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

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14 Abstract

- 15 Declining water quality, in particular elevated suspended sediments, pose a significant threat
- 16 to coastal coral reefs. We exposed juvenile anemonefish (*Amphiprion melanopus*) to two
- 17 suspended sediment concentrations (0 or 180 mgL⁻¹) for 7 days and examined their predator

18 escape performance and anti-predator behaviour in both clear water and suspended sediments

19 (0 and 180 mgL⁻¹, i.e., acute exposure). After 7-day exposure to suspended sediments, fish

20 responded faster to a mechanical stimulus and exhibited enhanced fast starts compared to

- 21 individuals reared in clear water, regardless of acute exposure. Fish were also less active and
- 22 avoided open areas when exposed to elevated suspended sediments in the test arena when

compared to clear water, irrespective of prior 7-day 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.
- 26 Keywords: suspended solids, sub-lethal effects, predator-prey interactions, turbidity, fish
- 27 health
- 28

30 Introduction

31 Suspended sediment concentrations in tropical coastal waters have increased substantially over the past few decades as a result of human activities including agriculture, 32 33 dredging, and shipping (Syvitski et al. 2005) and are altering the composition of biological communities (Fabricius et al. 2005). Elevated levels of suspended sediments can influence 34 coral reef fish assemblages indirectly through changes in the composition and structural 35 36 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 37 reef fishes, which may compound the negative effects of habitat degradation (reviewed in 38 Wenger et al. 2017). 39

Elevated suspended sediments reduce visual acuity and can thereby influence 40 41 important ecological processes such as predator-prey interactions (Wenger et al. 2017). 42 Reduced visual acuity can delay the detection of approaching predators, potentially altering 43 predation rates (Meager et al. 2006). While the early detection of predators is crucial, the 44 ability to escape a predator attack is equally important for prey survival (McCormick et al. 2018; Walker et al. 2005). Most prey fish escape predatory attacks via fast starts, i.e., short, 45 high-energy swimming bursts elicited by a sudden stimulus (Domenici and Blake 1997). 46 Prolonged exposure to elevated suspended sediments, however, has been shown to reduce the 47 aerobic scope (i.e., the capacity for aerobic activities) of some reef fishes (Hess et al. 2017); 48 this may compromise their capacity to engage in or recover from energetically costly 49 activities such as fast starts (Killen et al. 2015). Yet, the effects of suspended sediments on 50 the fast start performance of reef fishes are unknown. 51

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

54 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 55 al. 2015). Such changes can be linked to considerable non-consumptive costs (Hawlena and 56 Schmitz 2010; Preisser et al. 2005). For example, enhanced vigilance is associated with 57 increased metabolic costs and can trade-off with foraging (Lima 1998; Killen et al. 2015; 58 Preisser et al. 2005). Non-consumptive costs can result in reduced growth and condition 59 60 (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 61 62 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 63 individuals (Hoey and McCormick 2004). Despite its potential importance in shaping 64 65 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 66 behaviour of juvenile reef fishes is limited. 67

The aim of this study was to test the effects of suspended sediments on the fast start 68 performance and anti-predator behaviour of a common coral reef fish. Specifically, we 69 70 exposed juvenile cinnamon clownfish (Amphiprion melanopus) to suspended sediments for 7 days (0 or 180 mgL⁻¹) and examined their fast start performance and anti-predator behaviour 71 in both 0 and 180 mgL⁻¹ (i.e., after 5 min habituation time, referred to as "acute exposure" 72 73 hereafter) suspended sediment concentrations. Exposing fish to suspended sediments both acutely and for 7 days allowed us to distinguish between potential effects on fast starts and 74 anti-predator behaviour as a result of turbidity (e.g., sensory impairment) and potential effects 75 76 driven by physiological changes such as reduced aerobic scope following prolonged exposure to suspended sediments. 77

79 **Materials and methods**

Suspended sediment exposure 80

81	Amphiprion melanopus larvae were sourced from five captive breeding pairs
82	maintained at 28.5 \pm 0.5 °C and reared following standard protocols (electronic supplemental
83	material, ESM). At 35-days post-hatch, juveniles were exposed to 0 or 180 mgL ⁻¹ of
84	Australian bentonite (0.7 \pm 0.5 or 30.0 \pm 4 NTU, respectively) for 7 days. Bentonite clay is
85	representative of suspended sediments common to the Great Barrier Reef (GBR). The
86	sediment concentration and exposure duration were selected to represent conditions
87	frequently observed on inshore reefs of the GBR (Larcombe et al. 2001; Wenger et al. 2016).
88	Sediments were maintained in suspension using a series of pumps in external sumps (ESM).
89	

Fast start performance and anti-predator behaviour 90

After 7-day exposure, juvenile A. melanopus (18.7 ± 2.1 mm standard length; mean 91 \pm SE) were introduced into a circular (21 cm diameter) test arena contained within an 92 aquarium (ESM). The base of the arena was transparent, allowing the position of the 93 juveniles to be recorded as a silhouette via a mirror positioned at an angle of 45° below the 94 arena (Fig. S1). Juveniles were left undisturbed for five minutes, after which their behaviour 95 was recorded for two minutes (Casio ex-fh20 camera). Following this, individuals were 96 97 startled by a mechanical stimulus (a small weight), which was positioned above the arena and 98 released via an electromagnet (following Allan et al. 2014). Responses of fish were recorded at 480 frames second⁻¹. Each individual was tested twice, i.e. both in 0 and 180 mgL⁻¹ 99 suspended sediments in the arena (Fig. S2), and the presentation order of these trials was 100 randomized. In between the two trials, fish were housed in individual aquaria for 1.5 hours to 101 recover from escape responses. 102

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

To determine anti-predator behaviour, the position of individuals within the arena was determined every three seconds 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 percent 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).

115

116 *Statistical analyses*

Generalized linear mixed models were used to analyze the effects of acute and 7-day 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-centered 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.

124 **Results and Discussion**

After 7-day exposure to elevated suspended sediments (180 mgL⁻¹), juvenile A. 125 *melanopus* were faster to respond to the stimulus $(11.3 \pm 1.2 \text{ ms vs } 14.2 \pm 1.0 \text{ ms, mean} \pm$ 126 SE; n = 65, $\chi^2(1) = 5.36$, p = 0.02, Fig. 1a), exhibited higher turning rates (10.2 ± 0.3 deg ms⁻ 127 ¹ vs 9.2 \pm 0.3 deg ms⁻¹, $\chi^2(1) = 4.26$, p = 0.03, Fig. 1b), higher average escape speeds (72.1 \pm 128 3.5 cm sec⁻¹ vs 62.7 ± 3.4 cm sec⁻¹; $\chi^2(1) = 6.38$, p = 0.01, Fig. 1c), and moved further away 129 from the stimulus within the first 41 ms of the simulated attack $(34.4 \pm 1.6 \text{ mm vs } 29.5 \pm 1.5 \text{ mm vs$ 130 mm, $\chi^2(1) = 6.51$, p = 0.01, Fig. 1d) than fish exposed to clear water (0 mgL⁻¹ suspended 131 sediments) for 7 days. Maximum escape speeds and maximum acceleration were not 132 influenced by 7-day exposure to suspended sediments (Fig, 1e and f, see ESM for details). 133 Maximum acceleration, however, was influenced by acute exposure to suspended sediments, 134 with fish achieving higher maximum acceleration (40.8 ± 2.3 cm sec⁻² vs 36.8 ± 2.0 cm sec⁻², 135 $\chi^2(1) = 5.2$, p = 0.02, Fig. 1f) when the water in the test arena was turbid as opposed to when 136 it was clear. Acute exposure to suspended sediments did not influence any other fast start trait 137 (ESM). The shorter response latencies suggest that fish were more vigilant after 7-day 138 exposure to suspended sediments, and coupled with the higher escape speeds, turning rates, 139 and acceleration, these changes would be expected to increase chances of a fish to survive a 140 predator attack (Domenici and Blake 1997; Walker et al. 2005). 141

Acute exposure to suspended sediments led to changes in anti-predator behavior of juvenile *A. melanopus*. Fish moved significantly less $(38.6 \pm 4.8 \text{ cm vs} 51.8 \pm 4.8 \text{ cm}; n = 78,$ $\chi^2(1) = 13.47, p = 0.0002$, Fig. 2a) and spent less time in the open area of the arena (i.e., enhanced thigmotaxis) $(11.6 \pm 2.4 \% \text{ vs} 28.2 \pm 3.5 \%; \chi^2(1) = 11.16, p = 0.0008$, 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

148 clear water for 7 days (ESM). Exposure for 7-days would be expected to be sufficient for fish to habituate to suspended sediments, suggesting that the observed changes in behaviour (and 149 fast start performance) are not short-term reactions to a novel threat (i.e., turbidity), but rather 150 151 adjustments to changes in the environment. Juvenile A. melanopus are commonly found on turbid inshore reefs (Fautin 1992), where turbidity levels can be variable. Short periods 152 (minutes to hours) of elevated suspended sediments are caused by resuspension from waves 153 154 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). 155 156 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 157 cautious behavior when suspended sediment levels are high. 158

Contrary to expectations, neither 7-day nor acute exposure to suspended sediments 159 had negative effects on the fast start performance of fish. Exposure to suspended sediments 160 for 7 days was found to compromise the aerobic performance of juvenile A. melanopus (Hess 161 et al. 2017), yet the locomotor performance of fish in the present study was enhanced rather 162 than constrained. Similarly, acute exposure to suspended sediments did not influence the 163 ability of fish to detect a stimulus that was a short distance away (~5cm), simulating an 164 ambush attack. This distance may have not been sufficient for suspended sediments to 165 166 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, 167 however, that suspended sediments delay the visual detection of predators (Wenger et al. 168 169 2017) and attenuate sound transmission over longer distances (Brown et al. 1998). The observed enhanced fast starts and anti-predator behaviour following suspended sediment 170 exposure are typical responses to increases in perceived predation risk (Domenici 2010; Lima 171 1998) and were likely an attempt to compensate for this reduced ability to detect visual 172

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 antipredator behaviour would 177 translate into changes in predation rates in suspended sediments compared to clear water is 178 not known, since suspended sediments may also affect the detection of prey by predators (e.g. 179 Higham et al. 2015). A study on newly settled *Chromis atripectoralis* preved upon by an 180 ambush predator, Pseudochromis fuscus, documented that suspended sediments indeed 181 influenced predation rates, with increased predation at medium (30 mgL⁻¹) suspended 182 sediment levels, compared to low predation rates at both lower or higher levels of suspended 183 sediment (Wenger et al. 2013). 184

Enhanced fast starts and anti-predator behaviour, as observed in response to 185 suspended sediments, may lead to non-consumptive costs (Preisser et al. 2005). While A. 186 melanopus lives symbiotically with sea anemones (Fautin and Allen 1992), the area they use 187 for foraging (i.e., their home range) extends considerably beyond the area covered by their 188 189 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 190 only reduce movement within their home range, potentially limiting access to food, but may 191 192 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 193 habitats in elevated suspended sediments (Wenger and McCormick 2013). Furthermore, an 194 195 increase in perceived predation risk itself is associated with numerous negative effects, such as impaired growth efficiency and immunocompetence (Hawlena and Schmitz 2010). While 196 197 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.

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Fig. 1 Variables associated with fast starts of juvenile *Amphiprion melanopus* exposed to 0 or 180 mgL⁻¹ suspended sediments for 7 days and tested in both clear (closed circles) and turbid water (open circles), i.e. "acute exposure" (effect plots and associated adjusted means \pm SE). A) Latency to respond to a stimulus, b) turning rate, c) average escape speed, d) distance escaped within 41 ms of the reponse, e) maximum escape speed, and f) maximum

211 acceleration.

Fig. 2 Anti-predator behaviour of juvenile *A. melanopus* exposed to 0 or 180 mgL⁻¹ suspended sediments for 7 days and tested in both clear (closed circles) and turbid water (open circles), i.e. "acute exposure" (effect plots and associated adjusted means \pm SE). A) Percent of time spent > 2.5 body lengths away from the wall of the arena, and b) total distance moved during the 2 min trial.

- 217
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221 Data accessibility

- 222 https://cloudstor.aarnet.edu.au/plus/index.php/s/TUAtZEXLUJ2ZshL
- 223

224 **Conflict of interest statement**

225 On behalf of all authors, the corresponding author states that there is no conflict of interest.

226 Ethics statement

- 227 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).
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352 Supplementary methods

353 Suspended sediment exposure

Sediment was suspended in external 200 L sumps fitted with submersible pumps. 354 Each sump delivered water at a rate of 210 ± 30 mL min⁻¹ to the bottom of 18 replicate 355 conical experimental aquaria (3L). The water drained through an overflow outlet at the top of 356 the experimental aquaria back into sumps. Water temperature was maintained at 28.5 ± 0.5 °C 357 via 1000 W heaters (Eheim Gmbh & Co. KG, Deizisau, Germany) in each sump. Sumps were 358 flushed daily for 1 hour (> 100 % water exchange) to remove sediment and waste, after 359 which new sediment (Australian Bentonite) was added to the sumps. Temperature was 360 monitored daily and turbidity was monitored every four days (WP88 turbidity meter, Thermo 361 362 Fisher Scientific, QLD, Australia) throughout the experiments.

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364 *Larval rearing and exposure to experiments*

Breeding pairs of Amphiprion melanopus laid eggs on terracotta pots, which were 365 transferred to individual, black painted 40L hatching aquaria on the day hatching was 366 predicted (i.e. 6 – 8 days after egg deposition, Gordon et al. 2002). Aquaria were kept in a 367 1000L water bath to maintain temperature at 28.5 ± 0.5 °C and were flushed every morning 368 (prior to lights turning on) with filtered seawater for an hour to remove waste. To reduce 369 glare, algal paste (Nannochloropsis spp.) (ProAqua Pty Ltd, QLD, Australia) was added to 370 the water until the bottom of the aquaria was no longer visible. Branchionus spp. rotifers 371 were added at a density of 15 rotifers ml⁻¹ until 5 days post-hatch and were then reduced to a 372 density of 5 rotifers ml⁻¹ until day 8 post-hatch. Starting at day 5 post-hatch, Artemia spp. 373 nauplii were added to aquaria at a density of 1 nauplii ml⁻¹ twice daily until day 14 post-374 hatch, at which point larvae were fed flakes NRD 0.5 - 0.8 mm (Pro Aqua Pty Ltd) twice 375 daily. Most fish settled at approximately 8 days post-hatch. 376

- At 35 days post-hatch juveniles were randomly assigned to experimental aquaria at a
 density of 5 individuals per aquaria. Trials were run sequentially until a total number of 60
 individuals per treatment was reached.
- 380

381 Fast starts

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The following variables were measured:

Response latency was defined as the time interval between the weight entering the water and the first movement of the individual.

Turning rate was defined as the ratio of stage 1 angle and stage 1 duration (Domenici et al. 2008). Stage 1 angle was defined as the angle between the position of the fish (i.e. a line was drawn connecting the center of mass and the tip of the head) prior to the first detectable movement and at the end of stage 1. The end of stage 1 was reached when the turning rate of the fish reached zero for the first time (i.e., before a change in the direction of head rotation occured).

The remaining variables were determined based on stages 1 and 2 of the escape 391 392 response (i.e., the first two axial bends, Domenici and Blake 1997), which lasted 41 ms in this species. The position of the fish was determined for every frame (corresponding to a time 393 394 period of 2 ms between two frames) throughout the escape response. The distance moved and speed was calculated for each pair of consecutive frames. Acceleration was calculated as the 395 change in speed over time. Based on these measurements, the escape distance (i.e., sum of 396 397 distances moved within 41 ms), average and maximum escape speed, and maximum acceleration were determined. 398

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401 *Thigmotaxis*

Thigmotaxis, or "wall hugging" is a proxy for the shyness of an individual in a novel environment (Schnörr et al. 2012). As suggested by Schnörr et al. (2012), we used the proportion of time an individual spent within 2.5 body lengths from the wall to determine thigmotaxis.

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407 *Distance to the stimulus*

When suspended sediments were present in the test arena, fish were on average further away from the stimulus $(5.3 \pm 1.4 \text{ cm})$ when it entered the water than when the water was clear $(4.2 \pm 1.1 \text{ cm})$ (n = 65, $\chi^2(1) = 14.72$, p = 0.001), irrespective of 7-day exposure to suspended sediments ($\chi^2(1) = 0.02$, p = 0.89). To test whether distance to the stimulus had an effect on fast start variables, we initially included distance to the stimulus as covariate in

- 413 models. However, distance to the stimulus did not have a significant effect on any of the
- 414 variables, i.e. response latency, n = 65, $\chi^2(1) = 2.98$, p = 0.08; average escape speed, $\chi^2(1) =$
- 415 1.18, p = 0.28; maximum escape speed, $\chi^2(1) = 0.01$, p = 0.91; and distance travelled $\chi^2(1) =$
- 416 1.36, p = 0.24, and did not change the outcomes of any model. Therefore, distance to
- 417 stimulus was not included in the final models.
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Fig. S1. Experimental set up. 1) Electromagnet, accessible via a remote switch; 2) black weight with 438 439 tapered end used as a startling stimulus; 3) the stimulus fell through a tube ending 5mm above the 440 water surface to prevent fish from detecting the stimulus before entering the water surface. The 441 stimulus was released once the juveniles swam at least two body lengths away from the wall and one 442 body length away from the tube to avoid edge effects; 4) test arena (210 mm diameter) sitting in 5) an aquarium with opaque walls and top, illuminated by external LED lights (not shown), and filled to 8 443 444 cm with water to minimize vertical displacement; 6) the aquarium had a transparent bottom (indicated by the broken line), so the fish could be observed via a 7) mirror, sitting at an angle of 45° inside a 8) 445 box; 9) high speed camera pointed at the mirror. 446



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Fig. S2. Photograph of the experimental arena filled with clear water from the control a) and water 454 455 from the suspended sediment treatment b). The walls of the aquarium were opaque, while the bottom was transparent. 456

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2. Supplementary results 459

Juvenile A. melanopus exposed to suspended sediments for 7 days did not show any changes 460 in maximum acceleration ($\chi^2(1) = 0.26$, p = 0.60) or maximum escape speeds ($\chi^2(1) = 0.93$, p = 0.33) 461 462 compared to control fish. Acute exposure (i.e. suspended sediments present in the experimental arena) influenced maximum acceleration but not any other fast start variable, i.e. response latency (n 463 = 65, $\chi^2(1) = 2.57$, p = 0.11), turning rate ($\chi^2(1) = 2.19$, p = 0.13), average escape speed ($\chi^2(1) = 0.15$, 464 p = 0.70), maximum escape speed ($\chi^2(1) = 0.60$, p = 0.44), and distance travelled within the first 24 465 ms ($\chi^2(1) = 0.22$, p = 0.64). There were no significant interactions between 7-day exposure and acute 466 exposure, i.e. response latency ($\chi^2(1) = 0.09$, p = 0.75), turning rate ($\chi^2(1) = 0.31$, p = 0.57), 467 maximum acceleration ($\chi^2(1) = 1.70$, p = 0.19), average escape speed ($\chi^2(1) = 0.18$, p = 0.67), 468 maximum escape speed ($\chi^2(1) = 0.15$, p = 0.69), and distance travelled ($\chi^2(1) = 0.12$, p = 0.72). 469

470 Activity and thigmotaxis were influenced by suspended sediment concentrations in the test arena, but not by 7-day exposure to suspended sediments, i.e. activity (n = 78, $\chi^2(1) = 1.88$, p = 0.17) 471 and thigmotaxis ($\chi^2(1) = 0.64$, p = 0.42). There were also no significant interactions between 7-day 472 exposure and acute exposure, i.e. activity ($\chi^2(1) = 0.00$, p = 0.94), and thigmotaxis ($\chi^2(1) = 2.11$, p = 0.00, p = 0.94). 473 0.14). 474

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