Coral Reefs
https://doi.org/10.1007/s00338-018-01757-6

NOTE

Enhanced fast-start performance and anti-predator behaviour in a coral reef fish in response to suspended sediment exposure

Sybille Hess[1,2] · Bridie J. M. Allan[3] · Andrew S. Hoey[1] · Michael D. Jarrold[1,2] · Amelia S. Wenger[4] · Jodie L. Rummer[1]

Received: 16 November 2017 / Accepted: 21 November 2018

Abstract Declining water quality, in particular elevated suspended sediments, poses a significant threat to coastal coral reefs. We exposed juvenile anemonefish (*Amphiprion melanopus*) to two suspended sediment concentrations (0 or 180 mg L^{-1}) for 7 d and examined their predator escape performance and anti-predator behaviour in both clear water and suspended sediments (0 and 180 mg L^{-1}, i.e. acute exposure). After 7-d exposure to suspended sediments, fish responded faster to a mechanical stimulus and exhibited enhanced fast starts compared to individuals reared in clear water, regardless of acute exposure. Fish were also less active and avoided open areas when exposed to elevated suspended sediments in the test arena when compared to clear water, irrespective of prior 7-d exposure. While these changes are likely strategies to compensate for an increased perceived predation risk in suspended sediments, they may also be associated with non-consumptive costs for juveniles living on turbid reefs.

Topic Editor Morgan S. Pratchett

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00338-018-01757-6) contains supplementary material, which is available to authorized users.

✉ Sybille Hess
sybille.hess@my.jcu.edu.au

1 ARC Centre of Excellence for Coral Reef Studies, Townsville 4811, Australia

2 College of Science and Engineering, James Cook University, Townsville 4811, Australia

3 Department of Marine Science, University of Otago, Dunedin 9016, New Zealand

4 School of Earth and Environmental Sciences, University of Queensland, Brisbane 4072, Australia

Keywords Suspended solids · Sub-lethal effects · Predator–prey interactions · Turbidity · Fish health

Introduction

Suspended sediment concentrations in tropical coastal waters have increased substantially over the past few decades as a result of human activities including agriculture, dredging and shipping (Syvitski et al. 2005) and are altering the composition of biological communities (Fabricius 2005). Elevated levels of suspended sediments can influence coral reef fish assemblages indirectly through changes in the composition and structural complexity of benthic habitats (Brown et al. 2017; Hamilton et al. 2017). Recent studies, however, suggest that suspended sediments may also affect the physiology and behaviour of reef fishes, which may compound the negative effects of habitat degradation (reviewed in Wenger et al. 2017).

Elevated suspended sediments reduce visual acuity and can thereby influence important ecological processes such as predator–prey interactions (Wenger et al. 2017). Reduced visual acuity can delay the detection of approaching predators, potentially altering predation rates (Meager et al. 2006). While the early detection of predators is crucial, the ability to escape a predator attack is equally important for prey survival (Domenici and Blake 1997; Walker et al. 2005). Most prey fish escape predatory attacks via fast starts, i.e. short, high-energy swimming bursts elicited by a sudden stimulus (Domenici and Blake 1997). Prolonged exposure to elevated suspended sediments, however, has been shown to reduce the aerobic scope (i.e. the capacity for aerobic activities) of some reef fishes (Hess et al. 2017); this may compromise their capacity to engage in or recover from energetically costly

Published online: 26 November 2018

activities such as fast starts (Killen et al. 2015). Yet, the effects of suspended sediments on the fast-start performance of reef fishes are unknown.

A reduced ability to detect predators may decrease prey survival (Meager et al. 2006) and, as a consequence, may increase the perceived risk of predation in suspended sediments. Fish commonly respond to increases in predation risk with strategic changes in anti-predator behaviour or fast-start performance (Domenici 2010; Lima 1998; Ramasamy et al. 2015). Such changes can be linked to considerable non-consumptive costs (Hawlena and Schmitz 2010; Preisser et al. 2005). For example, enhanced vigilance is associated with increased metabolic costs and can trade-off with foraging (Lima 1998; Killen et al. 2015; Preisser et al. 2005). Non-consumptive costs can result in reduced growth and condition (Hawlena and Schmitz 2010; Lima 1998) and can have equal or greater effects on prey population dynamics than predation itself (Preisser et al. 2005). Non-consumptive costs are particularly important to consider for juvenile reef fishes, as survivorship is typically low during this critical life-history stage and has been related to the growth and condition of individuals (Hoey and McCormick 2004). Despite its potential importance in shaping juvenile—and hence adult—populations, our understanding of the effects of suspended sediments on perceived predation risk and associated changes in performance or anti-predator behaviour of juvenile reef fishes is limited.

The aim of this study was to test the effects of suspended sediments on the fast-start performance and anti-predator behaviour of a common coral reef fish. Specifically, we exposed juvenile cinnamon clownfish (*Amphiprion melanopus*) to suspended sediments for 7 d (0 or 180 mg L^{-1}) and examined their fast-start performance and anti-predator behaviour in both 0 and 180 mg L^{-1} (i.e. after 5 min habituation time, referred to as "acute exposure" hereafter) suspended sediment concentrations. Exposing fish to suspended sediments both acutely and for 7 d allowed us to distinguish between potential effects on fast starts and anti-predator behaviour as a result of turbidity (e.g. sensory impairment) and potential effects driven by physiological changes such as reduced aerobic scope following prolonged exposure to suspended sediments.

Materials and methods

Suspended sediment exposure

Amphiprion melanopus larvae were sourced from five captive breeding pairs maintained at 28.5 ± 0.5 °C and reared following standard protocols (electronic supplemental material, ESM). At 35-d post-hatch, juveniles were exposed to 0 or 180 mg L^{-1} of Australian bentonite (0.7 ± 0.5 or 30.0 ± 4 NTU, respectively) for 7 d. Bentonite clay is representative of suspended sediments common to the Great Barrier Reef (GBR). The sediment concentration and exposure duration were selected to represent conditions frequently observed on inshore reefs of the GBR (Larcombe et al. 2001; Wenger et al. 2016). Sediments were maintained in suspension using a series of pumps in external sumps (ESM).

Fast-start performance and anti-predator behaviour

After 7-d exposure, juvenile *A. melanopus* (18.7 ± 2.1 mm standard length; mean ± SE) were introduced into a circular (21 cm diameter) test arena contained within an aquarium (ESM). The base of the arena was transparent, allowing the position of the juveniles to be recorded as a silhouette via a mirror positioned at an angle of 45° below the arena (Fig. S1). Juveniles were left undisturbed for 5 min, after which their behaviour was recorded for 2 min (Casio ex-fh20 camera). Following this, individuals were startled by a mechanical stimulus (a small weight), which was positioned above the arena and released via an electromagnet (following Allan et al. 2014). Responses of fish were recorded at 480 frames s^{-1}. Each individual was tested twice, i.e. both in 0 and 180 mg L^{-1} suspended sediments in the arena (Fig. S2), and the presentation order of these trials was randomized. In between the two trials, fish were housed in individual aquaria for 1.5 h to recover from escape responses.

Analysis of videos

Videos were analysed in ImageJ (version 1.48, National Institute of Health, USA) using a manual tracking plug-in. To determine fast-start performance, the following variables were measured: (1) response latency, (2) turning rate, (3) maximum acceleration, (4) maximum escape speed, (5) average escape speed and (6) distance travelled (see ESM for more details). Variables 3–6 were measured within the first 41 ms of the response, i.e. during the first two caudal fin flips (Domenici and Blake 1997).

To determine anti-predator behaviour, the position of individuals within the arena was determined every 3 s from the videos of the initial 2-min observation period. These data were used to derive the total distance moved by individuals (as a proxy for activity) and the percentage of time they spent within 2.5 body lengths of the wall of the arena (i.e. thigmotaxis/avoidance of open areas; Schnörr et al. 2012) (ESM).

Statistical analyses

Generalized linear mixed models were used to analyse the effects of acute and 7-d exposure to suspended sediments and their interaction on fast starts, activity and thigmotaxis of juveniles in R (v.3.3.2) using the package lme4 (Bates et al. 2015). Fish standard length and distance between fish and the stimulus were mean-centred and included as covariates, and presentation order of trials and fish identity were included as random factors (ESM). Significance of fixed effects was evaluated via model comparison.

Results and discussion

After 7-d exposure to elevated suspended sediments (180 mg L^{-1}), juvenile *A. melanopus* were faster to respond to the stimulus (11.3 ± 1.2 ms vs. 14.2 ± 1.0 ms, mean ± SE; $n = 65$, $\chi^2(1) = 5.36$, $p = 0.02$, Fig. 1a), exhibited higher turning rates (10.2 ± 0.3 deg ms^{-1} vs. 9.2 ± 0.3 deg ms^{-1}, $\chi^2(1) = 4.26$, $p = 0.03$, Fig. 1b), higher average escape speeds (72.1 ± 3.5 cm s^{-1} vs. 62.7 ± 3.4 cm s^{-1}; $\chi^2(1) = 6.38$, $p = 0.01$, Fig. 1c) and moved further away from the stimulus within the first 41 ms of the simulated attack (34.4 ± 1.6 mm vs. 29.5 ± 1.5 mm, $\chi^2(1) = 6.51$, $p = 0.01$, Fig. 1d) than fish exposed to clear water (0 mg L^{-1} suspended sediments) for 7 d. Maximum escape speeds and maximum acceleration were not influenced by 7-d exposure to suspended sediments (Fig 1e, f, see ESM for details). Maximum acceleration, however, was influenced by acute exposure to suspended sediments, with fish achieving higher maximum acceleration (40.8 ± 2.3 cm s^{-2} vs. 36.8 ± 2.0 cm s^{-2}, $\chi^2(1) = 5.2$, $p = 0.02$, Fig. 1f) when the water in the test arena was turbid as opposed to when it was clear. Acute exposure to suspended sediments did not influence any other fast-start trait (ESM). The shorter response latencies suggest that fish were more vigilant after 7-d exposure to suspended sediments, and coupled with the higher escape speeds, turning rates and acceleration, these changes would be expected to increase chances of a fish to survive a predator attack (Domenici and Blake 1997; McCormick et al. 2018; Walker et al. 2005).

Acute exposure to suspended sediments led to changes in anti-predator behaviour of juvenile *A. melanopus*. Fish moved significantly less (38.6 ± 4.8 cm vs. 51.8 ± 4.8 cm; $n = 78$, $\chi^2(1) = 13.47$, $p = 0.0002$, Fig. 2a) and spent less time in the open area of the arena

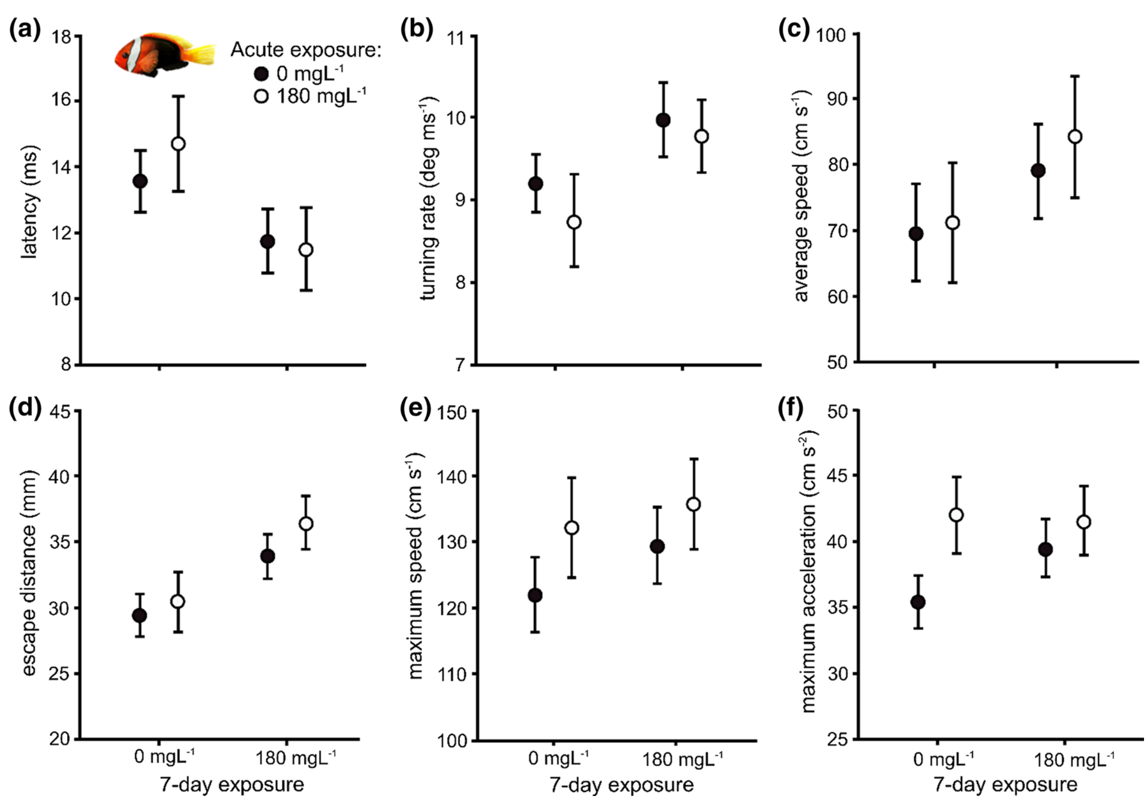

Fig. 1 Variables associated with fast starts of juvenile *Amphiprion melanopus* exposed to 0 or 180 mg L^{-1} suspended sediments for 7 d and tested in both clear (closed circles) and turbid water (open circles), i.e. "acute exposure" (effect plots and associated adjusted mean ± SE). **a** Latency to respond to a stimulus, **b** turning rate, **c** average escape speed, **d** distance escaped within 41 ms of the response, **e** maximum escape speed and **f** maximum acceleration

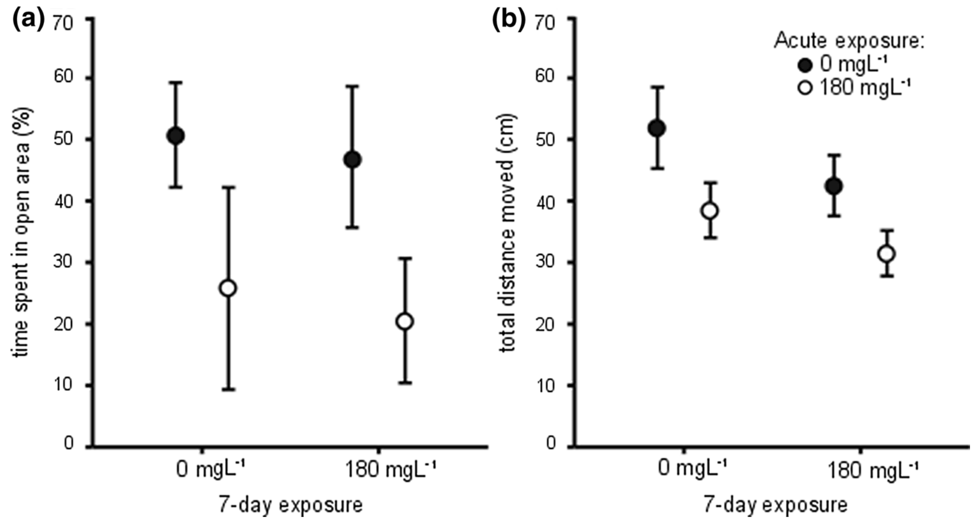

Fig. 2 Anti-predator behaviour of juvenile *A. melanopus* exposed to 0 or 180 mg L^{-1} suspended sediments for 7 d and tested in both clear (closed circles) and turbid water (open circles), i.e. "acute exposure" (effect plots and associated adjusted mean ± SE). **a** Percentage of time spent > 2.5 body lengths away from the wall of the arena and **b** total distance moved during the 2-min trial

(i.e. enhanced thigmotaxis) (11.6 ± 2.4% vs. 28.2 ± 3.5%; $\chi^2(1) = 11.16$, $p = 0.0008$, Fig. 2b) when exposed to suspended sediment in the arena compared to clear water. Fish exhibited these changes regardless of whether they were previously exposed to suspended sediments or clear water for 7 d (ESM). Exposure for 7-d would be expected to be sufficient for fish to habituate to suspended sediments, suggesting that the observed changes in behaviour (and fast-start performance) are not short-term reactions to a novel threat (i.e. turbidity), but rather adjustments to changes in the environment. Juvenile *A. melanopus* are commonly found on turbid inshore reefs (Fautin and Allen 1992), where turbidity levels can be variable. Short periods (minutes to hours) of elevated suspended sediments are caused by resuspension from waves and currents (Larcombe et al. 2001), while periodic events such as flood plumes can increase suspended sediment concentrations for days or weeks at a time (Wenger et al. 2016). Reductions in activity and enhanced thigmotaxis are strategies to decrease the likelihood of predator interactions (Lima 1998), suggesting that juvenile *A. melanopus* may adopt more cautious behaviour when suspended sediment levels are high.

Contrary to expectations, neither 7-d nor acute exposure to suspended sediments had negative effects on the fast-start performance of fish. Exposure to suspended sediments for 7 d was found to compromise the aerobic performance of juvenile *A. melanopus* (Hess et al. 2017), yet the locomotor performance of fish in the present study was enhanced rather than constrained. Similarly, acute exposure to suspended sediments did not influence the ability of fish to detect a stimulus that was a short distance away (~ 5 cm), simulating an ambush attack. This distance may have not been sufficient for suspended sediments to significantly reduce visual cues. Alternatively, fish may have used sound and/or water displacement, in addition to visual cues, to detect the stimulus. It is well established, however, that suspended sediments delay the visual detection of predators (Wenger et al. 2017) and attenuate sound transmission over longer distances (Brown et al. 1998). The observed enhanced fast starts and anti-predator behaviour following suspended sediment exposure are typical responses to increases in perceived predation risk (Domenici 2010; Lima 1998) and were likely an attempt to compensate for this reduced ability to detect visual and/or auditory cues associated with predators. Supporting this, a closely related species, *Acanthochromis polyacanthus*, has been found to enhance their anti-predator response to olfactory cues in suspended sediments to compensate for reduced visual cues (Leahy et al. 2011).

Whether the enhanced fast-start performance and anti-predator behaviour would translate into changes in predation rates in suspended sediments compared to clear water is not known, since suspended sediments may also affect the detection of prey by predators (e.g. Higham et al. 2015). A study on newly settled *Chromis atripectoralis* preyed upon by an ambush predator, *Pseudochromis fuscus*, documented that suspended sediments indeed influenced predation rates, with increased predation at medium (30 mg L^{-1}) suspended sediment levels, compared to low predation rates at both lower and higher levels of suspended sediment (Wenger et al. 2013).

Enhanced fast starts and anti-predator behaviour, as observed in response to suspended sediments, may lead to non-consumptive costs (Preisser et al. 2005). While *A. melanopus* lives symbiotically with sea anemones (Fautin and Allen 1992), the area they use for foraging (i.e. their home range) extends considerably beyond the area covered by their host (Ross 1978). Juveniles also frequently migrate between sea anemones (Ross 1978). More cautious behaviour, such as we observed in elevated suspended sediments, may not only reduce movement within their home range, potentially limiting access to food, but may also reduce the ability of juveniles to find a suitable anemone. Indeed, another damselfish species, *Pomacentrus moluccensis*, has been found to reduce movement between settlement habitats in elevated suspended sediments (Wenger and McCormick 2013). Furthermore, an increase in perceived predation risk itself is associated with numerous negative effects, such as impaired growth efficiency and immunocompetence (Hawlena and Schmitz 2010). While no studies, to date, have examined the metabolic costs of enhanced locomotor performance during fast starts, shorter response latencies have been linked to non-consumptive costs. Shorter response latencies are a result of enhanced vigilance, which is associated with increased metabolic costs (Killen et al. 2015) and is well known to trade-off with feeding in fish (Godin and Smith 1988; Preisser et al. 2005). Thus, while the enhanced fast-start performance and anti-predator behaviours can be perceived as beneficial when suspended sediment concentrations are high, such changes are likely associated with considerable costs for *A. melanopus* juveniles living on turbid reefs.

Acknowledgements We thank the team at MARFU, Ross Barrett and Sue Reilly for their technical support.

Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

Data accessibility https://cloudstor.aarnet.edu.au/plus/index.php/s/TUAtZEXLUJ2ZshL.

Ethical approval This research has been conducted according to the Australian code for the care and use of animals for scientific purposes and has been approved by the Animal Ethics Committee at James Cook University (animal ethics approval number A2218).

References

Allan BJ, Miller GM, McCormick MI, Domenici P, Munday PL (2014) Parental effects improve escape performance of juvenile reef fish in a high-CO_2 world. Proc R Soc Lond B Biol Sci 281:20132179

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Brown NR, Leighton TG, Richards SD, Heathershaw AD (1998) Measurement of viscous sound absorption at 50–150 kHz in a model turbid environment. J Acoust Soc Am 104:2114–2120

Brown CJ, Jupiter SD, Lin H-Y, Albert S, Klein C, Maina JM, Tulloch VJ, Wenger AS, Mumby PJ (2017) Habitat change mediates the response of coral reef fish populations to terrestrial run-off. Mar Ecol Prog Ser 576:55–68

Domenici P (2010) Context-dependent variability in the components of fish escape response: integrating locomotor performance and behavior. J Exp Zool 313:59–79

Domenici P, Blake R (1997) The kinematics and performance of fish fast-start swimming. J Exp Biol 200:1165–1178

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs:review and synthesis. Mar Poll Bull 50:125–146

Fautin DC, Allen GR (1992) Field guide to anemonefishes and their host sea anemones. Western Australian Museum, Perth

Godin JGJ, Smith SA (1988) A fitness cost of foraging in the guppy. Nature 333:69–71

Hamilton RJ, Almany GR, Brown CJ, Pita J, Peterson NA, Choat JH (2017) Logging degrades nursery habitat for an iconic coral reef fish. Biol Cons 210:273–280

Higham TE, Stewart WJ, Wainwright PC (2015) Turbulence, temperature, and turbidity: The ecomechanics of predator-prey interactions in fishes. Integr Comp Biol 55:6–20

Hess S, Prescott LJ, Hoey ASH, McMahon SA, Wenger ASW, Rummer JLR (2017) Species-specific effects of suspended sediments on gill structure and function in coral reef fishes. Proc R Soc Lond B Biol Sci 284

Hawlena D, Schmitz OJ (2010) Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. Am Nat 176:537–556

Hoey AS, McCormick MI (2004) Selective predation for low body condition at the larval-juvenile transition of a coral reef fish. Oecologica 139(1):23–29

Killen SS, Reid D, Marras S, Domenici P (2015) The interplay between aerobic metabolism and antipredator performance: vigilance is related to recovery rate after exercise. Front Physiol 6:111

Larcombe P, Costen A, Woolfe KJ (2001) The hydrodynamic and sedimentary setting of nearshore coral reefs, central Great Barrier Reef shelf, Australia: Paluma Shoals, a case study. Sedimentology 48:811–835

Leahy SM, McCormick MI, Mitchell MD, Ferrari MC (2011) To fear or to feed: the effects of turbidity on perception of risk by a marine fish. Biol Lett:rsbl20110645

Lima SL (1998) Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Adv Study Behav 27:215–290

Meager JJ, Domenici P, Shingles A, Utne-Palm AC (2006) Escape responses in juvenile Atlantic cod Gadus morhua L.: the effects of turbidity and predator speed. J Exp Biol 209:4174–4184

McCormick MI, Fakan E, Allan BJM (2018) Behavioural measures determine survivorship within the hierarchy of whole-organism phenotypic traits. Fun Ecol 32:958–969

Preisser EL, Bolnick DI, Benard MF (2005) Scared to death? The effects of intimidation and consumption in predator–prey interactions. Ecology 86:501–509

Ramasamy RA, Allan BJ, McCormick MI (2015) Plasticity of escape responses: prior predator experience enhances escape performance in a coral reef fish. Plos One 10:e0132790

Ross RM (1978) Territorial behaviour and ecology of the anemonefish *Amphiprion melanopus* on Guam. Ethology 36:71–83

Schnörr S, Steenbergen P, Richardson M, Champagne D (2012) Measuring thigmotaxis in larval zebrafish. Behav Brain Res 228:367–374

Syvitski JPM, Vorosmarty CJ, Kettner AJ, Green P (2005) Impact of humans on the flux of terrestrial sediment to the global coastal ocean. Science 308:376–380

Walker J, Ghalambor C, Griset O, McKenney D, Reznick D (2005) Do faster starts increase the probability of evading predators? Fun Ecol 19:808–815

Wenger AS, McCormick MI (2013) Determining trigger values of suspended sediment for behavioral changes in a coral reef fish. Mar Pol Bul 70:73–80

Wenger AS, McCormick MI, McLeod I, Jones G (2013) Suspended sediment alters predator–prey interactions between two coral reef fishes. Coral Reefs 32:369–374

Wenger AS, Williamson DH, da Silva ET, Ceccarelli DM, Browne NK, Petus C, Devlin MJ (2016) Effects of reduced water quality on coral reefs in and out of no-take marine reserves. Cons Biol 30:142–153

Wenger AS, Harvey E, Wilson S, Rawson C, Newman SJ, Clarke D, Saunders BJ, Browne N, Travers MJ, Mcilwain JL (2017) A critical analysis of the direct effects of dredging on fish. Fish Fish 18:967–985