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**Title Page**

**Sediment pollution impacts sensory ability and performance of settling coral-reef fish**

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Author Contributions: YN, DL, DB, JO, HB and GC conceived and designed the experiments. DL, JO, HB and GW performed the experiments. GL, JO, DL, HB and GC analyzed the data. JO wrote the manuscript; other authors provided editorial advice.

28

**Abstract**

Marine organisms are under threat globally from a suite of anthropogenic sources, but the current emphasis on global climate change has deflected the focus from local impacts. While the effect of increased sedimentation on settlement of coral species is well studied there is little known about the impact on larval fishes. Here, the effect of a laterite “red soil” sediment pollutant on settlement behaviour and post-settlement performance/fitness of larval reef fish was tested. In aquarium tests that isolated sensory cues we found significant olfaction-based avoidance behaviour and disruption of visual cue use in settlement-stage larval fish at  $50\text{mgL}^{-1}$ , a concentration regularly exceeded *in situ* during rain events. *In situ* light trap catches showed a trend of lower abundance and species richness in the presence of red soil but were not significantly different due to high variance in the data. Prolonged exposure to red soil produced altered olfactory cue responses, whereby fish in red soil made a likely maladaptive choice for dead coral compared to controls where fish chose live coral. Other significant effects of prolonged exposure included decreased feeding rates and body condition. These effects on fish larvae occurred in the presence of a minor drop in pH and may be due to the chemical influence of the sediment. Our results show that sediment pollution of coral reefs may have more complex effects on the ability of larval fish to successfully locate suitable habitat than previously thought, as well as impacting on their post-settlement performance and ultimately recruitment success.

50

**Keywords:**

behavioural ecology; coral reefs; environmental pollution; larval settlement; olfaction;

53

**1. Introduction**

54

55 Coral-reef ecosystems, which compose some of the world's most species rich  
56 environments, are facing threats to their survival on many fronts (Hughes et al.  
57 2010). Apart from rising sea levels, surface temperatures, acidification and fishing  
58 pressure, coral reefs are also highly sensitive to the effects of anthropogenic land-  
59 based pollution (Bégin et al. 2014). Impacts of sediment pollution are already  
60 realised in some regions (Rogers 1990), however these effects are likely to worsen,  
61 as some 75% of the world's coral reefs are currently nearby human settlements and  
62 because human populations in nearly all countries with coral reefs are expected to  
63 double within the next 50 to 100 years (Mora et al. 2011). Sedimentation is one of  
64 the biggest localized sources of reef degradation because elevated amounts of  
65 sediment on coral reefs, generated by increased land development run-off and  
66 dredging projects, have resulted in reduced coral cover, diversity, health and  
67 productivity (Erftemeijer et al. 2012; Fabricius 2005). Sediment pollution also directly  
68 impacts on the fitness of coral reef inhabitants (Wong et al. 2013), though the  
69 indirect mechanisms leading to shifts in density and species richness of fishes on  
70 sediment-impacted reefs are still being determined (Edinger and Risk 2013).

71 For coral reef fish populations to persist, their larvae need first to identify  
72 suitable settlement habitat then establish in this habitat as juveniles and adults.  
73 Coral-reef fish larvae have well-developed sensory systems capable of detecting  
74 habitat-relevant cues to allow orientation towards suitable settlement habitat, as well  
75 as the swimming capability to influence the direction of travel in ocean currents  
76 (Kingsford et al. 2002). Visual and olfactory senses play important roles for larval fish  
77 in orienting swimming direction towards suitable habitat (Lecchini et al. 2014a;  
78 Lecchini et al. 2014b). Therefore sediment pollution likely influences coral reef fish  
79 recruitment through impacting the capacity of these fishes to detect these cues  
80 (Siebeck et al. 2014). Suspended sediment can disrupt the ability of larval fish to

81 select appropriate habitat, though our understanding of which cues are affected and  
82 the potential consequences for recruitment success is limited (Wenger et al. 2011).

83 Even if coral reef fish larvae can locate and settle on suitable habitat,  
84 sediment pollution may threaten the viability of reef fish populations through impacts  
85 on their post-settlement fitness. Growth and behavioural development of fish larvae  
86 during settlement not only determines their recruitment success (Shima and Findlay  
87 2002), but also the ability of juvenile fishes to compete for resources (i.e. food,  
88 shelter and living space) within coral reef environments (Thorrold and Milicich 1990).  
89 Larval growth may be disrupted by increased sediment levels (Wenger et al. 2013a).  
90 Even in cases where larval development is not inhibited the presence of suspended  
91 sediment may still increase predator-induced mortality of post-settlement individuals  
92 by disrupting sensory cues. Hence, sensory modalities are of primary importance for  
93 survival and therefore ecological fitness at both pre- and post-settlement stages  
94 (Wenger et al. 2013b).

95 Here we investigated the effects of red soil pollution on the settlement  
96 behaviour of coral reef fish larvae and the impacts of exposure to red soil pollution  
97 on post-settlement behaviour and performance. The term “red soil” refers to a laterite  
98 soil that causes high levels of silt and turbidity around the coral reefs in Okinawa,  
99 Japan, during run-off events exacerbated by increased land development. Although  
100 this run-off has been reduced since the enforcement of the Okinawa Prefecture Red  
101 Soil Erosion Ordinance in 1995 there is evidence that it is still a major contributor to  
102 degradation of Okinawan coral reef communities, disrupting settlement and growth of  
103 coral species, however the effect on larval fishes remains largely unknown (Omori  
104 2011).

105 Here we tested the hypothesis that red soil pollution affects settlement  
106 dynamics of larval fish by applying red soil treatments *in situ* to light traps catching  
107 larvae as they approach the reef to settle, specifically investigating the patterns of

108 species abundance and richness. We then tested the effect of red soil on sensory  
109 cue use for habitat location and selection in the laboratory by observing behavioural  
110 responses of newly caught settlement-stage larvae to visual and olfactory habitat  
111 cues in the presence and absence of red soil. To investigate the effects of prolonged  
112 exposure of red soil on post-settlement performance we reared wild-caught fish  
113 larvae under different red soil concentrations then applied similar choice experiments  
114 on sensory cue response, as well as monitoring feeding behaviour and body  
115 condition. This is the first study to combine *in situ* and *ex situ* techniques to  
116 investigate multi-faceted effects of sediment pollution on early-stage fishes from  
117 habitat selection to post-settlement fitness.

## 118 **2. Materials & methods**

### 119 **(a) Field experiments**

#### 120 *(i) Establishing coral species important for settlement*

121 The planktivorous damselfish *Chromis viridis*, highly abundant in tropical reefs  
122 and light trap catches of the area, was selected as the study species for behavioural  
123 and conditioning experiments. *In situ* settlement preference of coral species for *C.*  
124 *viridis* was determined using underwater visual surveys on reef habitat adjacent to  
125 the light trap positions recording abundance of settlement stage individuals and the  
126 coral species they were associating with. To determine whether *C. viridis* associated  
127 with particular species of corals by chance, the cover of reef by each coral species  
128 was quantified within the site. The most common coral that *C. viridis* associated with  
129 was determined by comparing frequencies of recruits on each coral species  
130 observed during surveys. To test if association of *C. viridis* recruits with a given coral  
131 species occurred by chance, a Chi-squared test adapted for low values (p-values  
132 evaluated by Monte Carlo simulation n=1000) was used to compare the proportion of  
133 *C. viridis* that associated with a coral species to the proportion of reef it covered.

#### 134 *(ii) In situ choice experiment*

135 To test the *in situ* settlement dynamics of larval fish in the presence of red  
136 soil, four light traps were deployed (for more description about these light-traps, see  
137 (Nakamura et al. 2009)) adjacent to fringing coral reefs surrounding the Sesoko  
138 Station (Tropical Biosphere Research Center, University of the Ryukyus) on the  
139 south-east side of Sesoko Jima, Okinawa (See Fig. 1A in supplementary material).  
140 Traps were set at one of four locations spaced at 50m intervals and randomly  
141 assigned one of four treatments upon each deployment: 1) Control: empty bottles  
142 added, 2) Red soil added, 3) Live coral added and 4) Both live coral and red soil  
143 added. Red soil was added by the attachment of three slow release 250mL bottles  
144 filled with red soil suspended in sea water to the top, bottom and inner chamber of  
145 the light trap. Live coral was added with a *Porites cylindrica* coral head ~20cm  
146 diameter attached in a mesh bag suspended within the light trap. Total abundance  
147 and species richness from each trap catch was recorded for a period of eleven  
148 consecutive days (01 to 11 July 2013). A one-way ANOVA was used to test for  
149 differences in mean abundance and species richness between treatments. Chi-  
150 squared tests were used on rank-frequency data from the light trap catches to  
151 investigate bias in light trap location, treatment type, and temporal effects. These  
152 data were then put into a general linear model (GLM) using Poisson distribution  
153 (usually adapted for abundance data) to compare the effect of each treatment on  
154 larval catch patterns. Only fish caught in the control light traps were used in  
155 subsequent experiments to avoid prior conditioning to coral or red soil.

156

## 157 **(b) Settlement-stage larval sensory experiments**

### 158 *(ii) Effect of sediment extract on olfactory cue use*

159 A two-channel Perspex choice flume of a similar design to that of Gerlach et  
160 al. (2007) was used to test preferences between olfactory cues in water sources with  
161 and without the presence of red soil. Each trial begins with a larva being placed in

162 the centre of the downstream end of the chamber to explore the chamber and  
163 acclimate to the water sources for a period of two minutes. Fish that did not swim  
164 actively or explore both sides of the chamber during these two minutes were  
165 discarded from the trials (<5% of fish tested were discarded). After the acclimation  
166 period, the position of the fish was recorded every five seconds for another two  
167 minute period as being on one side of the chamber or the other. Water sources  
168 entering the chamber from buckets gravity-feeding into the left and right side were  
169 then switched, with one minute being allocated for the water sources to exchange  
170 and flush completely, in order to control for side preference in individuals. After  
171 switching water sources, another two-minute acclimation period was given, followed  
172 by another two-minute observation period. In this way it is possible to tease apart  
173 choice for chemical properties of the water sources and side preference of the  
174 apparatus. Each individual was tested only once after which they were released back  
175 to the capture site and the chamber was rinsed thoroughly with freshwater. Flow rate  
176 was maintained at  $200\text{mL min}^{-1}$  and dye tests were conducted after each replicate to  
177 ensure a laminar flow on each side of the chamber without eddies or mixing of the  
178 two water sources.

179 Experimental treatments for each fish consisted of an initial control treatment  
180 where incoming water on both sides of the chamber was from the same source (i.e.,  
181 coral-soaked water vs coral-soaked water), followed by the experimental treatment  
182 testing preferences between water from two different sources, resulting in two  
183 comparable data sets for each fish. To test the effect of red soil on behavioural  
184 response to habitat cues, *C. viridis* larvae were given a choice between coral-soaked  
185 water and the same coral-soaked water with red soil added in two different  
186 concentrations. Twenty fish larvae were used per treatment. Coral-soaked water was  
187 produced in a 150L tank containing approximately 6kg of live *P. cylindrica* coral  
188 heads. After the flow-through system had been shut off for at least two hours water



189 was transferred to two 60L tanks. Depending on the treatment being tested 50 or  
190 200mgL<sup>-1</sup> of red soil was mixed into one of the tanks. The two water sources were  
191 then left to sit for a further 2 - 4 hours to allow time for the water containing the  
192 suspended red soil to equilibrate and become “clear” to minimise the effect of  
193 turbidity, creating a red soil “extract”. Olfactory preference data was analysed using  
194 Wilcoxon’s Signed Rank Test, a non-parametric test suited to the time proportion  
195 data and accounting for the repeated measures of the same individual.

196 *(ii) Effect of suspended sediment on visual cue use*

197 Larvae were tested in a three-compartment test chamber (60 x 12 x 10 cm).  
198 The side compartments were formed by two transparent plexiglass panels separated  
199 by 1cm placed to create barriers at 8cm from each end, resulting in a central  
200 compartment of 32cm length which was delimited into three equal parts. This  
201 experimental system isolates visual cues available to the individual placed in the  
202 central compartment from chemical cues present in the side compartments. Thus,  
203 only visual cues from coral colonies were influencing larval movement in the central  
204 compartment.

205 Before each trial, one live and one dead coral colony were placed in the side  
206 compartments behind the plexiglass barriers. A single larva was introduced into the  
207 middle of the central compartment for a one minute acclimation period during which  
208 an opaque screen was placed between the plexiglass barriers to block visual cues  
209 after which the screens were removed and the trial commenced. The position of the  
210 larva in the central compartment was recorded every five seconds for a period of one  
211 minute. This short test period also ensured that sediment added to the test chamber  
212 remained in suspension. The aquarium was emptied and washed with freshwater  
213 after each trial. To exclude a possible side bias of the fish, the order of adjacent  
214 compartments containing each coral type was randomized for each trial. Moreover,

215 water samples were taken and parameters of temperature, pH, salinity and turbidity  
216 were measured to ensure there was no biasing effect in these parameters.

217 Five treatments were applied as follows ( $n = 20$  per treatment):

218 1) Control – Habitat compartments (at each end): Live or dead coral, larval  
219 chamber (centre): no red soil added

220 2) Low -  $50\text{mgL}^{-1}$  red soil suspended in larval chamber

221 3) High -  $200\text{mgL}^{-1}$  red soil suspended in larval chamber

222 Each individual was only tested once. Visual preference data were analysed using  
223 Wilcoxon's Rank Sum Test, a non-parametric alternative to the two-sample t test.

224

### 225 **(c) Effect of prolonged exposure to sediment on sensory responses**

#### 226 *(i) Olfactory response*

227 To test the olfactory responses of settlement-stage larvae after being  
228 acclimated to different pollution levels, *C. viridis* larvae caught in light traps were  
229 placed into aerated non-flow-through 10 litre holding tanks and reared for five days,  
230 fed twice daily *ad libitum* with newly hatched *Artemia salina*. Three different  
231 treatments were applied to the rearing tanks: 1) Control (no red soil added), 2)  
232  $50\text{mgL}^{-1}$  red soil mixed into solution and 3)  $200\text{mgL}^{-1}$  red soil mixed into solution.  
233 After initial mixing red soil was not-remixed during the rearing period and allowed to  
234 settle in the tank. Ten fish larvae from each treatment were then selected for  
235 olfactory choice testing using the same methods previously described, but  
236 implementing a test between olfactory cues from water soaked with live coral and  
237 dead coral (coral rubble collected from the just below the intertidal zone of the reef  
238 area sampled in this study).

#### 239 *(ii) Visual response*

240 Individuals from the same treatments as used for the olfactory experiments  
241 above were also tested in the visual cue test chamber with the same protocol as the

242 newly caught larvae. Fifteen fish per rearing treatment were tested in clear water  
243 with live and dead coral colonies in the adjacent compartments at each end of the  
244 test chamber without red soil added. Instead of comparing red soil concentrations in  
245 the chamber, preferences of individuals swimming in clear water but from different  
246 rearing concentrations of red soil were analysed.

#### 247 **(d) Red soil acclimation effects on post-settlement performance**

##### 248 *(i) Feeding rates and condition*

249 To test the effect of red soil on post-settlement performance of *C. viridis*  
250 recruits, aquaria trials were used to compare feeding rates and physiological  
251 condition. Following capture 10 individual larvae were randomly selected and  
252 allocated to one of sixteen 15L plastic tanks - eight containing 50mgL<sup>-1</sup> of red soil  
253 and eight containing untreated seawater. Larvae were maintained for seven days,  
254 fed live *Artemia salina* ad libitum twice daily. Following this rearing period, fishes  
255 were filmed using HD video from above tanks for one minute following the addition of  
256 a standardised quantity of pellet food. Feeding rates (bites per minute) of all  
257 individuals within groups were counted whilst replaying this video footage. The wet  
258 weight (WW) and standard length (SL) of each fish was measured at the end of the  
259 conditioning period, allowing calculation of Fulton's condition (K) factor;  $K =$   
260  $100(WW/SL^3)$ . Tanks were lit naturally, aerated and contained a small piece of coral  
261 for shelter. Water was changed daily; ensuring concentrations of red soil were  
262 consistent. Feeding rates and body condition (Fulton's) were compared between red  
263 soil and no red soil treatments (fixed) and groups (random; nested within red soil  
264 treatment) using a two factor nested ANOVA (individual fish being the residual).

##### 265 **(e) Post-experiment red soil pH analysis**

266 Following the analysis of the data on the sensory responses of fish reared for  
267 a prolonged period under different sediment treatments further measurements of the  
268 effect on pH levels were required. Measurements were done on site using a 713 pH

269 meter (Metrohm Japan Ltd.) using 6 replicates in 1L bottles for each of the three  
270 treatment concentrations of red soil used for the rearing tanks (namely 0, 50 and  
271 200mgL<sup>-1</sup>). As with the rearing trials sediment was initially mixed and not disturbed  
272 for the remainder of the experimental period. Measurements of pH were taken at  
273 0hrs (turbid water) and 2 hrs (clear water after sediment had settled to bottom), then  
274 at 3 days and 7 days after the initial mixing.

### 275 **3. Results**

#### 276 **(a) Field experiments**

##### 277 *(i) C. viridis coral association*

278 Field surveys showed *C. viridis* associated with the branching coral, *Porites*  
279 *cylindrica*, significantly more frequently than expected by chance; 119 of 184  
280 individuals (64.7%) observed associated with *P. cylindrica*, which composed 4% of  
281 live, hard corals ( $\chi^2 = 1160$ ,  $df = 10$ ,  $P < 0.001$ ). This preliminary survey justified the  
282 use of *P. cylindrica* as a habitat cue in settlement cue experiments.

##### 283 *(ii) In situ larval abundance and species richness trends*

284 Forty-seven species of larval fish were caught in the light traps during the field  
285 experiment. No significant experimental bias of light trap position ( $\chi^2 = 16.8$ ,  $df = 3$ ,  $P$   
286  $> 0.05$ ) or time of deployment (Global  $\chi^2 = 0.6894$ ) was detected. Species  
287 abundance and richness between light trap treatments were not significantly different  
288 ( $F = 0.36$ ,  $df = 3,36$ ,  $P = 0.78$  &  $F = 1.57$ ,  $df = 3,36$   $P = 0.21$  respectively) due to high  
289 levels of variance in the data (Welch test for homogeneity of variance in abundance,  
290  $P = 0.49$ ) and species richness ( $P = 0.24$ ). Though light trap catches were highly  
291 variable, a similar trend for both species richness and abundance was apparent  
292 between treatments (see Fig. 2A in supplementary material). Total abundance was  
293 highest in treatments without red soil, with the live coral treatment attracting the most  
294 larvae (32%) followed by Control (empty light trap) (26%), red soil (24%) and live  
295 coral with red soil (18%). Light traps containing live coral only also attracted the

296 highest species richness (30%) followed by control (28%), red soil and live coral with  
297 red soil (21% each).

298 One of the four light trap positions showed an effect of the treatment type on  
299 the number of larvae caught that approached significance ( $\chi^2 = 18.6$ ,  $df = na$ ,  $P =$   
300  $0.07$ ) and a significant difference in species richness ( $\chi^2 = 37.9$ ,  $df = na$ ,  $P = 0.01$ ).  
301 Comparing catches at this location showed a significant difference in larval  
302 abundance between traps that contained live coral and those that did those that did  
303 not ( $\chi^2 = 10$ ,  $df = na$ ,  $P = 0.01$ ). General Linear Modelling indicates this difference  
304 was driven by an increasing trend in catch by light trap treatment, with significant  
305 coefficients ordered as Control + Red soil < Live Coral + Red Soil < Control < Live  
306 Coral, a similar trend seen in the non-significant mean abundance and species  
307 richness between treatments (see Table 1A in supplementary material). Comparing  
308 rank frequencies of larval abundance at each of the four light trap positions for each  
309 day with chi-squared tests showed no difference in three of the four light traps ( $\chi^2 =$   
310  $6.2$ ,  $df = na$ ,  $P = 0.69$ ), however the southerly light trap position showed significantly  
311 higher catch over time irrespective of which treatments were being applied ( $\chi^2 =$   
312  $10.8$ ,  $df = na$ ,  $P = 0.02$ ). It should be noted that this light trap was excluded from the  
313 GLM due to its potential bias.

## 314 **(b) Settlement-stage larvae sensory experiments**

### 315 *(i) Larvae avoid habitat chemical cues with sediment extract present*

316 No bias to the chamber or experimental conditions was detected in *C. viridis*  
317 larvae, with no side preference shown when presented with the same habitat cue on  
318 both sides of the chamber. Larvae spent approximately equal time on each side  
319 (mean  $\pm$ SE percentage of time spent in the left flow  $52 \pm 0.63\%$ ; and in the right  $48 \pm$   
320  $0.63\%$ ), justifying this comparison as a control treatment to test for experimental  
321 bias. Larvae responded to the red soil infused treatment water by spending  
322 significantly more time in the live coral soaked water (>70%), strongly avoiding the

323 water infused with  $50\text{mgL}^{-1}$  of red soil ( $Z = -3.643$ ,  $P < 0.001$ ). This effect was  
324 increased when the concentration of red soil was increased to  $200\text{mgL}^{-1}$  spending  
325 over 74% of time (Fig. 1) in the live coral water ( $Z = -3.642$ ,  $P < 0.001$ ). Turbidity  
326 measurements did show a slight increase in turbidity with red soil concentration from  
327 live coral water to 50 and  $200\text{mgL}^{-1}$  (0.12, 0.15 and 0.19 NTU/FTU respectively),  
328 however this difference was regarded as nominal.

329 *(ii) Visual cue use disrupted by suspended sediment*

330 Larvae presented with visual cues of both live coral and dead coral spent  
331 significantly more time swimming near the live coral than the dead coral (Wilcoxon's  
332 Rank Sum test,  $z$ -value = 3.0,  $p$ -value = 0.002), spending twice the proportion of time  
333 exploring the compartment closest to the live coral chamber compared to the  
334 compartment near the dead coral (56% vs. 26% respectively). When  $50\text{mgL}^{-1}$  of red  
335 soil solution was added to the central compartment with the larvae, this ability to  
336 visually discriminate between the live and dead coral chambers disappeared (see  
337 Fig. 2), with no significant difference in time spent at either end of the choice  
338 chamber (Wilcoxon's test,  $Z = 0.05$ ,  $P = 0.96$ ). Time spent exploring the chamber  
339 dropped dramatically when  $200\text{mgL}^{-1}$  of red soil solution was added to the chamber:  
340 larvae were in the central compartment 75% of the time, as opposed to only 28%  
341 under the  $50\text{mgL}^{-1}$  conditions. Again, approximately equal time was spent exploring  
342 compartments close to both live and dead coral (Wilcoxon's test,  $Z = 0.05$ ,  $P =$   
343 0.957).

344 **(c) Effect of prolonged exposure to sediment on sensory responses**

345 *(i) Choice behaviour in response to olfactory cues reversed or eliminated*

346 After 5 days of being reared in test aquaria, fish under red soil conditions  
347 displayed significantly different behaviour than those raised in "clean" control water  
348 (see Fig. 3). Individuals reared under control conditions strongly preferred live coral  
349 cues over dead coral cues (Wilcoxon's Rank Sum;  $Z = 2.81$ ,  $P = 0.01$ ), spending

350 over 70% of the time in the flow containing live coral cues. By comparison the fish  
351 reared in water containing  $50\text{mgL}^{-1}$  shifted their preference, displaying significant  
352 choice towards dead coral cues over live coral cues (Wilcoxon's Rank Sum;  $Z =$   
353  $2.20$ ,  $P = 0.03$ ), spending 63% the time in the flow containing dead coral cues. After  
354 being reared in  $200\text{mgL}^{-1}$  conditions there was no significant choice between the two  
355 cues (Wilcoxon's Rank Sum;  $Z = -0.05$ ,  $P = 0.96$ ).

356 *(ii) Choice behaviour undetectable in response to visual cues*

357 Larvae reared under control conditions spent equal time near the live and  
358 dead coral compartments (31% each). Responses of larvae reared with  $50\text{mgL}^{-1}$  of  
359 sediment were similar, with 32% and 29% of time spent near live and dead coral  
360 compartments respectively. Under  $200\text{mgL}^{-1}$  rearing conditions this dynamic  
361 changed somewhat, with the largest proportion of time spent near the dead coral  
362 compartment (40%). This change in choice behaviour is similar to what occurred in  
363 the olfaction trials, though the difference was not statistically significant (Wilcoxon's  
364 test,  $Z = 0.86$ ,  $P = 0.39$ ). Furthermore, position distributions were not significantly  
365 different between the rearing treatments for time spent close to both live coral (K-S  
366 Test,  $P = 0.99$ ) and dead coral (K-S Test,  $P = 0.93$ ).

367 **(d) Red soil acclimation effects on post-settlement performance**

368 *(i) Decreased feeding rates and body condition*

369 Feeding rates and condition were significantly impacted by the presence of red soil  
370 (See Fig. 4). Feeding rates were significantly slower for red soil conditioned than  
371 control fish ( $F_{1, 144} = 7.12$ ;  $P = 0.04$ ), whereas, within the sediment treated tanks  
372 there were significant differences among groups ( $F_{1, 144} = 3.65$ ;  $P = 0.02$ ). Condition  
373 was also significantly poorer in red soil than control fish ( $F_{1, 99} = 5.52$ ;  $P = 0.04$ ),  
374 though it did not significantly differ amongst groups within the sediment treatment  
375 tanks ( $F_{1, 99} = 0.15$ ;  $P = 0.12$ ). There was no difference in mortality between control

376 and red soil treated fishes; 25 and 20 individuals from 80 respectively in the  
377 sediment treatment tanks ( $t_{14} = 0.90$ ;  $P = 0.38$ ).

#### 378 (e) Post-experimental pH analysis

379 Average pH level declined with increasing sediment concentration.  
380 Immediately after mixing mean pH of control samples, 50mgL<sup>-1</sup> and 200mgL<sup>-1</sup> was  
381 8.1, 8.09 and 8.08 respectively. Measurements were similar at 2 hours after the  
382 sediment had settled out of suspension however while the mean pH of the control  
383 water remained stable over time the water treated with red soil became more acidic  
384 over time, reaching 8.08 and 8.04 after 7 days for the 50 and 200mgL<sup>-1</sup> treatments  
385 respectively (see Table 2A in supplementary material).

#### 386 4. Discussion

387 Larval fish behaviour is likely to influence their dispersal and orientation to  
388 suitable settlement habitat (Cowen et al. 2006), yet the impacts of sediment pollution  
389 on this process have been largely unresolved. We showed that in the presence of  
390 sediment pollution, such as that caused by red soil, tropical reef fish larvae could be  
391 inhibited from locating suitable coral habitats during settlement. Specifically, we  
392 found that in the presence of red soil, *C. viridis* larvae failed to distinguish suitable  
393 coral habitat visual cues and avoided coral habitat olfactory cues. This may lead to  
394 decreased chances for recruitment in areas prone to recurrent sediment pollution,  
395 such as Okinawa, Japan, compared to more pristine areas. Previous studies have  
396 reported avoidance behaviour in settlement-stage fish of either degraded (by algal  
397 phase shift (Lecchini et al. 2013)) or dying coral reef habitat (Feary et al. 2007), and  
398 our results suggest sensory cue use may be an important factor. Evidence for  
399 chemically mediated avoidance behaviour *in situ* has been shown using cues from  
400 degraded seaweed-dominated reef habitats, suggesting that olfactory cues from  
401 sediment-degraded reefs could affect recruitment densities and reef resilience  
402 (Dixson et al. 2014).



403 Evidence of negative impacts of sediment pollution on settlement behaviour of  
404 settlement-stage reef fish larvae have been found previously (Wenger and  
405 McCormick 2013), yet the field relevance of these results were previously untested.  
406 Here we provide the initial evidence that the presence of red soil near coral habitat,  
407 even administered in small amounts, may reduce settlement success in the field.  
408 Untreated light traps containing live coral with red soil absent caught a higher  
409 abundance and species richness than light traps with coral in the presence of red  
410 soil. The statistical significance of this result may have been affected due to a  
411 positional bias of the light traps, with the southerly light trap position (the direction  
412 from which the prevailing current flows) catching more larvae than the other three  
413 positions. High levels of variation in catch abundance, seen in our results, is also a  
414 notoriously typical effect on reliable light trap sampling (Leis et al. 2002). The non-  
415 significant trend of a negative response of settling fishes to red soil treatments was  
416 congruent with results obtained in the laboratory experiments.

417 Results showing either an avoidance of olfactory cues from habitat with red  
418 soil present or a disruption of the ability or inclination to utilise visual habitat cues in  
419 settlement stage coral reef fish larvae indicates that such pollution of coral reef  
420 environments may impact larval recruitment and survival. A reluctance or inability to  
421 approach potential habitats can extend the period spent by fish larvae in close  
422 proximity to the reef running the “predation gauntlet”, increasing the risk of predation  
423 (Almany and Webster 2006). Even prolonged exposure to non-predatory fish can be  
424 detrimental, with harassment of recruiting fish larvae by territorial residents observed  
425 to result in elevated predation risk or avoiding the habitat altogether (Leis and  
426 Yerman 2012). In addition to this, previous studies have shown an effect of sediment  
427 pollution on larval development whereby the PLD is increased (Wenger et al. 2013a).  
428 This effect could alter the timing and location of larval settlement, changing the  
429 natural distribution and recruitment of fish larvae through the modifications of their

430 movement towards habitat can affect the spatial and community demography of fish  
431 populations.

432 Even if fish larvae manage to settle on coral reef habitat degraded with  
433 sediment pollution, our results show that prolonged exposure to the presence of  
434 sediment could impact post-settlement behaviour and survival. Five days of  
435 exposure to water containing red soil significantly altered the response to olfactory  
436 cues from different habitat types, reversing the strong preference for live coral cues  
437 under control conditions to instead preferring those from dead corals. At a higher  
438 rearing concentration of red soil, response to olfactory cues was absent altogether.  
439 As the habitat cues presented to individuals here after the rearing period contained  
440 no sediment influence, it is assumed that the change in behaviour was due to  
441 physiological effects of exposure on the sense organ, rather than impairment of  
442 transmission of the cues themselves. The response to visual cues in individuals  
443 exposed for five days to sediment differed from newly caught larvae, no longer  
444 showing significant choice behaviour towards live coral over dead coral. This  
445 reduced exploration of the visual cue chamber may be an artefact of rearing in  
446 captivity or an ontogenetic change in behaviour, perhaps due to a reduction in the  
447 inclination to use visual habitat cues to orient movement by juveniles compared to  
448 settling larvae (Lecchini et al. 2007).

449 Reversal in normal behavioural responses to olfactory cues has been shown  
450 in response to increased water acidification, where a normal avoidance of predator  
451 cues became a strong attraction in fish larvae reared in water with higher acidity  
452 (Dixson et al. 2009). Furthermore, when the acidity of rearing conditions is  
453 increased further the fish larvae no longer responded to olfactory cues (Munday et  
454 al. 2009), similar to the trend in our results. The mechanism suggested for this is an  
455 alteration caused by the increased acidity of anion gradients across neuronal  
456 membranes which reverse normal receptor function (Nilsson et al. 2012). The

457 changes in behaviour seen in the rearing trials may be a similar response due to the  
458 acidity of red soil. Behavioural avoidance of acid sulphate soils by juvenile fish has  
459 been shown in juveniles of various fishes where pH levels were well within the range  
460 exhibited in natural systems (Kroon 2005). Red soil in Okinawa is acidic with a pH of  
461 ~5 (Mkadam et al. 2006), and analysis of rearing conditions used here showed pH  
462 decreased both with increasing concentrations of red soil and with time. Reductions  
463 in pH of a similar range (0.07) have been shown to elicit similar behavioural changes  
464 in juvenile coral trout (*Plectropomus leopardus*) (Munday et al. 2013). This acidic soil  
465 could influence the pH of water surrounding the reef on which it deposits, as has  
466 been shown with organic-rich soils (Weber et al. 2012).

467 Previous studies on the effect of red soil on water chemistry showed that as  
468 red soil concentration increased in a solution, availability of H<sup>+</sup> ions (increasing  
469 acidity) and heavy metals, particularly Al<sup>3+</sup> also increased (Kombo et al. 2005).  
470 Exposure to elevated concentrations of heavy metals can also lead to changes in  
471 behavioural responses of fish to olfactory cues (Scott and Sloman 2004). Increased  
472 Al<sup>3+</sup> concentrations can exacerbate the damage done to the olfactory epithelium by  
473 increased acidity alone, working synergistically to disrupt olfactory abilities in  
474 salmonid fish (Klaprat et al. 1988). Our results suggest that chemical properties of  
475 sediment pollution may cause greater impacts on coral reef environments than  
476 turbidity alone. Of course, it is not only the use of habitat cues that can affect the  
477 ecology of early-stage fishes. Chemical pollution of the aquatic environment may  
478 also disrupt communication, social recognition and shoaling in fish, which can have  
479 drastic effects on population fitness (Fisher et al. 2006; Ward et al. 2008).

480 Exposure to sediment pollution negatively impacted the condition and  
481 performance in *C. viridis*. Both feeding rates and condition reduced with increasing  
482 concentration of red soil. The sensory disruption detected in other individuals of the  
483 same cohort during this experiment as well as other physiological effects from

484 prolonged exposure to sediment pollution may have played a role in reduced  
485 foraging success. As evidence suggests that growth is a critical variable in the  
486 recruitment success and survival of post-settlement fish this is another aspect in  
487 which sediment pollution can impact on affected fish populations (Bergenius et al.  
488 2002). Our results concur with data on juvenile reef fish reared under similar  
489 concentrations of suspended sediment ( $0 - 180\text{mgL}^{-1}$ ), where reduced foraging  
490 behaviour led to reduced growth, condition and survival (Wenger et al. 2012). This  
491 effect has also been shown to reduce foraging success *in situ* when prey detection  
492 may be limited by absolute light levels rather contrast (Fiksen et al. 2002).

493 In conclusion, this experiment used a variety of techniques and life history  
494 stages to investigate the effect of sediment pollution on coral reef fish larvae around  
495 the crucial settlement period. At the settlement stage we found evidence of  
496 disruption of natural use of sensory cues related to locating suitable habitat by fish  
497 larvae in the presence of increased sediment levels. Following settlement (after five  
498 days captive rearing) metamorphosing post-settlement fish experienced reduced  
499 feeding behaviour and condition under the sediment treatments. Response to  
500 habitat-relevant sensory cues became confused, reversing the preference from live  
501 coral to dead coral in some cases in individuals which had experienced prolonged  
502 exposure to sediment concentrations. The responses to sediment pollution reported  
503 here are in many aspects the similar to those reported in from elevated levels of  $\text{CO}_2$   
504 which also can simultaneously affect a range of fish behaviours (Jutfelt et al. 2013).  
505 These include avoidance behaviour, reversal of behavioural responses to  
506 ecologically relevant sensory cues, reduced growth and reduced feeding rates  
507 (Baumann et al. 2012; Briffa et al. 2012; Cripps et al. 2011; Dixson et al. 2009;  
508 Munday et al. 2009). This suggests that the interaction of red soil with the  
509 surrounding water can cause chemically altered environments detrimental for fish  
510 survival. In any case, these behavioural changes can be biomarkers for significant

511 biological effects of sediment pollution in marine environments (Galloway et al.  
512 2004). If the impacts on sensory cue use in recruiting larval fishes influences the  
513 recruitment success of coral reef fish populations this can have implications for both  
514 fisheries and marine park management as import and export of larvae between  
515 populations and habitats may be constrained by degraded habitat (Dixson et al.  
516 2014).

517 The concentrations of sediment used in this experiment are regularly  
518 encountered on coral reef ecosystems across the world, for example on the Great  
519 Barrier Reef, Australia, sediment concentrations are regularly recorded near the  
520 lower level used here ( $50\text{mgL}^{-1}$ ) and can exceed the higher level ( $200\text{mgL}^{-1}$ ) during  
521 the wet season or as a result of dredging (Bak 1978; Wenger and McCormick 2013).  
522 This indicates negative impacts on settlement behaviour and success of reef fish  
523 larvae may be exacerbated if sediment load influx to coral reef environments  
524 increases due to anthropogenic activities. The close proximity of acidic sediment  
525 similar to Okinawa's red soil to coral reef environments (e.g. over 600,000ha of acid  
526 sulfate soil resides within the Great Barrier Reef (GBR, Queensland) catchment  
527 alone (Powell and Martens 2005)), means that chemical effects of sediment are  
528 likely to have substantial impacts on coral reefs and their inhabitants. Future work is  
529 required to better understand these effects and how they interplay with effects of  
530 sediment-induced turbidity.

531

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698 **List of Figures**

699

700 **Fig. 1** Mean percentage of time ( $\pm$ SE) spent by *Chromis viridis* larvae in each side of the olfactory  
701 choice chamber when presented with cues from live coral with and without red soil extract at different  
702 concentrations. \*\*\*  $P < 0.001$ , N.S. no significant choice behaviour (n = 20)

703 **Fig. 2** Mean percentage of time ( $\pm$ SE) spent by *Chromis viridis* larvae in compartments close to live  
704 coral, dead coral, and in the centre in the presence of suspended sediment at different  
705 concentrations. \*\*\*  $P < 0.01$ , N.S. no significant choice behaviour between live and dead coral cues (n  
706 = 20)

707 **Fig. 3** Mean percentage of time ( $\pm$ SE) spent by reared *C. viridis* larvae when presented with live coral  
708 and dead coral soaked water after 5 days of exposure to different red soil concentrations. \*\*\*  $P <$   
709 0.05, N.S. no significant choice behaviour between live and dead coral cues (n = 10)

710 **Fig. 4** Mean body condition and feeding rates ( $\pm$ SE) for *C. viridis* after rearing in the presence of red  
711 soil compared to control conditions  $P = < 0.05$  (n= 160)

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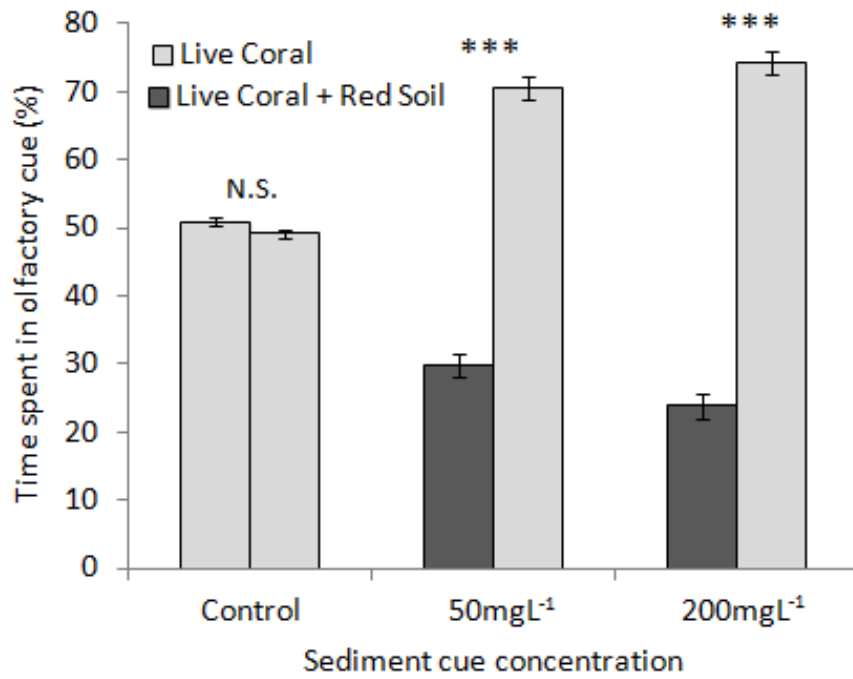
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724 Fig.1



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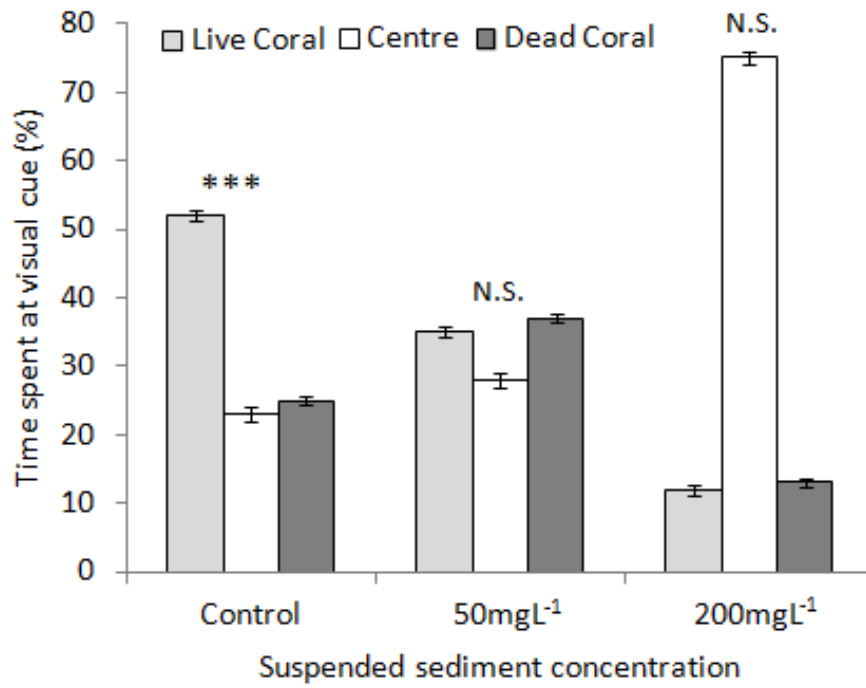
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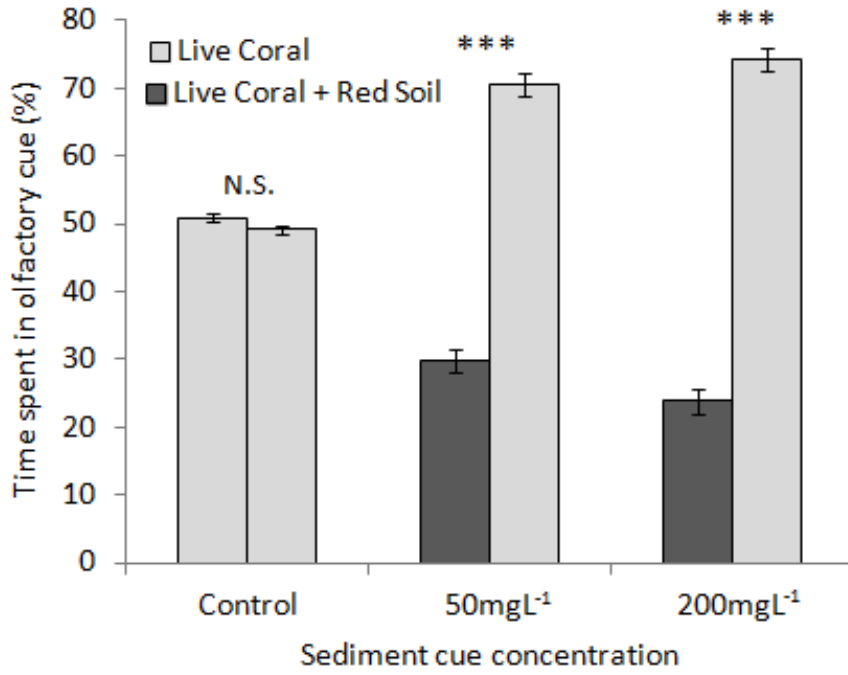
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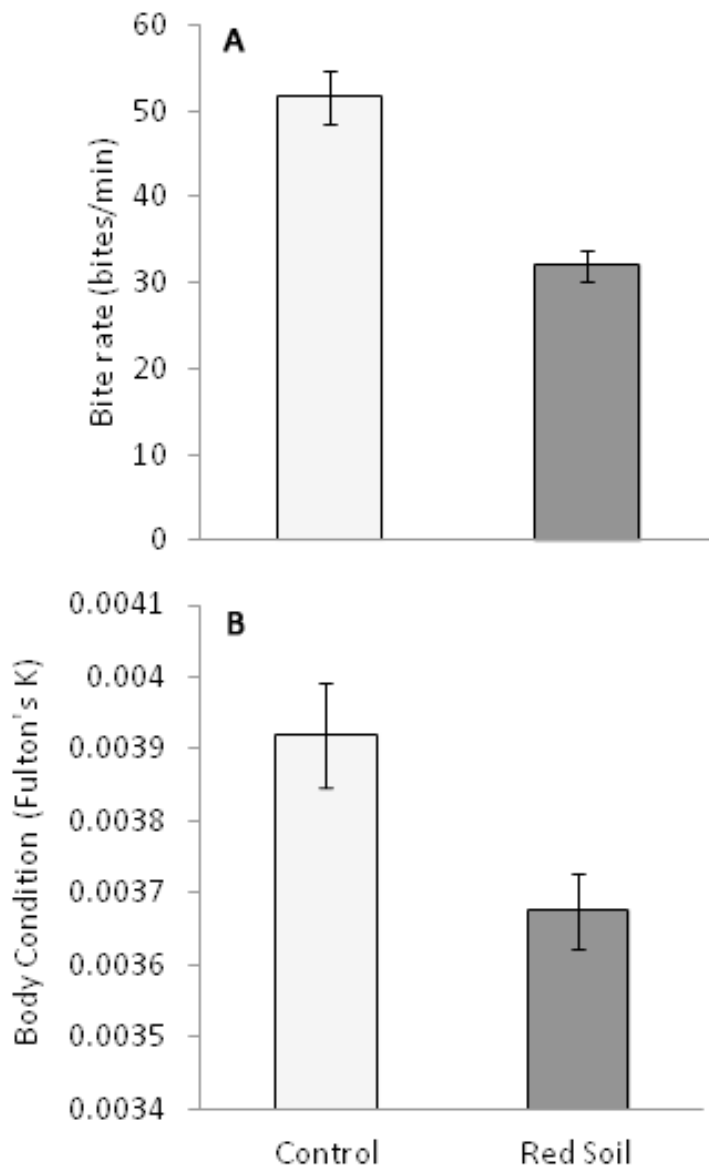
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