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1 **Species-specific impacts of suspended sediments on gill structure and function in coral**
2 **reef fishes**

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13 **Abstract**

14 Reduced water quality, in particular increasing suspended sediments, has been linked to declines in
15 fish abundance on coral reefs. Changes in gill structure induced by suspended sediments have been
16 hypothesized to impair gill function and may provide a mechanistic basis for the observed declines;
17 yet, evidence for this is lacking. We exposed juveniles of three reef fish species (*Amphiprion*
18 *melanopus*, *Amphiprion percula*, and *Acanthochromis polyacanthus*) to suspended sediments (0 -
19 180mgL⁻¹) for 7 days and examined changes in gill structure and metabolic performance (i.e. oxygen
20 consumption). Exposure to suspended sediments led to shorter gill lamellae in *A. melanopus* and *A.*
21 *polyacanthus* and reduced oxygen diffusion distances in all three species. While *A. melanopus*
22 exhibited impaired oxygen uptake upon suspended sediment exposure, i.e., decreased maximum
23 and increased resting oxygen consumption rates resulting in decreased aerobic scope, the oxygen
24 consumption rates of the other two species remained unaffected. These findings imply that species
25 sensitive to changes in gill structure such as *A. melanopus* may decline in abundance as reefs
26 become more turbid, while species that are able to maintain metabolic performance despite
27 suspended sediment exposure, such as *A. polyacanthus* or *A. percula*, may be able to persist or gain
28 a competitive advantage.

29

30

31 **Keywords: turbidity, suspended solids, dredging, fish health, coastal development, clownfish**

32

33 **1. Introduction**

34 Declining water quality is one of the leading causes of aquatic ecosystem degradation
35 globally [1, 2]. In particular, the input and resuspension of sediments are having a dramatic effect on
36 both sessile and mobile organisms [3]. Coastal development, agriculture, overgrazing, mining,
37 removal of riparian vegetation, dredging, and shipping have increased suspended sediments in
38 coastal waters over the past decades [1, 4, 5]. Continued population growth in coastal areas,
39 especially in the tropics [6], is likely to lead to further increases in suspended sediments. Increases in
40 suspended sediments have already led to biodiversity loss and fundamental changes in benthic and
41 fish assemblages on coral reefs [7-11]; however, the mechanistic basis for these declines is not fully
42 understood.

43 Declining water quality has been associated with reductions in abundance and/or diversity
44 of reef fishes on coastal reefs (e.g., Great Barrier Reef [9, 10], Caribbean [11], Pacific Islands [12,
45 13]). It is not clear, however, if these changes in fish assemblages are the result of the direct effects
46 of suspended sediments on fish behavior or physiology, and/or the indirect effects of suspended
47 sediments that manifest through the degradation of benthic habitats. The negative effects of
48 sediments on the abundance and composition of corals is well established [7, 14], and numerous
49 studies have documented declines in fish assemblages following coral loss [15, 16]. However, the
50 indirect effects of sediment-induced coral loss may be compounded by any direct impacts of
51 suspended sediments on fishes [3, 17]. For example, suspended sediments have been shown to
52 interfere with visual acuity and olfaction in some coral reef fishes, thereby affecting larval
53 settlement [18, 19] and prey capture [20-22]. Suspended sediments, however, may also have
54 important impacts on physiological processes, such as respiration, that could lead to negative effects
55 at the level of performance and fitness.

56 Most fish species rely on their gills to extract oxygen from water [23], and suspended
57 sediments and other pollutants have been hypothesized to interfere with this process [24]. Several
58 studies have shown that suspended sediments and other pollutants can irritate and damage gill
59 tissues, leading to changes in gill structure [25-28]. Specifically, exposure to suspended sediments
60 has been shown to reduce the length of gill lamellae, thereby reducing gill surface area, and to
61 damage the gill epithelium [29, 30], which is the primary site for oxygen uptake in most fishes [31].
62 To repair tissue damage and to reduce the impact of pollutants, gills often secrete mucous and grow
63 additional cell layers on the lamellae (referred to as hyperplasia), which increases the thickness of

64 the gill epithelium and oxygen diffusion distances [32, 33]. Reductions in gill surface area and
65 increases in oxygen diffusion distances are assumed to decrease the efficiency of gas exchange and
66 reduce the capacity of the gills for oxygen uptake [34, 35]. Indeed, some species are known to
67 undergo extensive modifications in gill surface area and oxygen diffusion distances to regulate ion-
68 and oxygen transport across the gills in response to changes in temperature, hypoxia, and air
69 exposure [36-41]. However, little is known as to whether changes in gill structure induced by
70 pollutants such as suspended sediments directly affect gill function and the metabolic performance
71 of fish (but see [28]).

72 The capacity to perform vital aerobic activities is tied to the capacity of the gills for oxygen
73 uptake [42, 43]. For example, the maximum rate of oxygen uptake of individuals (i.e., $\dot{M}O_{2max}$) has
74 been correlated with various activities linked to fitness and survival in fish, including locomotion and
75 competitive ability [43, 44]. Gill damage induced by suspended sediments may reduce the capacity
76 for oxygen uptake and limit oxygen delivery to tissues, especially during activities requiring high
77 levels of oxygen [45], thus compromising fish performance and ultimately reducing fitness and
78 survival of fish living on turbid reefs. The potential link between gill structure, metabolic
79 performance, and individual fitness may be an important - albeit understudied - driver of the
80 observed changes in fish assemblages with declining water quality [26, 28, 46]. Determining the
81 extent to which structural gill changes induced by suspended sediments affect the metabolic
82 performance of individual species is critical to understand current and future changes in coastal fish
83 assemblages as water quality decreases.

84 The aim of this study was to investigate whether changes in gill structure resulting from
85 exposure to suspended sediments will compromise gill function and metabolic performance of
86 juvenile coral reef fishes, thereby providing a mechanistic link between declining water quality and
87 fish health. To do so, we examined the effects of a range of ecologically relevant suspended
88 sediment concentrations on the gill morphology and oxygen consumption rates of three common
89 damselfish species using histology and intermittent-flow respirometry, respectively. The suspended
90 sediment concentrations used reflect those currently experienced on inshore reefs of the Great
91 Barrier Reef during re-suspension events such as currents, waves, and flood plumes [47, 48]. These
92 suspended sediment concentrations are likely to become more frequent in the future as population
93 growth, coastal development, and associated terrestrial run-off in tropical coastal areas rapidly
94 increase [2, 6].

95

96

97 2. Methods

98 *Experimental protocol*

99 Larvae of *Amphiprion melanopus* (cinnamon clownfish), *Amphiprion percula* (false orange
100 clownfish), and *Acanthochromis polyacanthus* (spiny chromis) were sourced from captive breeding
101 pairs between January and May 2016 and maintained until experimentation (see Supplemental
102 Materials for detailed description). At 30 days after hatching, juvenile *A. melanopus* and *A.*
103 *polyacanthus* were randomly assigned to one of five suspended sediment concentrations (i.e., 0, 45,
104 90, 135 or 180 mgL⁻¹) corresponding to turbidity levels of 0.5 ± 0.5, 7.0 ± 2.7, 14.2 ± 3.0, 21.3 ± 3.4,
105 and 30.1 ± 3.7 NTU, respectively. Juvenile *A. percula* were randomly allocated to one of three
106 suspended sediment concentrations (i.e., 0, 135 or 180 mgL⁻¹) due to the limited number of larvae
107 available. Water temperature was maintained at 28.5 ± 0.5°C for all fish. For each of the three
108 species, four to six replicate aquaria were established for each of the suspended sediment
109 concentrations, and five randomly selected individuals were placed in each aquarium. Fish were
110 maintained in the experimental aquaria for seven days and fed with flakes NRD 0.5 – 0.8 mm (Pro
111 Aqua Pty Ltd) twice daily. Sediments were re-suspended in external sumps and delivered to aquaria
112 via submersible pumps (figure S1, see also supplementary materials for further information).
113 Australian bentonite, a clay with a small particle size range (< 63 µm) and representative of
114 sediments found in suspension on the Great Barrier Reef [49], was used as the sediment. The
115 selected suspended sediment concentrations, turbidity levels, and length of exposure to suspended
116 sediments (i.e., 7 days) represent conditions that are currently observed on inshore reefs of the GBR
117 during regular re-suspension events (e.g., waves and currents) and periodic events, such as flood
118 plumes [47, 48, 50].

119

120 *Gill histology*

121 Following respirometry trials to measure oxygen consumption rates (see below), twelve
122 individuals (out of 20 exposed individuals) for each species and sediment treatment were randomly
123 selected for histological analyses. These fish were euthanized in an ice-water slurry, fixed in Bouin's
124 solution for 24-48 hours, and then transferred to 70% ethanol. Fish were then serially dehydrated
125 (Shandon Southern Duplex Processor BS5), embedded in paraffin wax blocks (Shandon Histocentre
126 3, Thermo Electron Corporation), and sectioned (5 µm thick) longitudinally with a microtome.
127 Sections (5 µm thick) were stained with Mayer's Haematoxylin and Eosin to allow the primary gill
128 filaments, secondary lamellae, gill epithelium, and supporting pillar cell system to be distinguished

129 visually (figure S2). Lamellae were photographed (Olympus DP12 Microscope Digital Camera System)
130 at 400x magnification, and 15 randomly selected lamellae per fish were analyzed in ImageJ (Version
131 1.48, National Institute of Health, USA).

132 Morphological features of the lamellae (i.e., total and functional lamellar length, filament
133 thickness, and thickness of the lamellar epithelium/oxygen diffusion distance) were measured
134 following [26] (figure S3a-c). In brief, total length of lamellae was measured from the tip of the
135 lamellae to the base (including the filament epithelium) and functional length from the tip to the
136 edge of the filament epithelium (figure S3a). The thickness of the filament epithelium was measured
137 in between two lamellae (figure S3a). The total area of the lamellae and the area of the pillar cell
138 system of the functional lamellar length was measured, and the difference between the two was
139 divided by twice the functional length to determine oxygen diffusion distance (figure S3c) [26]. Note
140 that the oxygen diffusion distance is different from the thickness of the lamellar epithelium, as it
141 includes non-tissue space caused by epithelial lifting (i.e., detachment of the epithelium from the
142 pillar cell system, [51]). All filaments were analyzed blindly with respect to treatments.

143

144 *Oxygen consumption rates*

145 Oxygen consumption rates ($\dot{M}O_2$) of individuals were determined using intermittent-flow
146 respirometry [52]. Prior to respirometry, each fish was fasted for 24 hours to ensure a post-
147 absorptive state [53]. Then, each individual fish was manually chased in a circular container (60 cm
148 diameter, 10 cm water depth) until exhaustion [54]. Individuals were deemed exhausted when they
149 no longer displayed burst swimming, which always occurred within 2 - 3 min. This method assumes
150 that maximum oxygen uptake rates are achieved while fish recover from exhaustive anaerobic
151 exercise [55]. Upon exhaustion, fish were placed immediately into their respective respirometry
152 chambers (15.7 ml volume including tubing) and left to recover for 3 hours (see Supplementary
153 Materials for detailed description) while oxygen levels were continuously recorded. While adult fish
154 are usually monitored over 24 hours [56], smaller fish recover much faster from exhaustive exercise
155 and are commonly measured for 2 - 3 hours only to minimize stress and risk of starvation (e.g. [57,
156 58]). Flush pumps supplied each chamber with (clear) aerated, UV-filtered seawater from the
157 surrounding water bath every 10 min for 2 min, thus preventing oxygen levels from falling below
158 90% air saturation. Recirculation pumps ensured homogenous oxygen tensions throughout
159 chambers [56]. Background microbial respiration in empty chambers was measured before and after
160 each trial [56]. After the trial, fish were euthanized in an ice-water slurry, blotted dry, and fish
161 standard length (to the nearest mm) and mass (to the nearest 0.001 g) were recorded. Fish length

162 and mass (mean \pm SE), respectively, were as follows: *A. melanopus*, 13.5 \pm 0.3 mm and 98 \pm 6 mg; *A.*
163 *polyacanthus*, 17.6 \pm 0.3 mm and 174 \pm 8 mg; *A. percula*, 19.1 \pm 0.3 mm and 153 \pm 6 mg.

164 Oxygen consumption rates (mg O₂ h⁻¹) during closed respirometry phases (i.e., non-flushing)
165 were calculated using linear least square regression in Labchart v. 6.1.3 (ADInstruments, Dunedin,
166 New Zealand). Background microbial respiration was subtracted from total respiration in chambers
167 to derive oxygen consumption rates of fish [56]. The highest value of oxygen consumption rates (30s
168 intervals) after exercise was taken as maximum oxygen consumption rate and usually occurred
169 during the first measurement cycle. Resting oxygen consumption rate was estimated as the mean of
170 the lowest 10% of all values, excluding outliers below or above 2 standard deviations [56]. Aerobic
171 scope was calculated as the difference between maximum and resting oxygen consumption rate (see
172 [57]).

173

174 *Statistical analyses*

175 All analyses were performed in R (v. 3.3.2, R Core Team 2013). Linear and generalized linear
176 mixed models (lme4 package, [59]) were used to analyze the effects of suspended sediment
177 concentrations on gill morphology. Total and functional lamellar length, and oxygen diffusion
178 distance were used as dependent variables, sediment treatment as a fixed effect and standard
179 length of fish as covariate, allowing for interactions between treatments and standard length.
180 Standard length was mean-centered to help with the interpretation of model intercepts. Fish
181 identity was included as random factor to account for repeated measurements per fish. Assumptions
182 of normality and homogeneity of residuals were visually assessed with Q-Q plots and frequency
183 distributions. Parameters were estimated using Restricted Maximum Likelihood, and *P*-values were
184 generated using Kenward-Rogers approximation [60]. If residuals of models did not meet
185 assumptions, generalized linear mixed models were used with a gamma distribution and log-link
186 function. Residuals were assessed for homogeneity, and checked for overdispersion. Parameters
187 were estimated using Laplace approximation, and *P*-values were generated using Wald Z test [60].
188 Interactions between the fixed factor and the covariate were dropped when not significant. The
189 effects of suspended sediments on oxygen consumption rates were analyzed using linear or
190 generalized linear models as described above. Maximum and resting oxygen consumption rates, and
191 aerobic scope (in mg O₂ h⁻¹) were dependent variables, sediment treatment was a fixed effect, and
192 body mass a covariate. Clutch identity was included as a random effect with random intercepts.

193 To display results visually, intercepts and standard errors produced by the model (i.e. after
194 correcting for fish size or mass) were plotted for each treatment. Parameters on log-scales were
195 transformed to facilitate visual interpretation.

196

197 **3. Results**

198 *Gill structure*

199 Exposure to suspended sediments significantly altered the gill structure of all three species
200 investigated, with the extent of the changes varying among species and suspended sediment
201 concentrations. Total lamellar length (see Supplementary Materials) and functional length of the
202 lamellae of both *A. melanopus* and *A. polyacanthus* were shorter following exposure to sediments,
203 while no changes were observed for *A. percula*. For *A. melanopus*, the functional lamellae length was
204 on average between 20.5% and 29.6% shorter exposed to any of the four suspended sediment
205 concentrations when compared to gills from control fish (45 mgL⁻¹: $t = -2.02$, $p = 0.0436$, 90 mgL⁻¹: t
206 $= -2.25$, $p = 0.0245$, 135 mgL⁻¹: $t = 3.62$, $p = 0.0002$, 180 mgL⁻¹: $t = -3.04$, $p = 0.002$, figure 1a, table S1).
207 For *A. polyacanthus*, functional lamellar length was on average between 21.7% and 30.6% shorter
208 upon exposure to three of four suspended sediment concentrations when compared to control fish
209 (45 mgL⁻¹: $t = -3.26$, $p = 0.0011$, 135 mgL⁻¹: $t = -3.07$, $p = 0.0021$, 180 mgL⁻¹: $t = -2.20$, $p = 0.027$, figure
210 1a, table S2).

211 All three species exhibited significant reductions in oxygen diffusion distances upon
212 suspended sediment exposure (figure 1b, tables S1-S3). In *A. melanopus*, oxygen diffusion distance
213 was reduced by 24.1% and 28.8%, respectively, in fish exposed to the two highest suspended
214 sediment concentrations (135 mgL⁻¹: $t = -1.96$, $p = 0.049$, 180 mgL⁻¹: $t = -2.28$, $p = 0.02$, figure 1b,
215 table S1). Similarly, oxygen diffusion distance was between 24.9% and 28.8% shorter in *A.*
216 *polyacanthus* exposed to three of four suspended sediment concentrations when compared to
217 control fish (45 mgL⁻¹: $t = -2.68$, $p = 0.007$, 135 mgL⁻¹: $t = -2.69$, $p = 0.007$, 180 mgL⁻¹: $t = -2.20$, $p =$
218 0.02 , figure 1b, table S2). In *A. percula*, reductions in oxygen diffusion distance by as much as 18.3%
219 were evident in fish from both examined suspended sediment treatments (135 mgL⁻¹: $t = -2.12$, $p =$
220 0.04 , 180 mgL⁻¹: $t = -3.25$, $p = 0.003$, figure 1b, table S3).

221

222 *Oxygen consumption rates*

223 Despite the observed changes in gill morphology in all three species of fish exposed to
224 suspended sediments, oxygen consumption rates were only affected in one of the three species (*A.*

225 *melanopus*). Specifically, maximum oxygen consumption rates were reduced by as much as 17.5%
226 following exposure to the two highest suspended sediment concentrations relative to control fish
227 (135 mgL^{-1} : $t = -2.39$, $p = 0.016$, 180 mgL^{-1} : $t = -2.01$, $p = 0.044$), but no changes were evident in fish
228 exposed to 45 or 90 mgL^{-1} (figure 2a, table S4). Resting oxygen consumption rates in *A. melanopus*
229 were elevated on average by 36.3% to 64.3% for three of the four suspended sediment
230 concentrations when compared to control fish (45 mgL^{-1} : $t = 2.92$, $p = 0.004$, 90 mgL^{-1} : $t = 3.00$, $p =$
231 0.003 , 180 mgL^{-1} : $t = 2.61$, $p = 0.011$, figure 2a, table S4). Reflecting changes in maximum and resting
232 oxygen consumption rates, aerobic scope was reduced by as much as 39.3% in fish upon exposure to
233 all suspended sediment concentrations when compared to control fish (45 mgL^{-1} : $t = -2.42$, $p =$
234 0.015 , 90 mgL^{-1} : $t = -2.60$, $p = 0.009$, 135 mgL^{-1} : $t = -3.85$, $p = 0.001$, 180 mgL^{-1} : $t = -2.31$, $p = 0.020$,
235 figure 2b, table S4). No effects on maximum or resting oxygen consumption rates or aerobic scope
236 were detected for *A. polyacanthus* or *A. percula* exposed to suspended sediments (tables S5 & S6).

237 To further explore the connection between oxygen consumption rates and changes in gill
238 morphology, we analyzed the relationship between aerobic scope and the squared mean functional
239 lamellar length (as a proxy for gill surface area) of *A. melanopus* using linear regressions. Separate
240 analyses were used for *A. melanopus* exposed to 0 and 180 mgL^{-1} suspended sediments. While there
241 was a significant correlation between aerobic scope and squared mean functional lamellar length in
242 *A. melanopus* juveniles exposed to control conditions ($R^2 = 0.34$, $F_{1,13} = 6.82$, $p = 0.02$), these two
243 variables were not significantly correlated in juveniles exposed to 180 mgL^{-1} suspended sediments
244 ($R^2 = 0.00$, $F_{1,8} = 0.03$, $R^2 = 0.00$, $p = 0.85$).

245

246 4. Discussion

247 Changes in the gill structure of fishes exposed to elevated suspended sediment
248 concentrations have been hypothesized to reduce metabolic performance and thereby lead to
249 declines in the diversity and abundance of fish assemblages on turbid reefs [26, 28, 46]. Our results
250 confirm that short-term exposure to suspended sediments led to changes in the gill structure of all
251 three examined species; however, these morphological changes only translated to impaired
252 metabolic performance (i.e., oxygen consumption rates) in one species (*A. melanopus*). These
253 findings imply that species that are sensitive to changes in gill structure such as *A. melanopus* may
254 decline in abundance as reefs become more turbid, while species that are able to maintain
255 metabolic performance despite suspended sediment exposure, such as *A. polyacanthus* or *A.*
256 *percula*, may be able to persist or gain a competitive advantage. Our results highlight that suspended

257 sediment can have direct physiological consequences for some coral reef fish and provide further
258 insight into how reduced water quality can shape coral reef communities.

259 The interspecific variation in the effect of suspended sediment exposure on oxygen uptake
260 rates observed in this study may be related to differences in environmental tolerances among
261 species. Following suspended sediment exposure, *A. melanopus* exhibited increases in resting
262 oxygen consumption rates and reductions in both maximum oxygen consumption rates and aerobic
263 scope. In contrast, the congener *A. percula* and confamilial *A. polyacanthus* both maintained oxygen
264 uptake rates despite similar changes in gill structure. The widespread distribution pattern of *A.*
265 *polyacanthus* spanning both turbid inshore and clear offshore reefs may explain the high tolerance
266 of this species to suspended sediments [61]. The differential responses of the closely related *A.*
267 *percula* and *A. melanopus*, however, is counter to expectations based on their current distributions.
268 While the current distribution of *A. melanopus* includes turbid reefs [62], this species was the most
269 heavily affected by suspended sediments in the present study. In contrast, the species least affected
270 by suspended sediments, *A. percula*, is typically rare in turbid environments [61], and the effects of
271 suspended sediments on gills may hence not influence the distribution of this species.
272 Understanding which species are sensitive versus those that are tolerant to changes in suspended
273 sediment concentrations will be critical for the effective conservation of inshore coral reefs.

274 Our results document that juvenile *A. melanopus* exposed to elevated suspended sediment
275 concentrations had a reduced capacity for oxygen uptake, as indicated by reductions in maximum
276 oxygen consumption rates (i.e. $\dot{M}O_{2max}$). This may have been the result of gill damage, leading to the
277 observed reductions in lamellar length and thus a reduction in gill surface area available for gas
278 exchange. Aerobic scope was positively correlated with the squared functional lamellar length (as a
279 proxy for gill surface area) in control fish, supporting the idea that the reduction in $\dot{M}O_{2max}$ may have
280 been caused by gill damage. Interestingly, there was no significant relationship between aerobic
281 scope and functional lamellar length in fish upon suspended sediment exposure. The reasons for this
282 are currently not known; however, it is important to note that *A. melanopus* also showed reductions
283 in oxygen diffusion distances in response to suspended sediments; this would have been likely to
284 enhance oxygen uptake efficiency, i.e. it may have compensated partly for reductions in gill surface
285 area [35] and may have weakened the relationship between aerobic scope and functional lamellar
286 length. An alternative hypothesis for the drivers of the observed reduction in $\dot{M}O_{2max}$ could be that
287 suspended sediment exposure may have elicited a stress response, which may have influenced
288 $\dot{M}O_{2max}$. However, there is limited information available on the effects of stress on $\dot{M}O_{2max}$.
289 Considering the multiple stressors that fish experience on degraded reefs, this would be an
290 interesting avenue for further research. Regardless of the underlying mechanisms, a reduced $\dot{M}O_{2max}$

291 suggests that oxygen delivery to tissues may be insufficient during activities with elevated oxygen
292 demand, such as during swimming [43, 63].

293 Individuals exposed to suspended sediments exhibited increased oxygen consumption at
294 rest (i.e., $\dot{M}O_{2rest}$), which is commonly observed in fish exposed to poor water quality (e.g. [64-66]).
295 This finding indicates that inhabiting areas with elevated suspended sediments incurs an energetic
296 cost. The increase in $\dot{M}O_{2rest}$ may have been the result of a stress response, behavioral and
297 physiological acclimation to suspended sediments, tissue repair at the gills, an enhanced immune
298 response, and/or inefficient oxygen uptake [67, 68]. Further, the reduction in aerobic scope of *A.*
299 *melanopus* exposed to suspended sediments suggests a compromised capacity to perform vital
300 aerobic activities, such as growth, development, and locomotion [69]. A reduction in aerobic scope
301 may be especially problematic in juvenile fish, which exhibit exceptionally high growth rates [70] but
302 low survival rates [71]. Factors that reduce growth or survival during early life history stages can
303 have strong effects on recruitment patterns [72, 73]. While *A. melanopus* is common on turbid reefs
304 today [64], our findings suggest that this species could decline in abundance as suspended
305 sediments continue to increase into the future, or may shift to alternative/less suitable habitats (e.g.
306 reefs further offshore). Any potential habitat shifts by *A. melanopus* are likely to increase
307 competition among anemonefish species for host anemones in these habitats, and (depending on
308 the outcomes) may interfere with the other species' niche rangers.

309 In contrast to *A. melanopus*, exposing juvenile *A. percula* to suspended sediments had no
310 detectable effect on the lamellar length and hence, surface area for gas exchange, or oxygen
311 consumption rates. This is counter to expectations, given the current distribution of *A. percula*. The
312 reason why *A. percula*, unlike *A. melanopus* and *A. polyacanthus*, did not exhibit any reductions in
313 lamellar length upon suspended sediment exposure remains unclear. However, *A. percula* juveniles
314 were on average larger in size than *A. melanopus* and *A. polyacanthus*, and may thus potentially
315 have been more tolerant [3]. Regardless of the underlying mechanism, these findings highlight that
316 there are inter-specific variations in response to suspended sediments. Considering the limited
317 impact of suspended sediments on the physiology of *A. percula* in the present study, its absence on
318 turbid reefs is most likely driven by other factors, such as the habitat preferences of its primary host,
319 the sea anemone, *Heteractis magnifica*, which requires clear water [61]. However, the present study
320 may have underestimated the effects of suspended sediments on oxygen consumption rates of fish.
321 It is well known that suspended sediments adhere to the mucous layer on the gill epithelium [24]; it
322 was not possible in the present study to examine whether this may have reduced oxygen uptake,
323 since oxygen consumption rates were determined in the absence of suspended sediments. It will be
324 important for future studies to examine whether the presence of suspended sediments may affect

325 oxygen uptake, and whether this may compound the negative effects of gill changes induced by
326 suspended sediments.

327 Following exposure to elevated suspended sediments, *A. polyacanthus* exhibited similar
328 changes in gill structure (i.e., reduced functional lamellar length) to *A. melanopus*; however, these
329 changes did not translate to any negative effects on metabolic performance, and the reasons behind
330 this are currently unclear. As mentioned above, it is possible that the observed reductions in oxygen
331 diffusion distances (i.e., a thinner gill epithelium) may have compensated for declines in oxygen
332 uptake due to reductions in surface area. Further, oxygen uptake capacity is also influenced by
333 factors other than gill structure, including haemoglobin oxygen carrying capacity and affinity, heart
334 rate, stroke volume, and cardiac output [34, 74]; some or all of these traits may have also been
335 modified to enhance oxygen transport. It is also possible that the capacity for oxygen uptake at the
336 gills in this species may be much higher than either the capacity to deliver oxygen to tissues or the
337 maximum oxygen demand of tissues [40, 75]. Not all species perfuse all of the available lamellae,
338 and thus do not use their gill surface area to its full potential [76, 77]. This may allow them to
339 tolerate some gill damage without adversely affecting oxygen uptake [28]. While the underlying
340 mechanisms are not fully resolved, it is likely that the ability to tolerate or compensate for changes
341 in gill structure may allow *A. polyacanthus* to persist on reefs that become increasingly more turbid,
342 which could provide an important competitive advantage to this species.

343 The underlying mechanisms that led to a reduction in oxygen diffusion distances upon
344 suspended sediment exposure in all three species are not clear. The onset and intensity of gill
345 changes in response to suspended sediments varies considerably between species, life-stages,
346 angularity of sediment particles, sediment concentration, and exposure duration [3, 78, 79]. The
347 reported structural changes induced by suspended sediments, however, are nonspecific [24, 51],
348 and the majority of studies examining the effects of prolonged exposure to suspended sediments (>
349 3 days) have documented the growth of protective cell layers, i.e. an increase - rather than a
350 decrease - in oxygen diffusion distances (e.g. [28, 30, 80]). For example, an increase in oxygen
351 diffusion distances was observed in a previous study on settlement-stage *A. percula* exposed to the
352 same sediment type, exposure duration, and concentration (yet at an earlier developmental stage)
353 as used in the present study [26]. The only study that has reported a reduction in oxygen diffusion
354 distances in response to prolonged suspended sediment exposure (6 weeks) examined this in green
355 grouper (*Epinephelus coioides*), a coral reef fish living on turbid inshore reefs [25]. The observed
356 reductions in oxygen diffusion distances in green grouper and the three coral reef fishes examined in
357 the present study may have been caused by tissue abrasion [25]. However, when exposed to hypoxia
358 [24, 36], elevated temperatures [37], air [38, 39] and even some pollutants [81], some fish species

359 are known to actively alter oxygen diffusion distances to regulate oxygen uptake. As suggested by
360 [25], the observed reductions in oxygen diffusion distances may have thus been the result of a re-
361 arrangement of cell layers to enhance oxygen uptake, rather than gill damage (see also [40, 41, 81]).
362 Regardless of the underlying mechanisms, reductions in oxygen diffusion distances may enhance the
363 susceptibility of fish to parasites and pathogens and may interfere with ion- and osmoregulation
364 [41].

365

366 **5. Conclusion**

367 Up to half of the world's coral reefs are threatened by poor water quality [82], with
368 continued and rapid expansions of coastal human populations likely to exacerbate the inputs and
369 resuspension of terrestrial sediments [2, 6]. Identifying the mechanisms that drive changes in coral
370 reef fish assemblages in response to human impacts is of key interest for the conservation of coral
371 reefs [83, 84]. Our findings suggest that *A. melanopus*, a species frequently found on turbid reefs
372 today [61], may decline in abundance or disappear from turbid reefs as suspended sediments
373 increase, due to the impacts of suspended sediments on the oxygen uptake rates of juveniles. Other
374 species, such as *A. polyacanthus* or *A. percula*, may be insensitive to short-term exposure to
375 suspended sediments and may remain unaffected or even gain a competitive advantage under
376 certain conditions. However, while juvenile *A. polyacanthus* and *A. percula* did not suffer any
377 reductions in metabolic performance upon suspended sediment exposure, the observed changes in
378 gill structure may potentially compromise their capacity to cope with other environmental factors
379 that affect oxygen demand or oxygen availability, such as increasing water temperatures, ocean
380 acidification or falling oxygen levels caused by climate change [85]. The combined effects of
381 suspended sediments, elevated temperature and hypoxia on gill structure and function of reef fish
382 will thus be important to consider in future studies. The present study shows that investigating the
383 effects of suspended sediments on physiological processes plays an important role in the
384 identification of winners and losers under future suspended sediment conditions and can provide
385 crucial information for the conservation of coral reefs.

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390 **Figure captions**

391 **Figure 1.** Effects of suspended sediments on **a)** functional lamellar length and **b)** oxygen diffusion
392 distance in *A. melanopus* (black circles), *A. polyacanthus* (white circles), and *A. percula* (black and
393 white circles). Circles and bars represent intercepts and standard errors, respectively, as estimated
394 by general- and linear mixed models after accounting for fish length. Asterisks indicate significant
395 differences when compared to the control group at $\alpha < 0.05$.

396 **Figure 2.** Effects of suspended sediments on oxygen consumption of *A. melanopus*. **a)** Maximum
397 oxygen consumption rates ($\dot{M}O_{2max}$, black circles) and resting oxygen consumption rates ($\dot{M}O_{2rest}$,
398 white circles), and **b)** aerobic scope. Circles and bars represent intercepts and standard errors,
399 respectively, as estimated by general- and linear mixed models after accounting for fish mass.
400 Asterisks indicate significant differences when compared to the control group at $\alpha < 0.05$.

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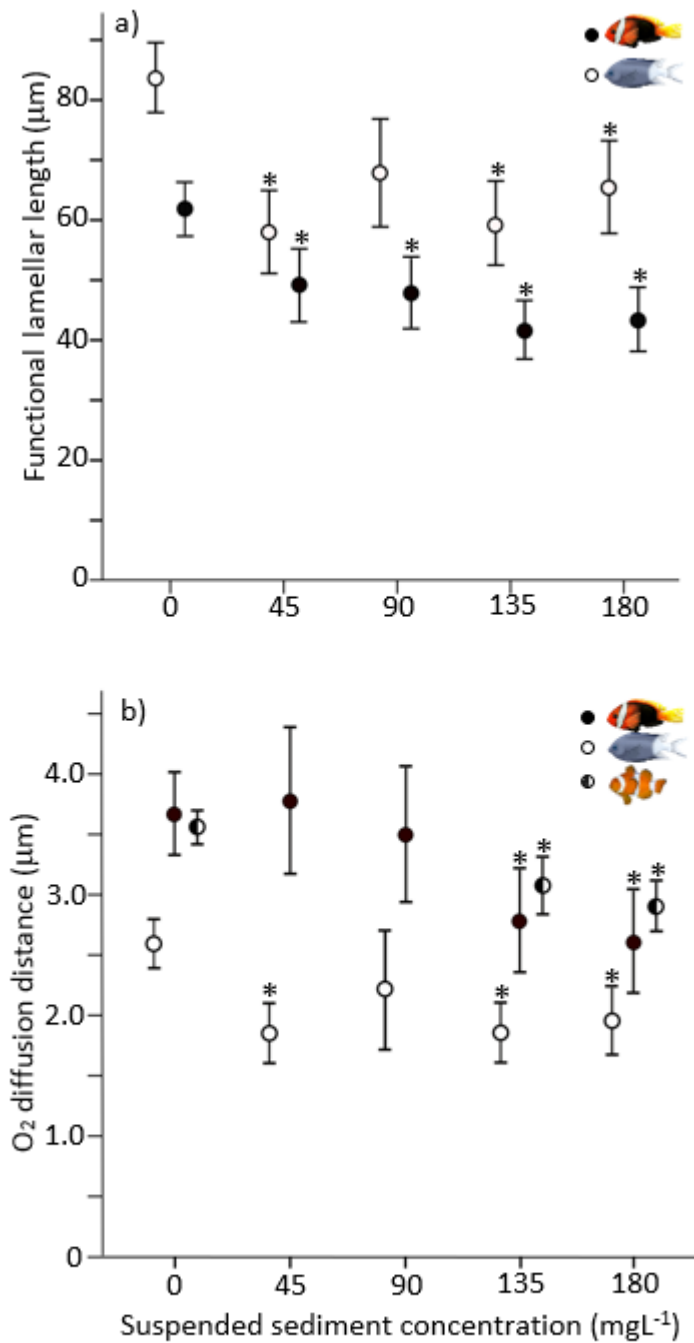


Figure 1.

420

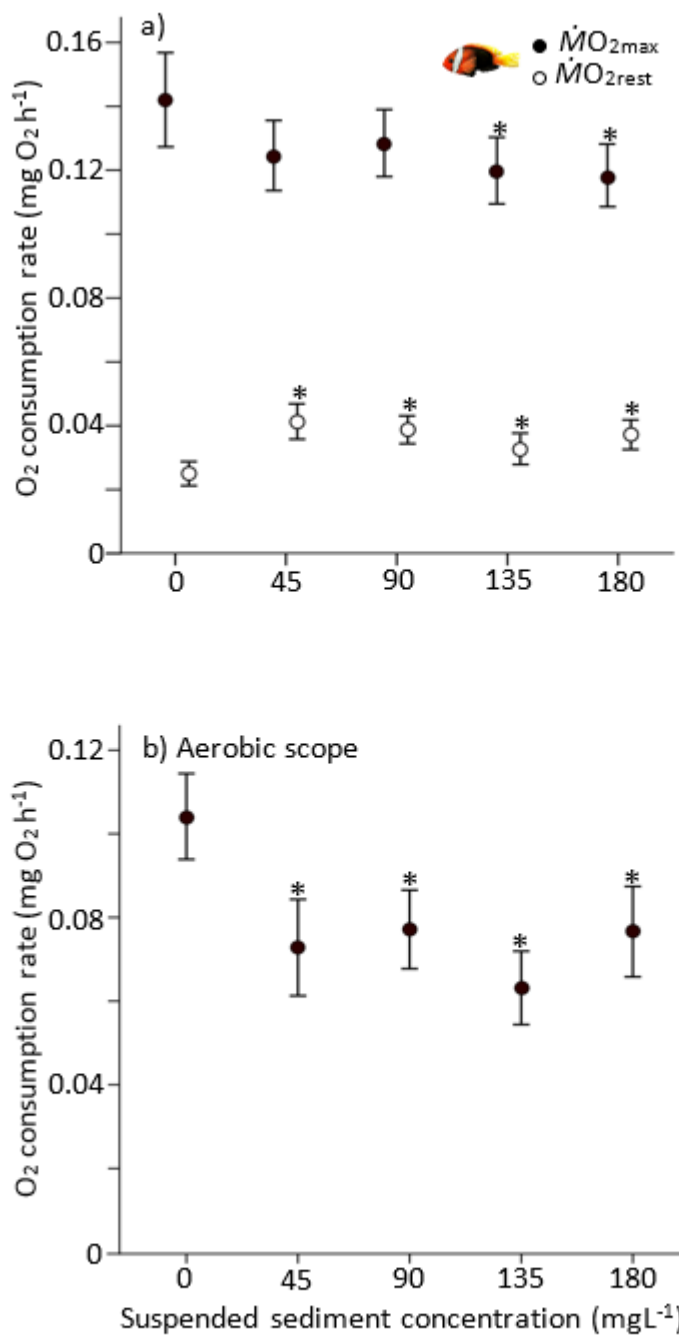


Figure 2.

422

423 **Datasets**

424 Datasets used in this article have been archived in the Research Data Repository (Tropical Data Hub)
425 at James Cook University. Please note that the data is currently under embargo. A DOI has been
426 reserved [86], which will be activated on publication. The datasets can be accessed from the
427 following link:

428 <https://cloudstor.aarnet.edu.au/plus/index.php/s/fsNjcmCyRwDmOXC>

429 **Ethics statement**

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

433 **Competing interests**

434 The authors have no competing interests.

435 **Author contributions**

436 SH, ALH, ASW, JLR conceived and designed the study; SM, SH raised fish; SH conducted experiments
437 and performed respirometry; LP analyzed gill morphology; SH carried out the statistical analyses; all
438 authors wrote the manuscript and gave final approval.

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