was placed on the bottom of the tanks and lifted straight up after a five-minute acclimation period.

The settlement trials were run in 250 L (100 x 50 x 50 cm) rectangular 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 (~24 cm). The outer edge of each habitat was against the tank walls. Between each trial, the coral heads were haphazardly rearranged in the tank to ensure that settlement was based on habitat type and not location of the coral heads, direction of sunlight or other outside stimuli.

Although it is generally thought that coral reef fish settle at night, it has been noted that in many damselfish species, diurnal settlement represents a substantial portion of observed settlement patterns (e.g., Robertson et al., 1988; Leis and Carson-Ewart, 1999). Consequently, trials were run throughout the day. This allowed for the use of both visual and chemosensory cues for settlement choice. Ninety minutes after the fish was added, their settlement choice was recorded. Settlement was defined as any individual within 5 cm of a coral head. In the medium and high levels of suspended sediment, the fish could not be observed because of the high turbidity. Therefore, after ninety minutes, clear glass jars were placed over each coral head. There was at least 5 cm between the coral head and the sides of the jars. A pilot study was conducted to ensure this retaining method did not influence the settlement choice of individual fish. Specifically, when the glass jars were placed over the coral heads in clear water, the fish swam further into the coral head it had settled on and was thus contained under the jar. The experimental tanks were then flushed by turning on the water to reduce the level of suspended sediment, to allow visual observation of settlement choice. Between each trial, each tank was flushed with fresh seawater to remove any sediment and chemical cues.

3.3.2 Experiment 2: effects of suspended sediment on chemosensory discrimination

To determine a potential mechanism underlying the results from experiment one, a second experiment was carried out to test whether juvenile damselfish discriminate between water based on sediment load, and whether or not sediment-enriched water impairs the ability to distinguish chemical stimuli from different habitat types. The experiment was carried out in Kimbe Bay, West New Britain, Papua New Guinea (5°30'S, 150°05'E) using *P. moluccensis*. Newly settled recruits [13.2 mm ± 0.167 (mean ± SE)] were collected off live coral using diluted clove oil (Munday and Wilson, 1997). It was not possible to run the chemosensory trials on pre-

settlement individuals. The experiment focused on *P. moluccensis* as it has been shown that pre-settlement and post-settlement *P. moluccensis* exhibit the same habitat preferences (Öhman et al., 1998). Other chemosensory studies have also shown that laboratory reared naïve larvae and field caught juvenile damselfishes can exhibit identical habitat preferences (Dixson et al., 2008). To test whether chemoreception was influenced by sediment, seawater was enriched with specific chemical cues and individuals were given a pair-wise choice between different water sources. The chemical cues that were tested against each other were as follows: (1) live coral in clear water vs. clear water alone, (2) sediment-enriched water vs. clear water, (3) live coral in clear water vs. dead coral in clear water, and (4) live coral in sediment-enriched water vs. dead coral in sediment-enriched water. Fifteen trials using different juvenile fish were performed for each combination of chemical cues.

Because this experiment was focused on a specific mechanism (i.e., chemoreception), water was enriched with settled muddy sediments taken from coastal reefs instead of with bentonite. This was to ensure that we were testing whether sediment from coral reefs impaired chemoreception. To minimize confounding factors, the sediment was not collected directly below live or dead coral. In addition, colonies of live and dead *Pocillopora damicornis* were collected off the reef and placed in separate 10 L buckets containing offshore (~1km) seawater. The sediment and the colonies were soaked in the water for two hours, allowing their chemical cues to absorb 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 x 4 cm) (Gerlach et al., 2007; Dixon et al., 2008). A constant gravity-driven flow of 100 mL min⁻¹ per channel was maintained throughout all trials. Flow rates were measured using a flow meter. 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 two minutes. At the end of the acclimation period, the position of the fish on each side of the chamber was recorded every five seconds for a two-minute period. After the two-minute 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 one-minute rest period and then allowed another two-minute 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. Additionally, between each trial the choice chamber was emptied and then filled with new treatment water so that no chemical cues from the previously tested fish remained. The few individuals that displayed clear side preferences during their trial were excluded from any analysis.

3.3.3 Data analysis

For the settlement trial, a row by column frequency table was used to assess whether there was an overall relationship between suspended sediment and habitat choice at settlement. Furthermore, a chi-squared goodness of fit was used to test whether the three habitats were chosen in equal frequency. For the chemosensory trials, the data from before and after the side switch were pooled. A distribution-free Randomization test was performed to see if the mean proportion of time the fishes spent in a particular water stream differed from random

3.4 RESULTS

3.4.1 Effects of sediment on habitat choice at settlement

There was no significant relationship between any level of suspended sediment (including the control) and the overall settlement habitat choices for either *P. amboinensis* (frequency table, $df=6$, $p=0.11$) or *P. moluccensis* ($df= 6$, $p=0.42$). However, when the observed habitat selection choices were compared to values representing equal likelihood of choosing each of the three habitat types, there was a significant difference between random habitat choice and specific habitat choice for the control levels of both *P. amboinensis* and *P. moluccensis* (Table 3.1). In the control (clear water), *P. amboinensis* chose live coral 8 out of 10 times and *P. moluccensis* chose live coral 7 out of 10 times (Table 3.2). However, starting in the low level of sediment, *P. amboinensis* only chose live coral 3 out of 10 times and *P. moluccensis* chose live coral 5 out of 10 times (Table 3.2). In the medium and high levels of suspended sediment, *P. amboinensis* continued to choose live coral only 3 out of 10 times, without showing increased preference for another habitat type (Table 3.2). In both the medium and high levels of suspended sediment, one individual of *P. moluccensis* did not choose any habitat. Therefore, in both the medium and high levels of suspended sediment, *P. moluccensis* chose live coral 3 out of 9 times, without showing increased preference for another habitat type (Table 3.2). Overall, in both species, there was no significant habitat preference in the low, medium, or high turbidity conditions, indicating that impaired choice occurs at relatively low sediment levels (Table 3.1)

Table 3.1 Chi squared goodness of fit examining whether significant preferences in habitat association in late stage larvae of *Pomacentrus amboinensis* and *P. moluccensis* were apparent between live coral, partially dead coral, and dead coral in aquaria. Asterisks denote significant ($p < 0.05$) results.

Species	Treatment	X ²	df	p
<i>P. amboinensis</i>	Control	10.4	2	<0.01*
	Low	0.2	2	0.9
	Medium	0.2	2	0.9
	High	1.4	2	0.49
<i>P. moluccensis</i>	Control	6.2	2	<0.05*
	Low	5	2	0.08
	Medium	0	2	1
	High	0	2	0.72

Table 3.2 Habitat choice of late stage larvae of *Pomacentrus amboinensis* and *P. moluccensis* in increasing levels of suspended sediment in aquaria.

Species	Treatment	Live Coral	Partially Dead Coral	Dead Coral
<i>P. amboinensis</i>	Control	8	0	2
	Low	3	3	4
	Medium	3	3	4
	High	3	5	2
<i>P. moluccensis</i>	Control	7	1	1
	Low	5	5	0
	Medium	3	3	3
	High	3	4	2

3.4.2 Effects of sediment on chemosensory discrimination

In clear water, juvenile *P. moluccensis* made choices based on chemical stimuli consistent with the habitat choice experiment. Juveniles preferred live coral in clear water to clear water (Randomization test, $p < 0.05$), overall spending 60.7 ± 8.43 % (mean \pm S.E.) of the time in the live coral water stream (Fig. 3.1). Juveniles chose live coral in clear water over dead coral in clear water (Randomization test, $p < 0.05$), spending 60.5 ± 6.27 % of the time in the live

coral stream (Fig. 3.1), showing they can clearly detect and respond to live coral through chemical cues.

Although 9 out of 15 individuals of *P. moluccensis* showed a preference for clear water over sediment-enriched water, the overall proportion of time spent in clear water over sediment-enriched water was not significant (Randomization test, $p=0.153$), with the fishes spending 56.6 ± 7.32 % of the time in clear water (Fig. 3.1). Though *P. moluccensis* was not repelled by the chemical cues from sediment, when the choice between live coral in sediment-enriched water vs. dead coral in sediment-enriched water was tested, there was not a significant preference for live coral over dead coral in sediment-enriched water (Randomization test, $p=0.661$). Overall, *P. moluccensis* only spent 47.3 ± 7.26 % of the time in the water stream with live coral and sediment cues, indicating the sediment-enriched water impairs habitat choice (Fig.3.1). This result also corresponds with the habitat choice experiment, with preference for live coral diminishing as sediment is added.

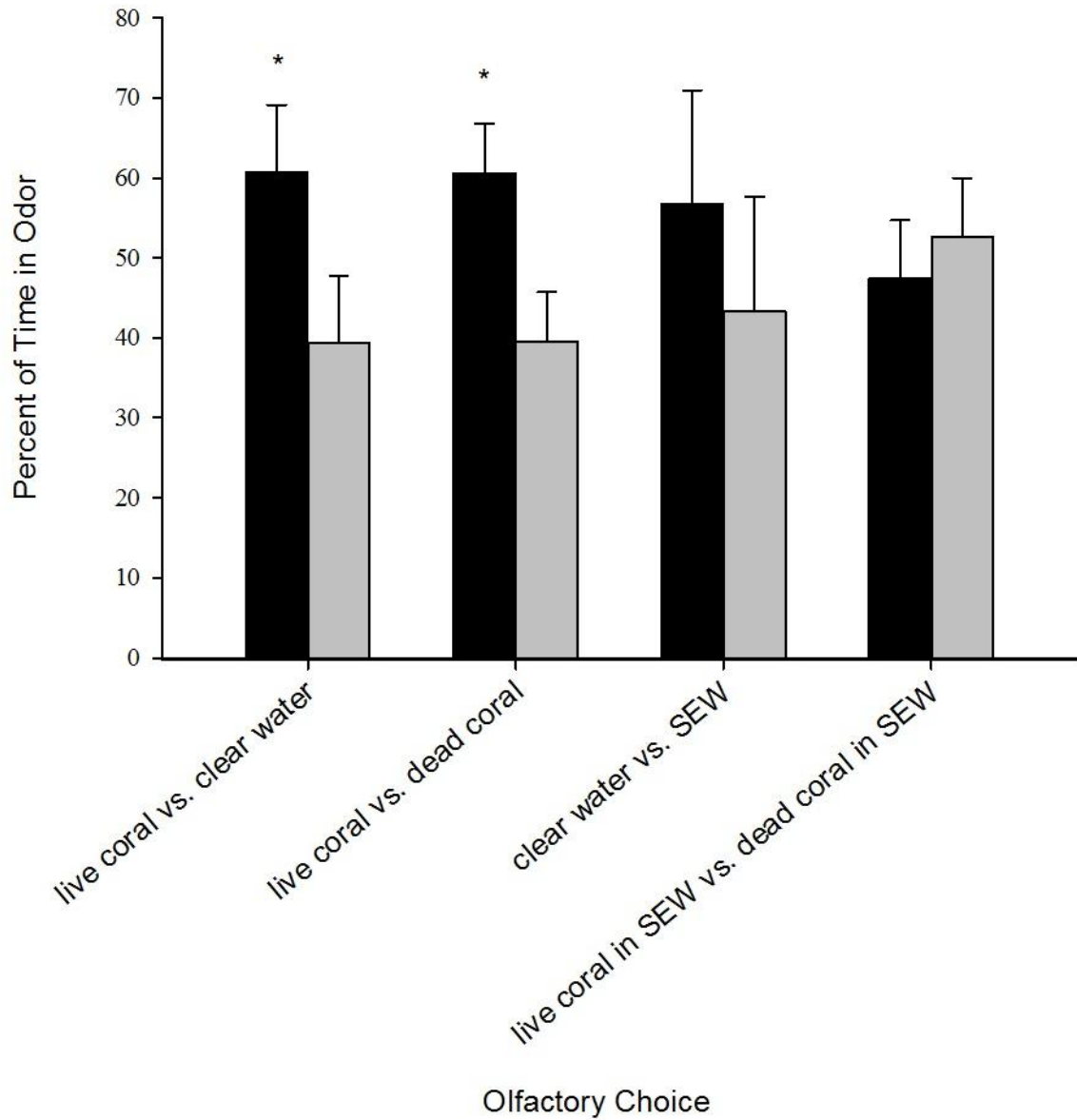


Figure 3.1 Percent of time newly settled *P. moluccensis* associated with specific chemical cues. SEW stands for sediment-enriched water. Black bar refers to first variable in x-axis text. Asterisks denote significant preferences ($p < 0.05$) in chemical cue association as determined by Randomization tests.

3.5 DISCUSSION

Successful recruitment by coral reef fishes is necessary to sustain local populations and the inability to find suitable habitat can lead to major changes in population dynamics (Holbrook et al., 2000; Halpern et al., 2005). This study provides the first demonstration of how sediment can directly affect the settlement choice of coral reef fishes and the disruption of sensory mechanisms used in habitat choice. We show that an increase in suspended sediment concentrations significantly modifies the selection of habitats by the two coral reef damselfishes *Pomacentrus amboinensis* and *P. moluccensis*. Both species clearly preferred live coral when settling in clear water. However, in turbid conditions above 45 mg l^{-1} , no habitat choice could be detected. In the second experiment, when in clear water, *P. moluccensis* preferred the chemical cues of live coral to dead coral but were not able to distinguish between live coral and dead coral in sediment-enriched water. Although the first experiment used naïve, light-trap caught fish and the second experiment used reef-captured juveniles, the patterns of choice were the same; a result confirmed by Öhman et al. (1998), who also found that pre-settlement and post-settlement juvenile *P. moluccensis* exhibit identical habitat choices. These findings suggest that as sediment loads increase above a minimum threshold, coral reef fishes may start to settle on non-preferred habitats, which could have negative demographic consequences.

Habitat selection is an important step in survival of coral reef fishes and they derive many benefits from associating with their preferred habitat. Any interference in the mechanisms used to select habitat may reduce the survivorship of recruiting individuals. For many species of coral reef fishes, live coral is the preferred habitat and studies have shown that when live coral cover decreases, more fish species decline than just species with obligate coral associations (e.g., Jones et al., 2004). The structural complexity of live coral provides shelter from predation (Beukers

and Jones, 1997; Coker et al., 2009). Additionally, the darker color of live coral compared to dead coral may allow the fish to hide more easily, and chemical cues stemming from the live coral may mask any chemical cues of the fish, leading to reduced predation (Feary et al., 2007b; Coker et al., 2009; McCormick, 2009). There are also fitness consequences for coral reef fishes that are not on their preferred habitat. A recent study found slower growth rates in live coral dwelling fishes placed on habitat with little to no live coral, compared to individuals placed on 100% live coral cover (Feary et al., 2009). Reduced growth rate can increase the time it takes to reach maturity, which could have greater implications for the long-term persistence of local populations (Jones, 1991; Brunton and Booth, 2003).

If reef fish do not initially settle on their preferred habitat, it is unlikely that they will be able to move to a suitable habitat, due to low migration success (Booth, 1995; McCormick, 2009). In increasing levels of suspended sediment, any potential post-settlement migration may be further limited by a reduction in the visual field (Asaeda et al., 2002), although this effect remains to be evaluated.

This study demonstrates that suspended sediment can interfere with chemoreception used during settlement. Coral reef fishes rely strongly on chemical cues to find their habitat (e.g., Sweatman, 1983; Munday et al., 2009) and the increased sediment may act to mask or confuse otherwise clear chemical signals, leading to random or wrong choices. The masking of chemical cues was observed in individuals of *P. moluccensis* that were no longer able to distinguish between live coral and dead coral in sediment-enriched water. On turbid reefs, if suitable habitat is unavailable or not detected, the fish may either find different reefs on which to settle or simply fail to recruit. Though we know that sediment interacts with chemical cues, further exploration is needed to determine whether the cues from sediment overpowers other chemical cues or whether

it binds to chemosensory receptors in some way. It is important to better understand what is occurring because chemosensory mechanisms are widely employed by marine life. Though our study specifically focuses on marine fishes, our results could have broad implications for other taxa as well. For instance, marine planktonic ciliates have been shown to use chemical signals to find their prey (Verity, 1988). Chemosensory cues also enable the settlement and metamorphosis of corals and gastropods (Morse et al., 1996; Hadfield et al., 2000). Consequently, if sediment is causing a disruption in chemosensory cues, then it is likely that sediment will affect a large suite of coral reef species.

Sediment may not only reduce the successful choice of habitat, it may also fully inhibit settlement to a particular reef. If high levels of sediment reduce ambient stimulus cues then settlement-sized fish may not be able to exploit habitat cues to orient towards a particular reef (Kingsford et al., 2002). Srinivasan and Jones (2006) showed that for PNG, periods of low recruitment coincide with turbid water conditions associated with the summer monsoon. Although we did not find a significant preference for clear water over sediment-enriched water, *P. moluccensis* did show a tendency for clear water. Consequently, sediment may directly cause recruitment failure for an area if larvae are unable to successfully find a reef or if they prefer to remain in clear pelagic water rather than enter turbid water.

Suspended sediment may act in another way to inhibit habitat selection success. Suspended sediment causes an increase in turbidity, which can reduce the visual field of fish (Newcombe, 2003; Fabricius, 2005). It has been well documented that reef fish use visual cues to find their habitat (Booth, 1992; Lecchini et al., 2005). Therefore, a loss in visual acuity due to high turbidity may lead to a modification of habitat choice, with the fish settling on the first shelter they find. Both experiments of this study were conducted during daylight hours, meaning

that visual cues could have potentially alleviated some of the effects of suspended sediment. However, in experiment one, although there was a very clear preference for live coral in the control treatment, this preference disappeared completely once sediment was added. Diurnal trials allowed for the use of both visual and chemosensory cues, and it is clear that one or both of these sensory mechanisms is impaired by sediment load. The mechanism by which sediment is impairing habitat choice in the first experiment requires further investigation. Increasing suspended sediment almost certainly impairs vision once it reaches a certain level. However, since bentonite is devoid of reef cues, it is not evident how it affects chemoreception. Because this part of the study did not isolate visual cues from chemical cues during the settlement trials, further work is needed to investigate whether a reduction of visual cues may play a role in limiting habitat selection success and whether the type of sediment used affects chemoreception. It is also important to note that because trials for experiment one were run during the day only, these results do not necessarily apply to larvae settling at night. Further work is required to determine whether nocturnal habitat choice is also influenced by increasing sediment levels.

While sediment loading to the marine environment is increasing worldwide (Rogers, 1990), the present study shows that suspended sediment concentrations on coral reefs are currently reaching detrimental levels for successful settlement of coral reef fish. All concentrations of suspended sediment examined in this study have been previously recorded on reefs worldwide (Rogers, 1990; Larcombe et al., 1995; Wolanski et al., 2008). Though severely high levels of suspended sediment (similar to the 180 mg l^{-1} examined here) occur less frequently, reefs may still regularly experience such concentrations for a period of days (Larcombe et al., 1995). Furthermore, we show that even at relatively low levels of suspended sediment (45 mg l^{-1}), which at present occur frequently and consistently on a range of reefs

within the GBR (Larcombe et al., 1995), recruiting coral reef fishes lose the ability to distinguish among habitats. Suspended sediment concentrations have been recorded above 40 mg l⁻¹ for up to 29% of the time and above 20 mg l⁻¹ for up to 41% of the time over a four-month period near reefs on the inner shelf of the GBR (Larcombe et al., 1995). This may also mean that even during calm weather with reduced suspended sediment, these reefs are still enriched with chemical cues from sediment. Therefore, while levels of suspended sediment may only be reaching detrimental levels 29% of the time, it is likely that the sediment will be having a broader impact than just during these re-suspension events. Since many coral reefs may chronically experience levels of suspended sediment here shown to seriously impact coral reef fish, it is necessary to examine lower levels of suspended sediment in order to determine the threshold concentration where suspended sediment become detrimental.

The impact of suspended sediment may also depend on its source. Offshore sediment is predominately calcareous based, whereas inshore coral reefs have a much higher proportion of terrigenous sediment (Larcombe et al., 2001), which may also contain chemical contaminants (Fabricius, 2005). It may be that the effects of suspended sediment combined with any additional pollutant will be much greater than would be seen with pure sediment. Although this study did not isolate additional components in the sediment, it is important to consider that the sediment on inshore reefs is likely to be enriched with terrestrial contaminants (Fabricius, 2005). The deleterious effects of agriculture pollutants, heavy metals, and sewage on coastal ecosystems have been widely chronicled (e.g., GESAMP, 2001; Fabricius, 2005). Inshore coral reefs may experience different levels of exposure to these contaminants and it is likely that species in areas more prone to declining water quality will behave differently. Further exploration is therefore necessary to determine how fishes will respond to different types of pollutants.

This study clearly demonstrates that sediment may directly affect the successful recruitment of coral reef fishes. The longer-term consequences of impaired habitat choice require further investigation. In addition, the direct effects of suspended sediment need to be examined in relation to other factors that may have a detrimental effect on the availability of preferred settlement habitats. Clearly, coral reefs are subject to multiple threats, including sedimentation, overfishing, cyclones, Crown of Thorns Starfish outbreaks, and climate change, including bleaching and ocean acidification (Bellwood et al., 2004; Pratchett, 2005; Munday et al., 2008). These disturbances may all reduce live coral cover, with sediment further suppressing growth and recovery of coral (Jones et al., 2004; Fabricius, 2005). By determining threshold concentrations of sediment that will directly impact reef species, we can begin to provide a good basis for future management strategies to reduce sediment loading onto coral reefs.

CHAPTER 4: DETERMINING TRIGGER VALUES OF SUSPENDED SEDIMENT FOR BEHAVIORAL CHANGES IN A CORAL REEF FISH[†]

[†] **Wenger AS**, McCormick MI (2013) Determining trigger values of suspended sediment for behavioral changes in a coral reef fish. *Mar Pol Bull* 70:73-80

4.1 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⁻¹), 10 mg l⁻¹ (~1.7 NTU), 20 mg l⁻¹ (~3.3 NTU) and 30 mg l⁻¹ (~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⁻¹ and 30 mg l⁻¹, suggesting a sediment threshold for behavioral changes. Inshore areas of the Great Barrier Reef, *P. moluccensis* may encounter sub-optimal conditions between 8-53% 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.

4.2 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. Tilman et al., 2001; Lotze et al., 2006; Diaz and Rosenberg, 2008). 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 (Cloern, 2001; Lotze et

al., 2006; Brodie et al., 2012). Among these shallow marine environments, coral reefs are especially sensitive to increased sediment and turbidity (Furnas, 2003; Fabricius, 2005; Brodie et al., 2012). 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 five-fold 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., 2013).

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 (Rogers, 1979; Anthony and Fabricius, 2000), 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 (Letourneur et al., 1998; Fabricius et al., 2005; 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 (Öhman et al., 1998; Jones et al., 2004; McCormick et al., 2010). 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 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. Sweatman, 1983; Lecchini et al., 2005; Munday et al., 2009; McCormick et al., 2010). Once settled, fish continue to use sensory cues to gain information about their environment (Odling-Smee and Braithwaite, 2003; Kroon, 2005). 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 (Odling-Smee and Braithwaite, 2003; Gaillard et al., 2010; Coker et al., 2012). 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 mg l^{-1} (~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 (Syms and Jones, 2000; Bellwood et al., 2006), 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.

4.3 METHODS

4.3.1 Study species

Juvenile *Pomacentrus moluccensis* (16.9 ± 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 ± 0.02 , A. 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 48h prior to experiments. This time frame was determined based on how quickly the fishes began to swim and eat normally.

4.3.2 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 ($14^{\circ}40'$ S; $145^{\circ}28'$ E). *Pocillopora damicornis*, a complex branching coral used by many coral-dwelling fishes for habitat (e.g. Feary et al., 2007b), was chosen for this habitat choice experiment. Three habitat types were used: live coral, partially dead coral (~25% live coral cover), and dead coral (covered by some benthic invertebrates and algae), all of which were structurally intact (Feary et al., 2007b). The proportion of live coral in the partially dead colonies was determined based on the required total diameter for each colony. 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 mg l⁻¹), 10 mg l⁻¹ (~1.7 NTU), 20 mg l⁻¹ (~3.3 NTU) and 30 mg l⁻¹ (~5 NTU). The relationship between mg l⁻¹ bentonite and turbidity (NTU) was determined *a priori* through calibrations. 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 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., 2011, 2012) 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; A. 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 (~10 minutes), one fish was placed into a clear Perspex box in the center of each tank. After a three-minute 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 minutes for 90 minutes. Choice was defined as any individual within 5 cm of a coral head.

4.3.3 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 *Pocillopora 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⁻¹). The bentonite and the coral colonies were soaked in individual bins for 24 hours, 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 x 4 cm, L x 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⁻¹ per channel, which was maintained throughout all trials, and then into the flume chamber (Gerlach et al., 2007; Dixon et al., 2008). 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 two minutes. At the end of the acclimation period, the position of the fish on each side of the chamber was recorded every five seconds for a two-minute period. After the two-minute 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 one-minute rest period and then allowed another two-minute 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.

4.3.4 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 4.1). We extracted data from the literature about the frequency with which turbidity exceeded 5

NTU (the high level of sediment in this study; Table 4.1). In Larcombe et al. (1995), a calibration was made between mg l^{-1} and turbidity in the study region, which they determined to be ~1:1. The results of the study are reported in mg l^{-1} 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^{-1} conversion was not available for all studies.

Table 4.1 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 (percent)	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., 2013	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

4.3.5 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.

4.4 RESULTS

4.4.1 Experiment 1: habitat choice in increasing levels of suspended sediment

Pomacentrus moluccensis in all treatments showed unequal frequency in which they associated with one of the 3 habitat types according to the chi-squared goodness of fit test (Table 4.2). *Pomacentrus moluccensis* preferred live coral in the control, low, and medium treatments, associating with it $61.1 \pm 8.3\%$, $51.6 \pm 8.6\%$, and $49.4 \pm 8.4\%$ of the time, respectively (Fig. 4.1). In the high sediment treatment, *P. moluccensis* preferred partially dead coral over the other

habitats, spending $45.5 \pm 9.9\%$ of the time associating with it and only spent $23.3 \pm 8.9\%$ of the time associating with live coral (Fig. 4.1). 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. 4.1). There were no significant differences between any of the treatments in time spent associating with partially dead and dead coral (ANOVA, $p > 0.05$).

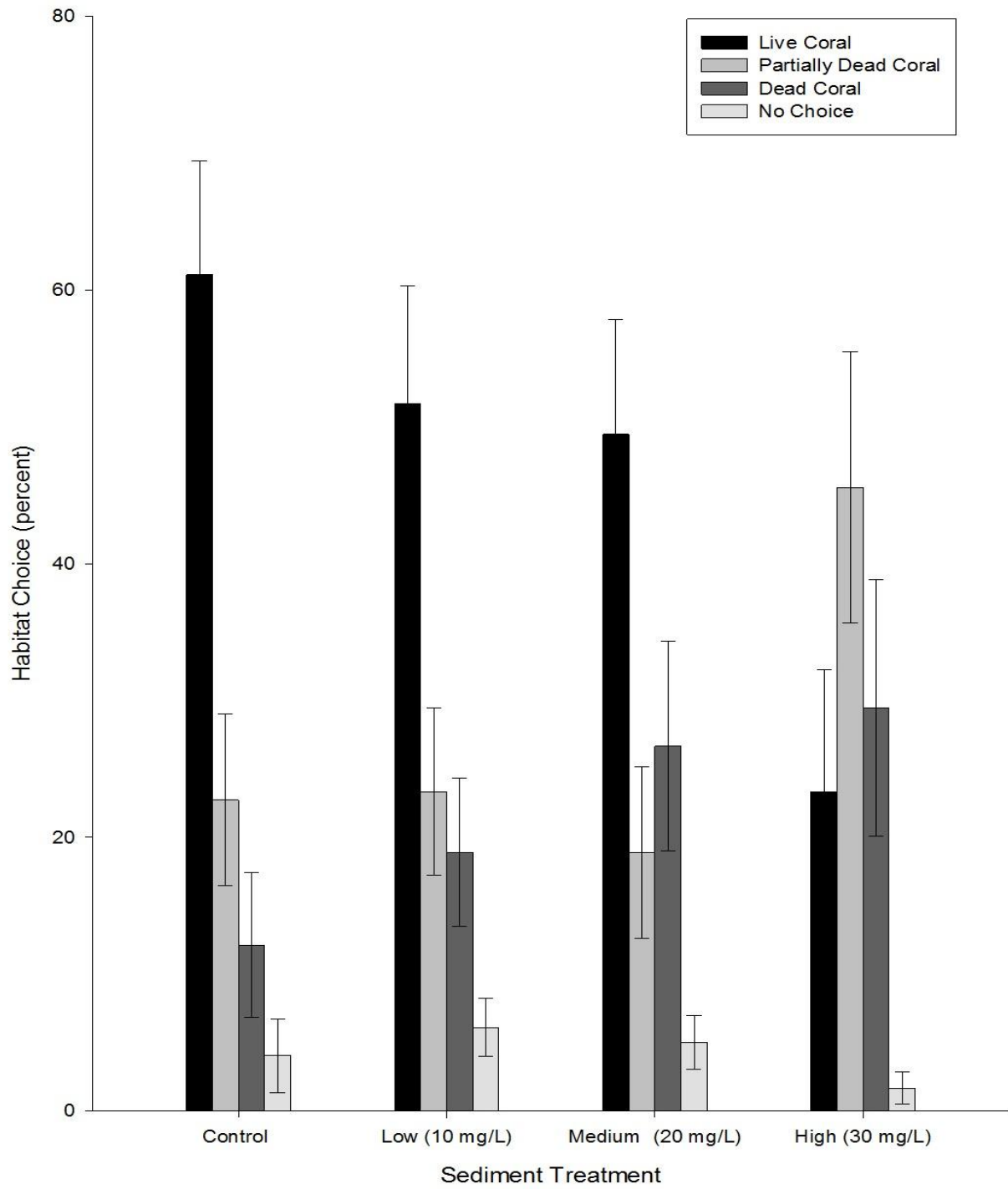


Figure 4.1 Proportion of time (\pm SE) that *Pomacentrus moluccensis* associated with each habitat type in the four sediment treatments.

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. 4.2a). 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 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. 4.2c).

Table 4.2 Propensity of *Pomacentrus moluccensis* to have an uneven settlement distribution among three settlement habitats in a choice experiment.

Treatment	X^2	df	p
Control	40.02	2	<0.0001
Low (10 mg l ⁻¹)	19.34	2	<0.0001
Medium (20 mg l ⁻¹)	15.38	2	0.0005
High (30 mg l ⁻¹)	7.94	2	0.02

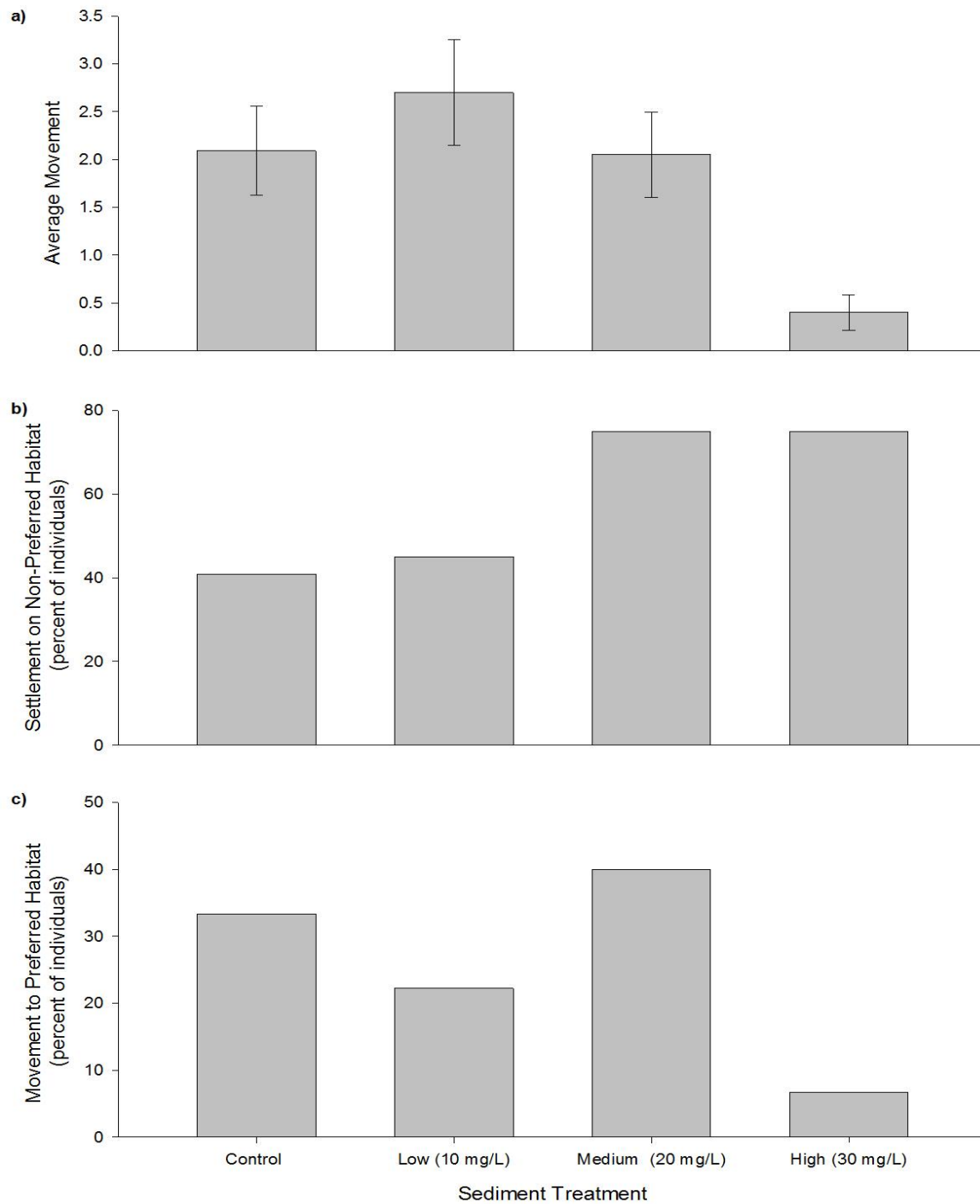


Figure 4.2 Differences between treatments of *Pomacentrus moluccensis* in a) movement (\pm SE) between habitat types, b) proportion of individuals that initially settled on partially dead and dead coral and c) proportion of individuals that successfully relocated to live coral after initially choosing partially dead or dead coral.

4.4.2 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.

4.4.3 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. (2013) 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 4.1) and this affects the percentages of time that turbidity exceeded 5 NTU. Overall, the frequency that 5 NTU was exceeded ranged between 8-53%, 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 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 2 sites so it is unclear if *P. moluccensis* is found there.

4.5 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 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., 2013). 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 (Öhman et al., 1998; McCormick and Weaver, 2012). 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 (Lewis 1997; Grüss et al., 2011). 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 (Snover, 2008; Grüss et al., 2011). 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^{-1} , $\sim 7.5 \text{ NTU}$) 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, 2009, 2012). 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 (McCormick, 2009; Coker et al., 2012). 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 (Larcombe et al., 1995; Anthony and Hoegh-Guldberg, 2003). 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^{-1}) with a slight adjustment during the wet season (2.4 mg l^{-1}) (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^{-1} 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^{-1} . The wet season corresponds with a high fish recruitment season on the Great Barrier Reef (McCormick, 2003; Brodie et al., 2007) 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 two 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., 2013). 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.

CHAPTER 5: INCREASING SUSPENDED SEDIMENT REDUCES FORAGING, GROWTH AND CONDITION OF A PLANKTIVOROUS DAMSELFISH[†]

[†]Wenger AS, Johansen JL, Jones GP (2012) Increasing suspended sediment reduces foraging success of a planktivorous damselfish. *J Exp Mar Biol Ecol* 428:43-48

5.1 ABSTRACT

Increasing sediment inputs into many coastal marine environments are having a profound influence on shallow marine habitats and their constituent species. Coral reef habitats appear to be particularly sensitive, with increased sediment deposition and turbidity regimes associated with declines in the abundance and diversity of coral reef fishes due to an indirect effect of habitat loss. The direct causes of these declines are largely unknown. In this study we tested the hypothesis that suspended sediment can negatively affect the foraging efficiency, nutritional state and survival of the planktivorous coral reef damselfish, *Acanthochromis polyacanthus*. Food acquisition, growth rate and body condition were measured in juvenile *A. polyacanthus* subjected to four experimental concentrations of suspended sediment (up to 180 mg l⁻¹; 30 NTU). There was a clear effect of suspended sediment on food acquisition. Fish took longer to find food and consumed less of the food provided with increasing sediment. The decline in food acquisition was associated with a significant reduction in juvenile growth and body condition. Fish reared in the medium and high sediment treatments increased in size by less than half the growth rates observed in the control group. Fish held in the control and low sediment treatment had double the surface area of hepatocyte vacuoles in the liver (a proxy for lipid storage) than the fish held in the medium and high sediment treatments. Suspended sediment also caused a significant increase in mortality of the juvenile fish in the high sediment treatment. Mortality reached almost

50% in the high sediment treatment, with no mortality in the control and less than 10% in the intermediate treatments. This study underscores the need to ameliorate increasing suspended sediment in inshore waters due to its potential impact on the growth and survival of planktivorous organisms, which form a vital trophic link between secondary production and fish biomass.

5.2 INTRODUCTION

Urbanization and increased agricultural activities are causing long-term changes to many of the key physical characteristics in coastal aquatic environments (Tilman et al., 2001; Lotze et al., 2006; Brodie et al., 2012). Many shallow water coastal habitats have already been severely modified through changed sedimentation regimes, increased nutrient loading, elevated turbidity and reduced light penetration (Cloern, 2001; Fabricius, 2005; Diaz and Rosenberg, 2008; Fabricius et al., 2013). Coral reef habitats and dependent species are particularly sensitive to sediment deposition and re-suspension (Rogers, 1990; Richmond, 1993; Fabricius, 2005; Ryan et al., 2008, Wenger et al., 2011). An increase in suspended sediment concentrations can lead to increased turbidity and reduced light attenuation (Kleypas, 1996; Fabricius, 2005) resulting in reduced photosynthesis, decreased calcification rates and a shallower depth range of coral (Fabricius, 2005). The effects of sediment on coral distribution and dynamics can have substantial indirect effects on other organisms associated with coral reefs, such as coral reef fishes (Rogers, 1990). Large-scale changes in the distribution and diversity of reef fishes along terrestrial run-off gradients (Letourneur et al., 1998; Fabricius et al., 2005; Mallela et al., 2007) suggest that there is a relationship between sediment load and fish occurrence. Suspended sediment is known to reduce the ability of some coral reef fish species to locate suitable habitat during settlement (Wenger et al., 2011). However, for most coral reef fishes the influence of

suspended sediment on the fitness-associated traits of individuals and their population consequences are unknown.

In coral reef fishes, like most other organisms, food acquisition is one of the key daily activities dictating individual performance such as growth, reproduction and life expectancy (Kerrigan, 1994; Donelson et al., 2008). Ultimately foraging success can strongly affect patterns of distribution, abundance and population dynamics (Jones and McCormick, 2002). Coral reefs have a high diversity of planktivorous fishes that acquire planktonic prey primarily through visual detection (Williams and Hatcher, 1983; Hobson, 1991; Rowland, 1999). Any reduction in the visual field due to suspended sediment has the potential to affect prey intake and growth in planktivorous fishes. Reduced growth in planktivorous fishes may lead to higher mortality by increasing the time individuals are available to a large number of gape-limited predators (Sirois and Dodson, 2000; Holmes and McCormick, 2010). Additionally, effective foraging enables individuals to allocate excess energy to storage for future energy demands such as reproduction, predator avoidance or periods of low food availability (Green and McCormick, 1999; Post and Parkinson, 2001; Donelson et al., 2008).

Few studies have examined the impact of suspended sediment on foraging in fishes. A number of freshwater studies found that suspended sediment inhibited the foraging of planktivorous feeding juveniles and adults by reducing the distance at which food could be detected (Gardner, 1981; Asaeda et al., 2002; Sweka and Hartman, 2001, 2003). In contrast, Granqvist and Matilla (2004) found no effect of suspended sediment or reduced light on foraging by *Perca fluviatilis* (Linnaeus, 1758), a species that may be adapted to the turbid conditions of the Baltic Sea. This varied response to suspended sediment makes predictions on the effect of elevated sediment on coral reef fishes difficult.

The aim of this study was to experimentally evaluate whether increasing concentrations of suspended sediment impaired the ecological performance of juvenile *Acanthochromis polyacanthus* (Pomacentridae; Bleeker, 1855), a planktivorous coral reef fish found on turbid, inshore reefs in the Indo-Pacific. Concentrations of suspended sediment were manipulated under controlled aquarium conditions to test whether there were direct effects of suspended sediment on foraging success and food consumption. We then examined the indirect effect of suspended sediment, as a result of lowered food consumption, on individual growth, physiological condition and mortality. The suspended sediment concentrations used were levels recorded on reefs worldwide, ranging from pristine, sediment-free conditions to high levels observed on inshore reefs in the Great Barrier Reef (GBR) during extreme periods of terrestrial run-off and re-suspension events.

5.3 METHODS

5.3.1 Study site and species

This experiment was conducted over a six-week period from September to October 2010 at the Marine and Aquaculture Research Facility Unit at James Cook University, Townsville, Australia. Juvenile *A. polyacanthus* were sourced from a captive breeding program at this facility. Eight-week old juveniles were maintained in holding tanks in a temperature-controlled laboratory (27° C). Light levels were set to a 12h:12h L: D regime. All sides of the tank were blacked out to reduce outside stimuli.

5.3.2 Experimental design

The effects of increasing suspended sediment concentrations on foraging success, growth rate, body condition and mortality of *A. polyacanthus* were examined by manipulating suspended sediment in replicate aquaria at four concentrations: (1) Control (0 mg l⁻¹); (2) Low (45 mg l⁻¹;

7.5 NTU), (3) Medium (90 mg l⁻¹; 15 NTU), and (4) High (180 mg l⁻¹; 30 NTU). Australian bentonite, a commercially available clay used in previous turbidity experiments (e.g., De Robertis et al., 2003; Van de Meutter et al., 2005) was used to manipulate levels of suspended sediment. Muddy sediments and clays are common constituents of sediment on the inshore GBR (Carter et al., 1993; McCulloch et al., 2003). The sediment levels were selected to encompass the range of sediment concentrations that have been recorded on coral reefs (Table 5.1).

The experiment consisted of twelve 27 L (27 x 50 x 20cm) aquaria, with three replicate tanks for each sediment treatment. Groups of 8-9 juveniles were selected haphazardly from holding tanks (17.8 ± 0.2 mm, mean standard length ± SE) and placed in the 12 tanks supplied with a constant flow of filtered (50 µm) seawater at 27° (range: 26.5°- 28° C). Tanks were then randomly assigned to one of the four sediment levels. The feeding performance and growth of all fish in each tank were measured over a six-week period.

Table 5.1 Suspended sediment concentrations measured on different coral reefs

Location	Suspended sediment values (mg l ⁻¹)	Area of focus	Reference
GBR, Australia	39-670	flood plume	Devlin et al., 2001
GBR, Australia	5-45	inshore reef	Larcombe et al., 1995
Hawaii	0-100	fringing reef	Ogston et al., 2004
GBR, Australia	300	fringing reef	Wolanski et al., 2008
GBR, Australia	120	fringing reef	Hopley and Van Woesik, 1988

5.3.3 Sediment manipulations and foraging

In order to specifically test the effect of suspended sediment on foraging and not the effect of sediment exposure on *A. polyacanthus*, the fish were only exposed to suspended sediment during feeding. Thirty-minutes before each feeding trial, the water was turned off in the experimental tanks so that no sediment could leave the tanks during the trials. The required concentration of sediment for each treatment was then manually dissolved into the tanks to avoid clumping and to ensure homogenous level throughout the tank (Robertis et al., 2003). Though sediment was not added to the control tanks, the action of adding sediment was mimed in each control tank to simulate secondary disturbance effects. The fish were fed once per day at the same time daily with 4 mg of INVE 5/8 enriched food pellets per fish (Donelson et al., 2008).

The food was added in three consecutive 30-s intervals to determine the time taken to react to food. Trials run prior to the experiment determined that 30 seconds was sufficient for juvenile *A. polyacanthus* to consume all food in the water column under clear water conditions. During the first addition of food, the reaction time to the food was recorded; defined as the time in seconds from when the food was added to the tank to when the first fish began eating. This resulted in one reaction time per tank per feeding trial. The location within the tank where food was added was changed daily to minimize learned behavior and to keep food encounters randomized.

Thirty seconds after the final addition of food for each feeding trial, any food remaining on the bottom was siphoned out and through a 200 μm plankton mesh. It was not possible to remove the food from the plankton mesh due to the consistency of the food. Therefore, the amount of food remaining was categorized as large (>75% remaining), intermediate (25-50%

remaining), small (<25% remaining), or no food remaining. Once the feeding trials were complete, the water flow through the system was turned on, enabling the sediment to be flushed.

5.3.4 Growth and mortality

The measurement of the growth of individual fish within tanks was facilitated by tagging each fish with a distinctive color of fluorescent elastomer (Hoey and McCormick, 2006). The dye was subcutaneously injected into each fish with an insulin needle. The fish were then allowed to acclimate for two weeks prior to commencement of the experiment. The standard length of each fish was measured two days before the start of the experiment and at fortnightly intervals until the completion of the experiment, giving a total of four length measurements for each fish. Mortality was recorded over the course of the experiment. The date, sediment treatment and tank number of the deceased fish were recorded and the food level in the tank was adjusted so that each fish still received the same amount of food.

5.3.5 Body condition

The physiological condition of the fish in different sediment regimes was assessed by comparing the densities of liver hepatocyte vacuoles (an indicator of lipid and glycogen stores in the liver) (Theilacker, 1978; Green and McCormick, 1999). At the end of the experiment the fish were euthanized and preserved in 10% phosphate buffered formalin. After two weeks, the livers were removed and dehydrated in a graded ethanol series and embedded in paraffin wax. Wax blocks of hepatic tissues were sectioned at 5 μm , and stained using Mayer's hematoxylin and eosin to emphasize hepatocyte vacuoles. Images of each liver were captured at 400x magnification. A grid was overlaid onto each image and the proportion of points (99) that intercepted a vacuole was recorded. Three counts of hepatocyte vacuolation were made per section from two randomly chosen sections, giving six estimates for each fish.

5.3.6 Statistical analysis

A randomization-based nested ANOVA was used to determine if there were significant differences in reaction time, food remaining and hepatocyte vacuolation between replicate tanks within each sediment treatment and between sediment treatments. Each recorded value was randomly assigned to particular groups 4999 times to produce an f-value distribution curve. The observed f-statistic was then compared to this distribution curve. The randomized version was used to avoid violating assumptions associated with the theoretical f-value distribution curve and because it was a more powerful and versatile test (Manly, 1997). Post-hoc multiple pair wise comparisons of reaction time, food remaining and hepatocyte vacuolation between sediment treatments were analyzed using randomization-based two-sample t-tests with a Bonferroni correction. Growth rates were determined by calculating proportional growth (the percent increase in size from the start of the experiment) for each fish. To test if there were (i) differences in proportional growth between replicate tanks within each sediment treatment, (ii) when differences in growth started occurring between sediment treatments, and (iii) if there was a difference in final growth rates between sediment treatments, randomization-based nested ANOVAs were used. Post-hoc comparisons were made with randomization-based t-tests with a Bonferroni correction. The differences in total mortality between sediment treatments were analyzed through a Chi-Square test of homogeneity.

5.4 RESULTS

5.4.1 Reaction time

The concentration of suspended sediment had a significant effect on the time taken for individuals to begin foraging (nested ANOVA, $F_{3, 480}=51.2$, $p<0.0001$). The reaction time to food increased dramatically with increasing sediment, from only 1.1 ± 0.07 seconds (mean \pm S.E.) in the control to 23.3 ± 3.7 seconds in the high sediment treatment (Fig. 5.1a). Fish in the low sediment treatment also had a fast reaction time of 3.3 ± 1.2 seconds, but it was significantly slower than in the control (Fig. 5.1a; t-test, $p<0.0001$). The medium and high sediment treatments had significantly slower reaction times than both the control and the low sediment treatment tanks (based on post-hoc multiple pair-wise comparisons). Though one of the high sediment treatment tanks had a significantly higher average reaction time than the other replicates (one way ANOVA, $F_{2, 120}=4.2$, $p=0.017$), there was not a significant difference in reaction time between the medium (19.1 ± 3.6 seconds) and high sediment treatment fish (t-test, $p=0.159$) and there was not a significant difference between any of the other tanks within replicate treatments (nested ANOVA, $F_{6, 360}=0.37$, $p=0.89$).

5.4.2 Food remaining

Concentration of suspended sediment also had a significant effect on the proportion of food consumed during feeding trials (nested ANOVA, $F_{3,216} =86.4$, $p<0.0001$), with food remaining increasing in relation to sediment load (Fig. 5.1b). There was no significant difference between any of the tanks within replicate treatments (nested ANOVA, $F_{8, 216}=1.2$, $p=0.32$). There was an overall decline in food consumption, with food consumption significantly greater in the control treatment and the low sediment treatment, compared with both the medium or high sediment treatments (Fig. 5.1b). However, although the fish in the low sediment treatment

consumed all of their food $51.7 \pm 0.4\%$ of the time, compared to $86.9 \pm 0.9\%$ of the time in the control, there was no difference in food consumption between the control and low sediment treatment. The fish in the medium and high sediment treatment consumed all of their food only $8.7 \pm 0.19\%$ and $9.1 \pm 1.3\%$ of the time, respectively, and did not differ significantly from each other (Fig. 5.1b) (based on post-hoc multiple pair-wise comparisons).

5.4.3 Body condition

The fish in the medium and high sediment treatments showed a significant decline in body condition, as measured by density of hepatocyte vacuoles (Fig.5.1c; ANOVA, $F_{3,354}=123.4$, $df=3$, $p<0.0001$). Fish in the control and low sediment treatment had the same density of hepatocyte vacuoles, averaging $20.8 \pm 0.7\%$ and $20.7 \pm 1.4\%$, respectively (Fig. 5.1c). Hepatocyte vacuolation was significantly greater in both the control and low sediment treatments than in either the medium and high sediment treatment. There was not a significant difference in vacuole density between the medium and high treatment, averaging $11.5 \pm 0.9\%$ and $8.7 \pm 0.7\%$ vacuolation, respectively (based on post-hoc multiple pair-wise comparisons).

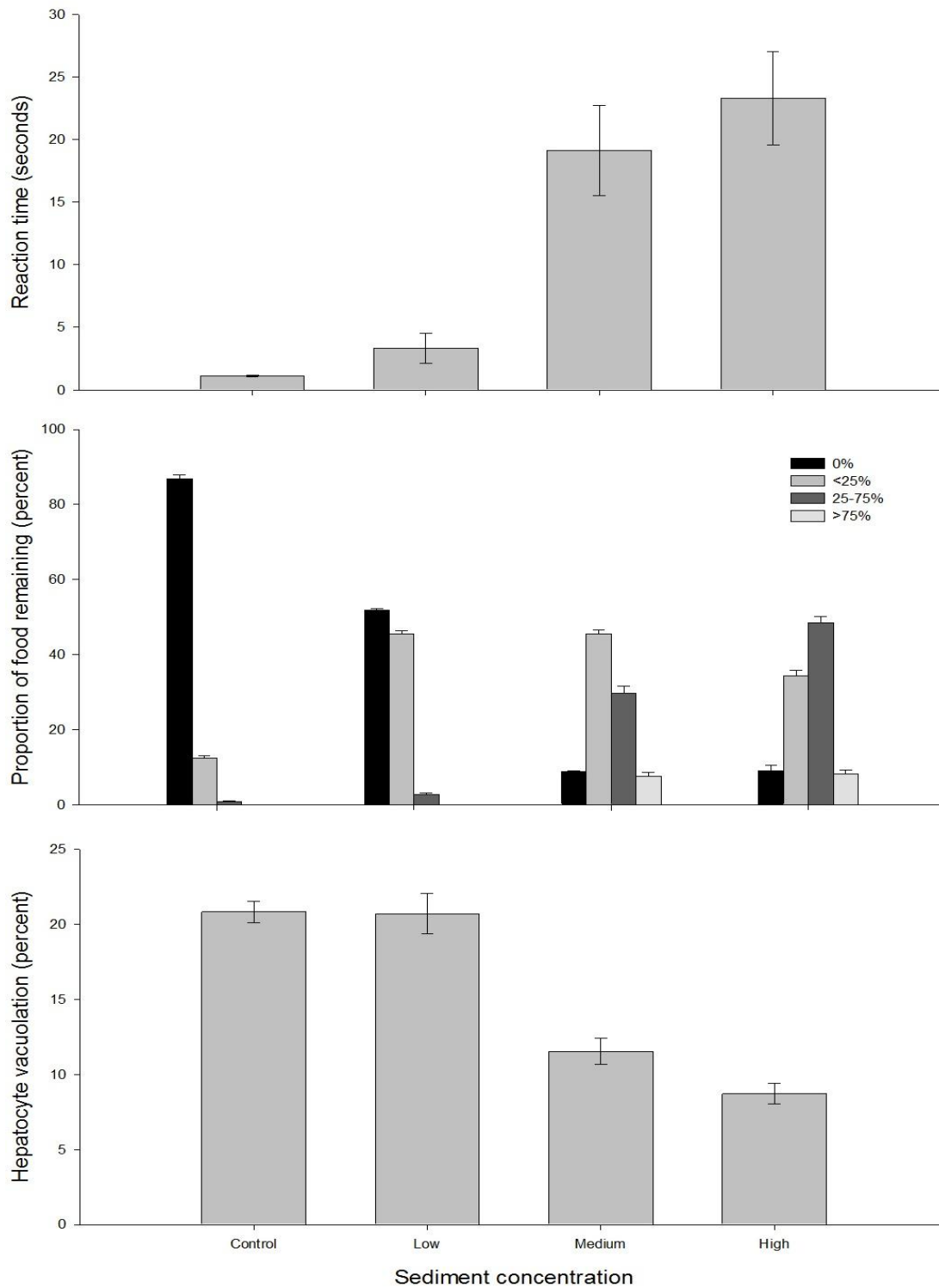


Figure 5.1 The effect of increasing concentrations of suspended sediment on the mean (\pm SE) of a) the reaction time to the first addition of food ($n=42$); b) the amount of food remaining ($n=42$) and c) hepatocyte vacuolation density in *Acanthochromis polyacanthus*.

5.4.4 Growth

Sediment concentration had a substantial negative influence on juvenile growth rates. Significant differences in growth occurred within the first two weeks of the experiment (Fig. 5.2a; nested ANOVA, $F_{3,76}=11.76$, $p<0.0001$), with the fish in the control treatment showing significantly higher growth rates than the fish in the medium and high sediment treatment, though not when compared to growth in the low sediment treatment fish (based on post-hoc multiple pair-wise comparisons). By the end of the experiment, the fish in the control treatment had significantly higher proportional growth than all the other treatments (Fig. 5.2a; ANOVA, $F_{3,76}=15.42$, $p<0.0001$), whereas the low, medium, and high treatment fish did not have significantly different growth rates from each other at the end of the experiment (based on post-hoc multiple pair-wise comparisons). Over the course of the experiment, the fish in the control increased in length by $27.0 \pm 1.8\%$ compared to an overall growth of $18.1 \pm 1.9\%$, $14.5 \pm 1.2\%$, and $13.3 \pm 2.1\%$ for the low, medium and high sediment treatment fish, respectively (Fig. 5.2a). The final proportional growth of fish in the high sediment treatment (13.3%) was less than the proportional growth of the control treatment fish within the first two weeks of the experiment (14.1%).

5.4.5 Mortality

Mortality was higher in the high sediment treatment compared to the other sediment treatments (Fig. 5.2b; Chi-Square test of Homogeneity, $X^2=22.4$, $df=3$, $p<0.0001$). No fish died in the control treatment and only two fish died in both the low and medium sediment treatments. However, the high sediment treatment levels experienced significant mortality, with 11 fish out of 26 fish dying. Upon closer examination, mortality was particularly high in two of the high sediment treatment tanks (44% and 67%), but was quite low in the third sediment treatment tank

(12.5%). Mortality occurred from day 16 and increased steadily throughout the duration of the experiment (Fig. 5.2b). In total, only 58% of fish in the high sediment treatment remained at the end of the experiment, compared to 100%, 92%, and 92% of fish remaining in the control, low and medium sediment treatments respectively.

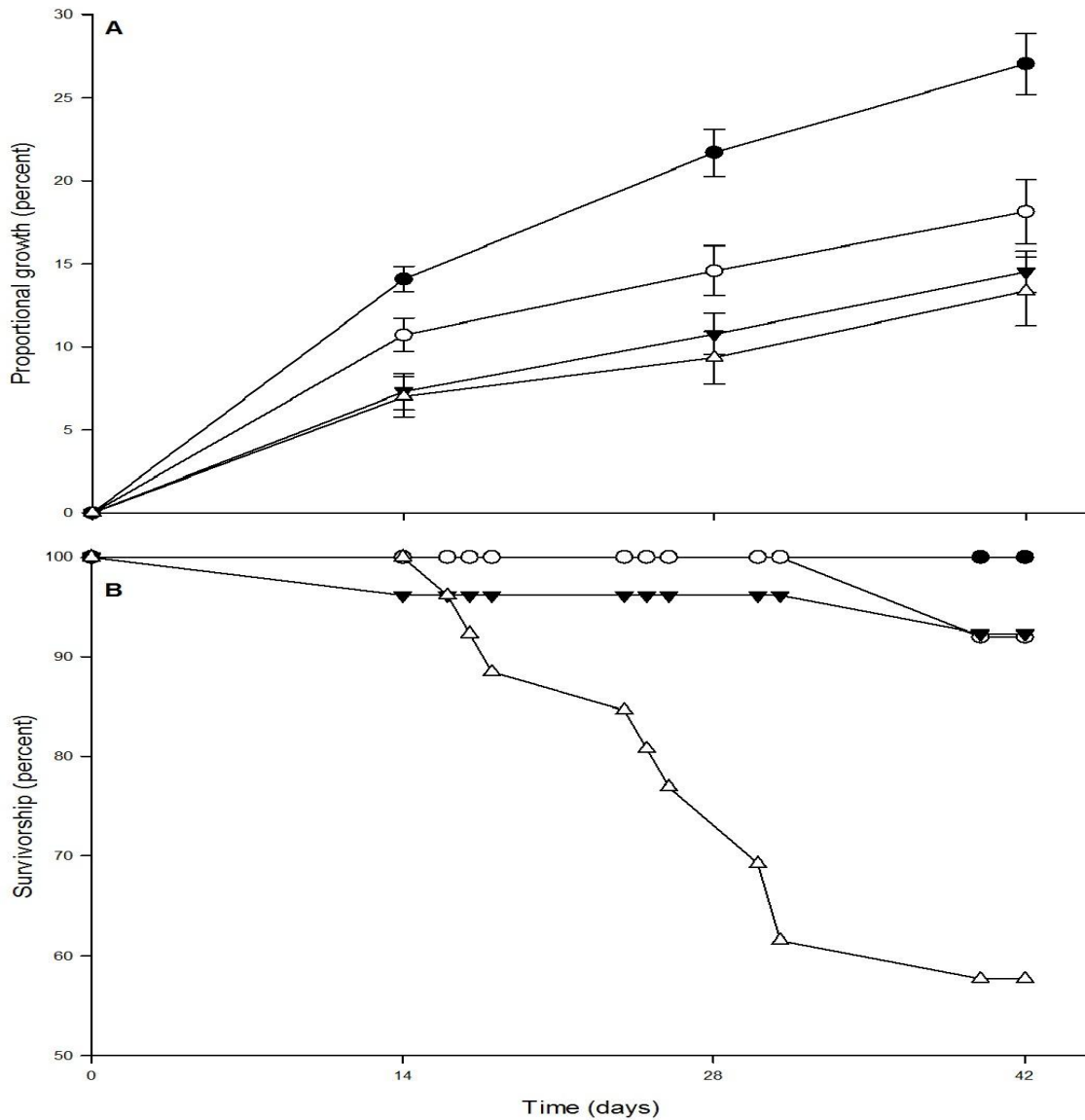


Figure 5.2 Changes over time in a) growth rate and b) survival of *Acanthochromis polyacanthus* in the control (closed circle), low (open circle), medium (closed triangle), and high (open triangle) sediment treatments

5.5 DISCUSSION

This study demonstrates that suspended sediment can have a marked effect on the foraging success of a juvenile planktivorous coral reef fish. This reduction in foraging success resulted in both lethal and sub-lethal effects on key biological functions that are critical to individual performance and demography including a reduction in food acquisition, reduced body condition, slower growth and increased mortality. The extremely high mortality observed in the high sediment treatment suggests that this level of suspended sediment is close to the tolerance limit of this planktivorous species.

The increase in suspended sediment concentrations reduced the visual cues necessary for foraging and led to a delayed reaction time to food and reduced food consumption. Sweka and Hartman (2003) reported similar results for the freshwater smallmouth bass, *Micropterus dolomieu* (Lacepède, 1802), which showed an exponential increase in reaction distance to prey as turbidity increased from 0-40 NTU (roughly 240 mg l⁻¹ bentonite, A. Wenger, unpublished data). The change in food consumption observed in the present experiment corresponds with previous studies that have examined the effect of increased suspended sediment on food consumption for planktivorous fishes. Johnston and Wildish (1982) found that larval Atlantic herring, *Clupea harengus* (Linnaeus, 1758), consumed significantly less prey as turbidity increased to 13 NTU (~78 mg l⁻¹ bentonite). For juvenile reef fish, the amount of energy that can go into growth and storage is contingent upon the amount of food they consume (Kerrigan, 1994; Pratchett et al., 2004). Therefore, the reduction in food consumption observed in this study has important implications for individual fitness and survivorship.

Lower foraging success in high suspended sediment concentrations resulted in lower growth rates for *A. polyacanthus* in this study. Growth rate is an important determinant of the survivorship of juvenile reef fish since many post-settlement processes are size dependent (McCormick, 2009; McCormick and Meekan, 2010; Perez-Dominguez and Munch, 2010; Grol et al., 2011). For example, if *A. polyacanthus* is experiencing slower growth rates due to reduced foraging in suspended sediment, they could face increased competition and a greater risk of predation (Holmes and McCormick, 2010; Forrester et al., 2011). Slow juvenile growth increases the time to sexual maturity and reduces the likelihood of an individual becoming a dominant male in sex-changing species (Walker et al., 2007; McCormick and Gagliano, 2008). A reduction in foraging success not only reduced growth rates in this experiment, it also had a major effect on physiological condition of the fish in sediment treatments. Energy reserves are a crucial safeguard against poor environmental conditions, such as low food availability (Green and McCormick, 1999; Post and Parkinson, 2001). Glycogen and lipid reserves allow fish to put energy into other necessary activities apart from foraging such as predator avoidance, territory defense, and reproduction (Jones, 1987; Miller et al., 1988; McCormick 2003; Donelson et al., 2008). A recent study has shown that juvenile damselfishes that settle with low body condition have a lower response to innate indicators of risk and are more likely to attempt to forage in high risk conditions, thereby reducing their potential survival (Lönngstedt and McCormick, 2011).

Because this experiment was run in a laboratory, there is the potential that some of the results seen in this experiment might be different for *A. polyacanthus* in the wild. For instance, juvenile *A. polyacanthus* experiencing high levels of suspended sediment in the wild could counteract a reduction in foraging efficiency by spending more time foraging, which was not possible in this experiment. A food supplementation experiment with *A. polyacanthus* found that

juveniles who were supplementary fed and had higher body condition also achieved higher survival in the field (Booth and Alquezar, 2002). However, Sweka and Hartman (2001) showed that for brook trout, *Salvelinus fontinalis* (Mitchill, 1814), even though individuals foraging in high sediment did not experience a reduction in food consumption, specific growth rates decreased as suspended sediment increased, due to an increase in energy used to forage. Therefore, in the natural environment, increased time spent foraging to compensate for a reduction in visual acuity may not yield a net energetic increase due to competing energy demands.

In this experiment, the reduced food consumption and lower energy storage in fish in the high sediment treatment resulted in high mortality. The observed mortality may be a result of insufficient energy to grow and to maintain basic functions (Suthers, 1998). Mortality started after two weeks and survivorship steadily declined throughout the experiment. Since mortality for juveniles on the reef is already quite high (Victor, 1986; Eckert, 1987), any process that further increases mortality could have profound effects on adult populations and subsequent recruitment (Jones, 1990).

When fish go through periods of starvation and then enter into a period of high food intake, they will often show compensatory growth, enabling them to grow rapidly and reach the size of continuously fed fish (Jobling and Koskela, 1996; Dutil et al., 2006; Gagliano et al., 2007). However, in many cases, compensatory growth results in a depletion of energy reserves (Post and Parkinson, 2001; Ali et al., 2003). In the present experiment, fish in the medium and high sediment treatment had low energy reserves and this would inhibit their ability to accelerate growth. In contrast, fish in the low sediment treatment did have energy stored in the liver, which could facilitate compensatory growth if turbidity conditions change. Interestingly, when fish

undertake compensatory growth they often overshoot the fish that have had optimal conditions continuously and this can lead to higher mortality at later life stages (e.g. Heath et al., 1999). The pulsed nature of high turbidity conditions associated with storm events or flood plumes means that fishes on inshore reefs may face situations where compensatory growth may occur. Further studies will be needed to determine whether this compensation has long term consequences for fitness and survival.

This experiment used levels of suspended sediment that have been consistently recorded on coral reefs. During the wet season in Australia, levels of suspended sediment can actually peak at concentrations that are much higher (300 mg l^{-1}) than the levels used in this study (Wolanski et al., 2008). It is important to note that re-suspension events are often pulse occurrences and are not consistently at the physiological limits of reef fishes (Larcombe et al., 1995; Wolanski et al., 2008). However, as the effects of 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 sediment flowing onto the reef and more opportunities for it to be suspended, reef fish will be exposed to an increasing level of suspended sediment year round (Fabricius et al., 2013). This study demonstrates that after a two-week exposure to concentrations of suspended sediment already reached on coral reefs, fish experience reduced growth rates and increased mortality. Given that fishes in early life history stages require more energy than adults to withstand starvation (due to high metabolic rates and low energy storage) and are more prone to mortality (Miller et al., 1988; Post and Parkinson, 2001), suspended sediment will differentially affect early life history stages of coral reef fishes.

In conclusion, this study provides clear evidence that prolonged exposure to suspended sediment can impair a fish's ability to find food, leading to a reduction in food consumption. This

decline in foraging success caused a reduction in growth and physiological condition, leading to an increase in mortality. This illustrates the need to fully understand the interaction between suspended sediment and foraging in coral reef fishes. Given the compounding effects of multiple pollutants, it is important to explore the coupled interaction between sediment and other contaminants. This is the first study to examine the relationship between suspended sediment and growth in a coral reef fish and it has important implications for water quality management on coral reefs. Small changes in mortality during early life history stages 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.

CHAPTER 6: SUSPENDED SEDIMENT ALTERS PREDATOR-PREY INTERACTIONS BETWEEN TWO CORAL REEF FISHES[†]

[†] **Wenger AS**, McCormick MI, McLeod IM, Jones GP (2013) Suspended sediment alters predator-prey interactions in two coral reef fishes. *Coral Reefs* 32:369-374

6.1 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 atripectoralis* exposed to *Pseudochromis fuscus*, a common predator of juvenile damselfishes, in aquaria with one of four turbidity levels. Increased turbidity led to a non-linear 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.

6.2 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 contrast with its background, making it easier for the predator to see them (e.g., Gregory and Northcote, 1993; Utne, 1997; Rowe and Dean, 1998; Utne-Palm, 1999). However, at higher levels of turbidity, foraging success declines, generating a non-linear 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 of 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 der 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 predation of juvenile salmonids by *Oncorhynchus 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 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.

6.3 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 *Chromis 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 hours 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 predation of *C. atripectoralis* was examined by adjusting suspended sediment levels in aquaria to four concentrations: (1) Control (0 mg l⁻¹); (2) Low (30 mg l⁻¹; ~5 NTU), (3) Medium (45 mg l⁻¹; ~7.5 NTU), and (4) High (60 mg l⁻¹; ~10 NTU). 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 x 30 x 30 cm) tanks, from 7 am to 7 pm in a temperature controlled laboratory (29 ° C) with artificial light. Each tank was fed by a submersible pump (1000 L h⁻¹) placed in an external 10 L aerated sump. Each sump also contained a disturbance pump (1000 L h⁻¹) 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., 2007b), 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., 2007a). 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 thirty minutes to acclimate before the barrier was carefully removed. Surviving *C. atripectoralis* were counted every two hours over a twelve-hour period. A total of twenty 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 if there were significant differences in predation between turbidity treatments after two hours and at the end of each trial.

6.4 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 non-linear, 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. 6.1). There were no significant differences in predation rates among the control, low and high turbidity treatments (Tukey's HSD, $p > 0.5$).

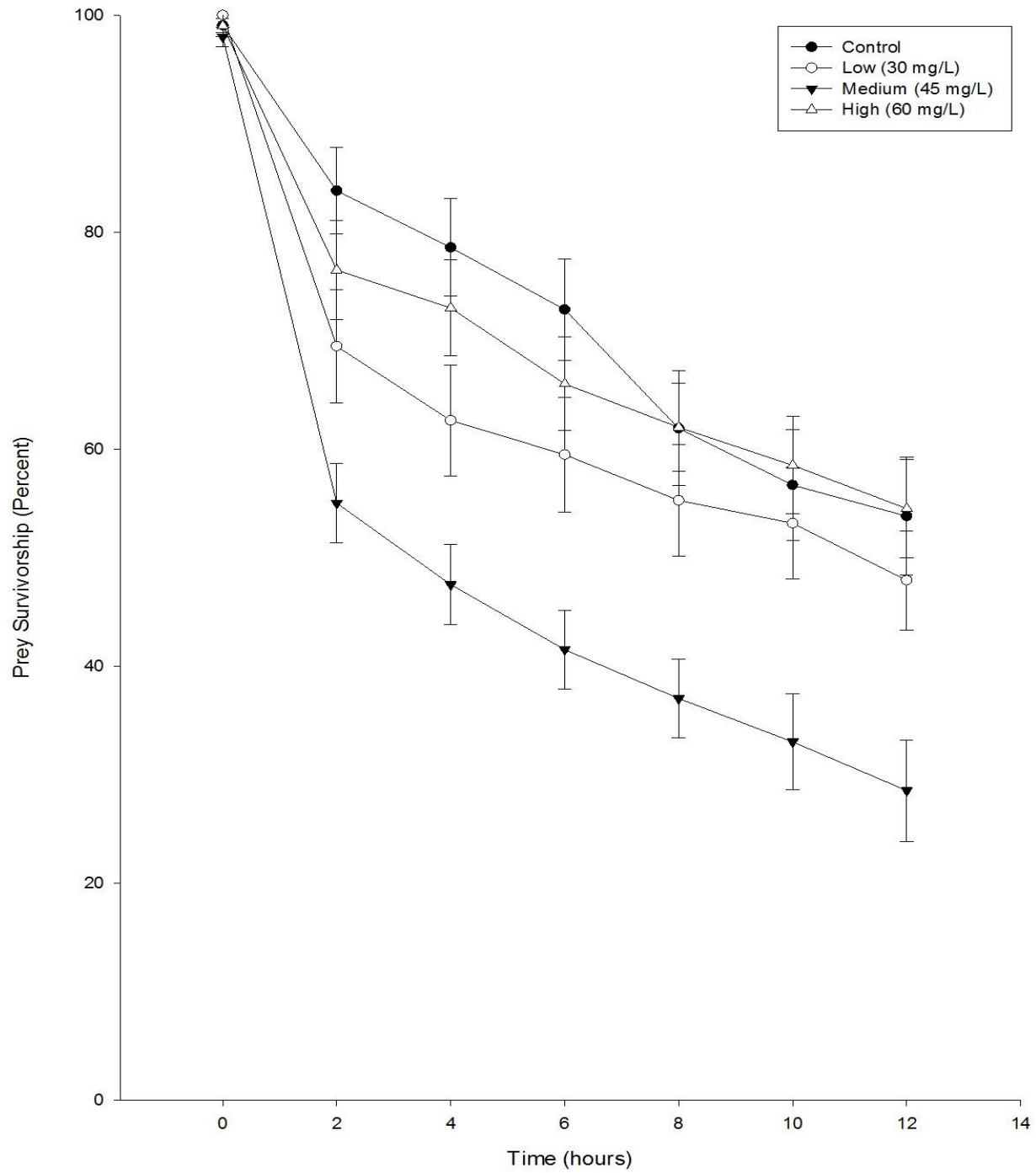


Figure 6.1 Differences over time in survival (\pm SE) of *Chromis atripectoralis* among four sediment treatments.

The non-linear relationship observed contradicts previous studies examining piscivory and turbidity (Hect and Van der 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 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.

P. 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 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 mg l^{-1} *Acanthochromis 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 mg l⁻¹ may be a threshold for visual cues in prey species. Miner and Stein (1993) 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 been what 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 two hours of the trial, consuming 15.4% ± 3.9%, 30.5 ± 5.2%, 43.8 ± 3.8% and 22.7 ± 4.5% of *C. atripectoralis* in the control low, medium and high treatments, respectively (Fig. 6.1).

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 two hours (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 two hours 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 two hours and show a similar linear decline between treatments (Fig.6.1). Though 45 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 con-specific 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 substratum 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 tropho-dynamics.

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 re-suspension, reef fish will be exposed to higher turbidity year round (Fabricius et al., 2013). 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.

GENERAL DISCUSSION

Increased sediment loading has been cited as one of the critical threats to coastal and inshore reefs, due to its negative effects on corals. Through behavioral and physiological work, each of the five chapters in this thesis examined a different component of early life history stages and processes. This thesis has provided extensive evidence that coral reef fishes are also vulnerable to suspended sediment, and has shown that they will be susceptible to direct pressure from suspended sediment in combination with indirect pressure due to habitat loss. The results of this thesis have agreed in some cases to previous literature from other aquatic environments, but have also revealed novel interactions between fishes and suspended sediment.

Chapter 2 provided the first example of how suspended sediment may affect larval development in a coral reef fish. The results of the study contradicted the hypothesis that suspended sediment would slow larval development, due to a reduction in foraging. Instead, I found that the pelagic larval duration was extended, and sometimes doubled, for individuals developing in suspended sediment. This was seemingly unrelated to size or body condition, suggesting another mechanism that is prolonging development. In Chapter 3, I demonstrate that suspended sediment can inhibit successful habitat selection, both through a reduction in visual cues and chemical cues. The reduction in visual cues happens at a sediment concentration that occurs relatively frequently on inshore reefs (Chapter 4). The lowered visual acuity also changes post-settlement movement, which is important both for emigration and for home range use. Chapter 5 showed that foraging in suspended sediment can lead to physiological consequences, such as lowered growth rates and body condition. In high levels of suspended sediment, and concentrations that are currently reached on inshore coral reefs, increased mortality can also

occur, most likely from starvation. Chapter 6 revealed that mortality can also occur through increased predation, though this is dependent on the level of sediment. The implications of these findings for coral reef fishes living in turbid environments, or environments at risk to increased turbidity are discussed below.

Increasing concentrations of suspended sediment

Throughout the chapters of this thesis, I used similar concentrations of suspended sediment to allow for a hierarchical assessment of the different ways suspended sediment influences coral reef fishes. The lowest concentration of suspended sediment that elicited a response was 15 mg l^{-1} , within which *Amphiprion percula* experienced a prolonged pelagic larval duration but were heavier, bigger and in better condition than larvae that developed in the control treatment.

When testing the effects of suspended sediment at 30 mg l^{-1} concentration, I found that the ability of *Pomacentrus moluccensis* to find suitable habitat types and to exploit their home range declined sharply. Additionally, the ability of *Pseudochromis fuscus* to capture their prey, *Chromis atripectoralis*, started to increase, with the predator seeming to have an advantage during the first two hours of the trial.

When the suspended sediment concentration increased to 45 mg l^{-1} , there were widespread behavioral changes, indicating that this sediment concentration could be an important threshold. The planktivorous damselfish *Acanthochromis polyacanthus* experienced a decline in food acquisition, which led to a significant reduction in their growth rate. Predation rates increased substantially between *P. fuscus* and *C. atripectoralis*, from 50% in the control to 71% in 45 mg l^{-1} of suspended sediment. In 60 mg l^{-1} , predation rates declined to 50% again, marking

the sediment threshold concentration for the predator. By 90 mg l⁻¹, *A. polyacanthus* juveniles were showing a substantial reduction in body condition due to reduced foraging success. Finally, in suspended sediment concentrations 180 mg l⁻¹, mortality reached almost 50% as a result of impaired foraging. When collated, it is clear that as suspended sediment increases, the consequences for coral reef fishes exposed to it continue to escalate.

Cumulative effects of suspended sediment

For coral reef fishes continuously experiencing elevated concentrations of suspended sediment, there may be a synergistic relationship among the effects of suspended sediment on individuals. For instance, if larvae experience a prolonged pelagic larvae stage, it is likely that fewer individuals will successfully make it to the reef, given that the chances of mortality increase the longer larvae are in the pelagic environment (Houde, 1987). If the fish then settle into sub-optimal habitat, they are more vulnerable to predation and may experience slower growth rates (Coker et al., 2009; Feary et al., 2009). If sediment concentrations continue to be elevated, then there may be increased competitive interactions due to the inability of individuals to undergo post-settlement emigration (Coker et al., 2012; McCormick, 2012). If coral reef fishes remain in their habitat and do not fully utilize their home range because they cannot properly assess predation risk, it is likely that there will be fitness consequences through a reduction in foraging and territorial defense (Lewis, 1997; Lönnstedt and McCormick, 2011). Chapter 5 clearly showed that suspended sediment reduces foraging, meaning that an individual would have to spend more time foraging to find adequate resources, though that requires an energetic trade-off between the energy used to forage and the energy gained from increased foraging. However, if an individual is unwillingly to move from their habitat (Chapter 4), there will be both the energetic costs from not maximizing foraging area and reduced foraging efficiency

(Chapter 5). If an individual risks spending more time foraging, there will be increased predation pressure if sediment concentrations fall below visual thresholds of predators (Chapter 6).

There is the potential, therefore, for negative feedback loops to exist in turbid environments, wherein individuals must trade-off between foraging in risky conditions or staying in their habitat, thereby decreasing foraging activity and remaining smaller, and more vulnerable to predation for longer (Holmes and McCormick, 2010). As a result of these different interactions there would likely be a reduced number of individuals making it to adulthood. Additionally, since sexual maturation and reproductive success are dependent on size and body condition (Miller et al., 1988; Donelson et al., 2008), there may be a lower number of adults that will be able to produce offspring.

Suspended sediment concentrations on coral reefs

Although sediment loading into coral reef environments is considered one of the major stressors to coral reefs (Burke et al., 2011), few studies have actually recorded suspended sediment, and they are predominately concentrated in the Great Barrier Reef. This knowledge gap makes it extremely difficult to assess which coral reefs are experiencing detrimental levels of turbidity. However, the sediment levels used within this thesis are all currently being reached on coral reefs (Table 2.1). Additionally, new evidence confirms that increased sediment loading is causing higher turbidity levels (Fabricius et al., 2013), therefore the higher concentrations of suspended sediment used in this thesis are likely to be observed more frequently.

Future research and conclusions

The insights arising from this thesis have provided a solid foundation for further research examining the relationship between suspended sediment and coral reef fishes. Since the work

presented here was all laboratory based, future work needs to concentrate on ground-truthing the results with fishes from inshore reefs and those vulnerable to dredging operations. Specifically, research should focus on local adaptation by examining species that have different probabilities of being adapted to inshore conditions. Additionally, more research needs to be done on inshore coral reefs outside of Australia. Currently, the majority of the work assessing turbidity on inshore reefs has been done on the Great Barrier Reef, and a lot of it has focused on the same region. Since coastal development is rapidly increasing in other parts of the world with coral reefs, it is important to focus research in areas that will experience increasing amounts of suspended sediment. This thesis investigated the effects of suspended sediment on pomacentrids. This family was used because species are ubiquitous and easy to capture and maintain in captivity. The knowledge gained provided proof of concept that suspended sediment can affect coral reef fishes. Future research should focus on how commercially and recreationally important fishes are affected, as the inshore populations of these species are easily accessible and heavily relied upon.

If the goal of coral reef management is to increase resilience, targeting water quality management is paramount. The lessons learned from this thesis should be incorporated into water quality management. Small scale ecological processes occur on short time scales, whereas some current management practices focus on annual means and may miss important interactions. Finally, suspended sediment from run-off and dredging is often combined with additional contaminants. The deleterious effects of agriculture pollutants, heavy metals, and sewage on coastal ecosystems have been widely chronicled (e.g., GESAMP 2001; Fabricius 2005). Future research needs to focus on the synergistic effects of multiple pollutants on coral reef fishes. Continued efforts to understand the complex relationship between declining water quality and coral reefs is essential for population persistence of inshore coral reef fishes.

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