1 **The influence of thermal extremes on coral reef fish behaviour in the**

2 **Persian Gulf**

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Abstract

Despite increasing environmental variability within marine ecosystems, little is known about how coral reef fish species will cope with future climate scenarios. The Arabian/Persian Gulf is an extreme environment, providing an opportunity to study fish behaviour on reefs with seasonal temperature ranges which include both values above the mortality threshold of Indo-Pacific reef fish, and values below the optimum temperature for growth. Summer temperatures in the Gulf are comparable to those predicted for the tropical ocean by 2090-2099. Using field observations in winter, spring and summer, and laboratory experiments, we examined the foraging activity, distance from refugia and resting time of *Pomacentrus trichrourus* (pale-tail damselfish). Observations of fish behaviour in natural conditions showed that individuals substantially reduced distance from refugia and feeding rate and increased resting time at sub-optimal environmental temperatures in winter (average SST = 21°C) and summer (average SST = 34°C), while showing high movement and feeding activity in spring (average SST= 27°C). Diet was dominated by plankton in winter and spring, while fish used both plankton and benthic trophic resources in summer. These findings were corroborated under laboratory conditions: in a replicated aquarium experiment, time away from refugia and activity were significantly higher at 28°C (i.e., spring temperature conditions) compared to 21 °C (i.e., winter temperature conditions). Our findings suggest that *P. trichrourus* may have adapted to the Arabian/Persian Gulf environment by downregulating costly activity during winter and summer and upregulating activity and increasing energy stores in spring. Such adaptive behavioural plasticity may be an important factor in the persistence of populations within increasing environmentally variable coral reef ecosystems.

Introduction

Over the last century sustained climate change has resulted in an average global sea surface temperature increase of 0.6°C, with predictions of further 4.0°C rises by 2100 (Collins et al. 2013; IPCC 2014). As the planet warms, the occurrence of extreme weather events will also increase (IPCC 2012) and, as the world's oceans absorb 93% of excess heat trapped by greenhouse gases (Laffoley and Baxter 2016), this will have major consequences for the biodiversity, functional structure and productivity of marine ecosystems (Folguera et al. 2011; Doney et al. 2012; Bellard et al. 2012; Thornton et al. 2014; Pecl et al. 2017). Alterations have already being documented in the diversity and assemblage structure in temperate seaweed and seagrass ecosystems (Wernberg et al. 2013; Vergés et al. 2014), coral reefs (Hughes et al. 2018) and costal temperate rocky reefs (Lejeusne et al. 2010; Albouy et al. 2014). Despite this, our understanding of the capacity for marine ecosystems to resist or show resilience to climate change is limited (Côté and Darling 2010).

Coral reefs are particularly susceptible to a range of natural and anthropogenic disturbances that have resulted in degradation and loss of coral on a global scale in recent decades (Wilkinson 1999; Cheal et al. 2017; Hughes et al. 2018). While these disturbances are clearly significant for the corals that serve as the biogenic engineers of these ecosystems, diverse and ecologically important reef-associated fish assemblages also often exhibit dramatic changes in composition and abundance with increasing environmental variation (Day et al. 2018; Richardson et al. 2018; Gordon et al. 2018). Indeed, in addition to susceptibility to habitat loss (Pratchett et al. 2018), coral reef fishes are also directly threatened by ocean warming due to their narrow thermal tolerance range (Tewksbury et al. 2008; Sunday et al. 2011). Experimental evidence suggests that coral reef fish may already be living close to their upper thermal limits (Rummer et al. 2014) and that population structure may be directly impacted by increased variability in water temperature (Folguera et al. 2011; Pratchett et al. 2015; Rodgers et al. 2018).

One of the primary responses to environmental temperature change is modification of behaviour, with the speed and scope of behavioural adjustment potentially determining survival (Tuomainen and Candolin 2011; Wong and Candolin 2015). Tropical reef fishes, however, have evolved in quite thermally stable environments and may have little ability to adjust their behaviour adaptively (Candolin 2018). Furthermore, as fish metabolism and

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85   neurophysiology are directly influenced by temperature (Pörtner and Farrell 2008; Pörtner et

86   al. 2010), environmental temperatures outside an individual's optimum range may have a

87   pervasive effect on ecological performance and survival via non-adaptive (dysfunctional)

88   modification of behaviour, altering individual feeding rate, risk-taking behaviour, activity

89   levels and habitat use (Figueira et al. 2009; Nagelkerken and Munday 2016). Despite this, a

90   growing body of research suggests adaptive behavioural plasticity in response to temperature

91   increases in coral reef fishes, often through temporary reductions in aerobically-costly

92   behaviours (i.e. activity and feeding) associated with increased (short-term) environmental

93   variance (Nowicki et al. 2012; Johansen et al. 2014; Scott et al. 2017; Chase et al. 2018).

94   Nevertheless, how well coral reef fishes will cope with ocean warming scenarios (ICCP

95   2014), and by what mechanisms, is still generally poorly understood.

96

97   One approach to understanding how individuals may behaviourally respond to environmental

98   variance is to study contemporary communities that exist within naturally variable

99   environments. The fauna associated with the high latitude reefs of the southern

100   Arabian/Persian Gulf (hereafter the 'Gulf') provide a natural test of the impact of extreme

101   water temperature variation on coral reef fish behaviour (Feary et al. 2010; Burt et al. 2011b).

102   The Gulf experiences the highest annual change in water temperature for coral reefs globally

103   (winter: <15°C, summer: >35°C), with fishes persisting for several months in conditions that

104   would be considered lethal to reef fishes in other parts of the world (Riegl and Purkis 2012;

105   Vaughan et al. 2019). Summer temperatures in the Gulf exceed the upper thermal limits of

106   most tropical reef fishes (Nilsson et al. 2009; Munday et al. 2009; Rummer et al. 2014;

107   Rodgers et al. 2018), while winter temperatures are well below the optimum temperatures

108   reported for reef fish elsewhere in the Indo-Pacific (Eme and Bennett 2008; Figueira and

109   Booth 2010; Nakamura et al. 2013). Indeed, contemporary summer water temperatures in the

110   Gulf are comparable to those predicted for tropical oceans at the end of this century (Riegl

111   and Purkis 2012; IPCC 2014), while winter conditions can be so severe as to induce cold

112   water coral bleaching (Shinn 1976; Coles et al. 1991).

113

114   Using a combination of *in situ* field observations and *ex situ* experimental manipulations, this

115   study examined the influence of extreme thermal variability on reef fish behaviour in the

116   southern Gulf. Using the locally abundant *Pomacentrus trichrourus* (pale-tail damselfish;

117   Günther, 1867) we performed field-based observations of behaviour across three thermally

118   distinct seasons separated by a 13 °C sea surface temperature (SST) range (winter: SST = 21

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119 °C, spring: 27 °C, and summer: 34 °C), monitoring individual distances from refugia, resting

120 times, feeding rate and diet across three sites in the southern Gulf. We predicted that fish

121 would respond to low and high water temperature extremes by modifying their behaviour

122 (i.e., exhibit behavioural plasticity) to different temperature conditions. Specifically, we

123 hypothesize that fish would minimize aerobically-costly behaviours (i.e., reduced distance

124 from refugia and feeding rate, whilst increasing resting time) when exposed to sub-optimal

125 temperatures in winter and summer, while compensating for energy losses and building up

126 energetic stores by increasing activity and feeding in spring. We also hypothesized that *P.*

127 *trichrourus* would exhibit flexibility in diet by shifting from a predominately planktonic diet

128 during optimal condition to a mixed planktonic and benthic diet when exposed to suboptimal

129 temperature. By restricting foraging movements in suboptimal conditions, fish may have to

130 become more generalist in their feeding habits, exploiting more easily accessible resources.

131 Finally, we performed an aquarium-based experiment exposing *P. trichrourus* to

132 temperatures typical of winter (21 °C) and spring (28 °C) in order to examine the hypothesis

133 that variation in behaviour observed in the field was directly mediated by temperature. The

134 results of this study have important implications for understanding how coral reef fishes may

135 use behavioural modification as a means to respond to the environmental variability that is

136 expected to increase under future climate change.

137

138

Materials and methods

140 The pale-tail damselfish is a small omnivorous damselfish common in southern Gulf coral

141 communities, often living in association with a single 'home' coral head (Allen 1991; Shraim

142 et al. 2017). Within the Gulf this species shows high abundance, a benthic life style with

143 diurnal behaviour, a strong association with the reef, and high territoriality to a small area

144 [territory size of 0.5 to 1.5 m^2]). It has a small body size (max 6 cm standard length - SL -)

145 and distinct differences in colour pattern between juvenile and adults (Randall 1995; Feary et

146 al. 2010). All individuals within this study were adults (~4 - 6 cm SL). The optimum

147 temperature for this species is modelled to be between 24.7 °C and 29.3 °C (mean 27.2 °C)

148 (Kaschner et al 2016).

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151 ***In situ* behavioural quantification of *P. trichrourus***

152 To determine the effect of seasonal changes in temperature on behaviour of *P. trichrourus* in

153 the Gulf, behavioural observations were replicated across three seasons: spring (April/May

154 2016, average SST = 27°C), summer (August/September 2016, average SST = 34°C), and

155 winter (February/March 2017, average SST = 21°C). Observations were undertaken at three

156 reef sites spaced ca. 40 km apart from one another along the Abu Dhabi coast (United Arab

157 Emirates – southern Gulf): Dhabiya (24°21'55.8"N, 54°06'02.9"E), Saadiyat (24°35'56.4"N,

158 54°25'17.4"E) and Ras Ghanada (24°50'53.4"N, 54°41'25.1"E) (Fig. 1). Sites were located at

159 similar distance from shore (between 5.8 and 3.8 km), with available habitat dominated by

160 hard-coral communities (ca. 40-55% live coral cover, Burt et al. 2011a) and were at 6 – 7m in

161 depth (Grizzle et al. 2015).

162

163 In situ *behavioural observation*

164 Observations were undertaken by scuba diving on cloudless days between 10:00 and 14:00,

165 reducing any influence of changing light levels on behaviour (Layton and Fulton 2014). In

166 each site, across seasons, replicate coral heads holding *P. trichrourus* individuals were

167 identified by visual searches made whilst swimming along haphazardly located transects of

168 the reef. Coral heads held one (56% of coral heads examined), two (34%), three (7%) or four

169 (2%) adult *P. trichrourus*. An individual *P. trichrourus* was haphazardly selected and its

170 territory identified and marked using numbered flags (Magalhaes et al. 2013). When several

171 adults shared the same coral head, in order to minimize the developmental variability among

172 individuals being sampled, the individual with the largest body size was selected. Following

173 marking of the territory, focal fish were allowed to acclimate for 4 min (), and then filmed for

174 2 minutes (using DBPOWER HD 1080P). A minimum distance of 3 m was maintained

175 between observer and subject. Observations were aborted if fish displayed any adverse

176 reactions to diver's presence (< 5% of individuals). Across sites and seasons, a total of 226

177 individual behavioural observations were recorded (winter: Dhabiya n = 26, Saadiyat n = 32,

178 Ras Ghanada n = 25; spring: Dhabiya n = 26, Saadiyat n = 32, Ras Ghanada n = 25; summer:

179 Dhabiya n = 23, Saadiyat n = 31, Ras Ghanada n = 29).

180

181 *Analyses of video quantifying* in situ *individual behaviour*

182 Mean distance from refugia was defined as the distance from the 'home' coral every ten

183 seconds (Beck et al. 2016) and estimated to the nearest 5 cm referenced against the territory

184 marking flag's length (25 cm) and the individual's body size (taken as 5 cm SL). Resting was

185 taken as total time (seconds) spent immobile (i.e. not active swimming, foraging or chasing

186 behaviour) across each 2-minute video. Feeding rate was the total number of bites during the

187 observation period, while diet was identified by classifying each food bite as either on pelagic

188 or benthic substrates. Benthic food bites were further classified as being on live coral, coral

189 rubble, turf or sand. Behavioural data were initially extracted from 15% of videos and

190 independently analysed and validated by two observers. As results differed by < 5 % between

191 observers, all remaining video analyses were carried out by one observer (DD).

192

193 In situ *environmental measurements*

194 To assess seasonal changes in abiotic variables in the Gulf, across the dates of all behavioural

195 observations, daily *in situ* SST (°C) and dissolved oxygen (DO, mg l^{-1}) measurements were

196 taken at 1200 hrs at each site using a YSI Professional Plus multi-parameter probe, while

197 underwater visibility (in m) was visually estimated *in situ*. Chlorophyll-a (chl-a, mg l^{-1})

198 measurements were downloaded as monthly composite data at 0.05 resolution from the

199 MODIS-aqua satellite (NASA, Ocean Ecology Laboratory), while salinity (psu), wind (m s^{-1})

200 and currents (m s^{-1}) were obtained from the NCEP climate forecast system version 2 (CFSv2,

201 Saha et al 2011). Salinity and current data were accessible as daily means (resolution 0.25-

202 deg x 0.25-deg), while wind data were taken at 1200 hrs (0.205-deg x ~0.204-deg) across all

203 experimental days.

204

205 To estimate the relative frequency of predation or competition across seasons and sites, the

206 abundance of predators (i.e. piscivorous fish with SL $\geq$ 15 cm observed interacting with *P.*

207 *trichrourus*) and competitors (i.e. fishes with comparable ecology/body size to *P. trichrourus*

208 observed chasing/being chased by *P. trichrourus*) entering each individual territory was

209 quantified for each observation.

210

211 **Aquarium-based behavioural quantification**

212 To experimentally determine the impact of water temperature on behaviour, we examined

213 time away from refugia and distance moved of *P. trichrourus* in controlled conditions in the

214 laboratory. Sixteen adults (mean body size 4.78 [± 0.13 SE] cm SL) were collected from

215 Saadiyat during winter. Eight individuals were randomly allocated to separate pierced 6L

216 bottles within either of two 900L holding tanks (control and experimental group). Each bottle

217 had a 10-cm-long plastic pipe provided for shelter. All tanks were kept at 21°C, 40 psu, 8.15

218 pH, 6.5 mg l^{-1} DO and 12 hours dark/light cycle reflecting *in situ* winter condition. 25%

219 water changes were performed weekly, with ammonia, nitrite and nitrate kept at 0 ppt. Fish

220 were fed *ad libitum* twice daily with commercial pellets.

221 After a week for acclimation, refuge use and movement of all individuals was tested at 21°C.

222 To do this a randomly chosen individual had its holding container submerged in an

223 experimental tank (80 L * 50 W *40 H [cm], filled to 20 cm H) and was left to acclimate for

224 10 minutes. The tank's base was divided into 40 squares (10 * 10 cm grid), a 10-cm-long

225 segment of plastic pipe was provided as shelter, and a DBPOWER HD 1080P video camera

226 was placed one metre above the tank. Following acclimation the individual was released and

227 led to the shelter; a transparent bottomless bottle was used to confine the individual which

228 was then left for 20 minutes. Subsequently the bottle was removed and behaviour videoed for

229 16 minutes. All videoing occurred between 1000 hrs and 1400 hrs, with a 25% water change

230 between individuals. Water temperature within the experimental holding tank was increased

231 to 28°C (~0.5°C/6 h) across four days, while the temperature within the control remained

232 constant (21 °C). Fish were then left for 7 days. As described above, all individuals were then

233 individually videoed and behaviours experimentally examined.

234

235 Within experimental videos, the first 5 minutes were discarded to allow time of acclimation

236 after activation of the video camera. Time away from refuge was quantified (in seconds)

237 when individuals moved 10 cm from the shelter. Distance moved was quantified (in cm) by

238 counting the number of grid-lines crossed over 11 min with one cross being assumed to equal

239 to 10 cm movement, independently of the distance from refuge.

240

241 **Statistical Analysis**

242 To determine whether abiotic and/or biotic factors significantly differed among seasons,

243 Kruskal-Wallis test was undertaken. Abiotic factors were then combined using Principal

244 Components Analysis, to identify the main axes of environmental variation among

245 observations; axes that explained more than 15% of the total variance (PC1 to PC3, hereafter

246 'environmental PCs') were retained and used in further analyses (Magalhaes et al. 2016).

247 To determine the impact of season, site, environmental PCs and predator/competitor

248 abundance on distance from refugia and resting time, a Generalised Linear Mixed Model

249 (GLMM) with Gaussian errors was used, while feeding rate against all predictor variables (as

250 above) was examined using a GLMM with Poisson error distribution and log link function.

251 Both distance from refugia and resting were not normally distributed and were, respectively,

252 log and log (X + 1) transformed prior to testing. In all tests, date of sampling was fitted as a

253 random effect and backwards model selection followed, using likelihood ratio tests to

254 examine the significance of each term removed from the model. To determine whether food

255 preference significantly differed between seasons, individual bites on substrate were analysed

256 using Kruskal-Wallis test.

257 To determine the effect of experimental change in temperature on time away from refugia

258 and distance moved, behavioural data before and after temperature manipulation from the

259 control and experimental groups were compared using Mann-Whitney U tests. All data were

260 analysed in R (R core development team 3.5.1, 2018).

261

Results

In situ environmental variation

264 Significant differences among seasons in SST, DO, chl-a, salinity and visibility were

265 apparent (Kruskal-Wallis test: $p < 0.05$ in all cases; Table S1). SST was highest in summer

266 and lowest in winter, while DO showed the opposite trend. Chl-a concentration was higher in

267 summer than the other seasons. PCA showed that 82% of the variation in the raw abiotic

268 variables was captured by the first three principal components, with a high score in PC1

269 (39%) being associated with low SST and chl-a, and high DO. A high score in PC2 (25%)

270 was associated with high salinity and low visibility, and a high score in PC3 (18%) was

271 associated with high water current (Table 1).

272 Across all sites and seasons, predator abundance was dominated by *Lutjanus ehrenbergii*,

273 comprising 97% of counts (Table S2). Predator abundance significantly differed among

274 seasons (Kruskal-Wallis test, H = 73.790, df = 2, $p < 0.001$), with predators being more

275 abundant in summer than spring or winter, while among sites predators were more abundant

276 in Dhabiya than Saadiyat or Ras Ghanada (Fig. S1). The predominant competitors were other

277 *P. trichrourus* and *Pomacentrus aquilis* individuals. Competitor abundance significantly

278 differing among seasons (H = 7.191, df = 2, $p = 0.027$), with slightly higher abundance in

279 spring than winter (Table S2).

280

In situ behavioural analysis

282 Season had a significant effect on *P. trichrourus* distance from refugia (Table 2), with

283 individuals showing a higher distance from refugia in spring than in either winter or summer

284   (Table S3). Although site itself did not have a significant effect on distance from refugia,

285   there was a significant interaction between site and season (Table 2), with individuals in Ras

286   Ghanada and Saadiyat showing higher distance from refugia in spring than winter or summer

287   compared to individuals from Dhabiya (Fig. 2a). Overall, *P. trichrourus* spent more time

288   resting during summer and winter than spring (Table S3). However, only the interaction

289   between site and season had a significant effect on resting time (Table 2); a clear pattern in

290   seasonal differences in resting was evident only in Ras Ghanada and Saadiyat compared to

291   Dhabiya (Fig. 2b). Season and the interaction between site and season had a significant effect

292   on individuals' feeding behaviour (Table 2), with bite rate being twice as high in spring as in

293   summer, and four times higher in spring than winter (Table S3). Clear seasonal changes in

294   feeding rate were apparent in Ras Ghanada and Saadiyat, while in Dhabiya the differences

295   between spring and summer were less clear-cut (Fig. 2c).

296

297   Significant differences in diet were apparent among seasons, with planktonic prey

298   representing 93% and 96% of food bites in winter and spring, respectively, while only

299   accounting for 73% in summer (Kruskal-Wallis, $H = 139.04$, $df = 2$, $P < 0.001$). Benthic food

300   bites were predominantly given on live corals (5 and 4% of total food bites in winter and

301   spring, 17% in summer) while coral rubble, turf and sand accounted for less than 1% of total

302   food bites in winter and spring, and $\leq 4\%$ in summer.

303

Laboratory behavioural assays

305   Before temperature manipulation there were no differences between the control and the

306   experimental group in both time away from refugia (Mann-Whitney U test, $W = 44$, $p = 0.14$)

307   and distance moved ($W = 40$, $p = 0.41$); however, differences in time away from refugia and

308   distance moved between the control and the experimental group become significant post

309   temperature manipulation ($W = 2$, $p = 0.001$ and $W = 3$, $p = 0.002$, respectively) (Fig. 3a, b).

310

Discussion

312   Although increasing variance in global SSTs may directly impact coral reef fish community

313   biodiversity (Pratchett et al. 2015; Pecl et al. 2017; Hughes et al. 2018), coral reef fish

314   populations might be able to mitigate the effect of rapidly changing environments through

315   behavioural plasticity (Nagelkerken and Munday 2016; Scott et al. 2017; Shraim et al. 2017;

316   Chase et al. 2018). We examined the impact of seasonal changes in biotic and abiotic

317 conditions on distance from refugia, activity and feeding ecology of the pale-tail damselfish

318 *P. trichrourus* within the southern Gulf. We found that *P. trichrourus* substantially increased

319 resting time and reduced distance from refugia and feeding rate at sub-optimal environmental

320 temperatures (both high and low) when observed *in situ* and when tested in the laboratory.

321 Individuals were also observed to shift from a planktonic-based diet to a mixed planktonic

322 and benthic diet during the Gulf's extreme summer season. Our results show considerable

323 scope for behavioural and trophic plasticity in *P. trichrourus*, which may allow this species to

324 cope with seasonal variance in environmental conditions, including those that are above the

325 mortality thresholds (Nilsson et al. 2009; Munday et al. 2009; Rummer et al. 2014; Rodgers

326 et al. 2018) and below the optimum temperature of Indo-Pacific reef fish (Eme and Bennett

327 2008; Figueira and Booth 2010; Nakamura et al. 2013).

328

329 We observed substantial behavioural and trophic plasticity in *P. trichrourus'* populations

330 among seasons. In particular, *P. trichrourus* were observed to reduce distance from refugia

331 and feeding rate and increase resting time in winter and summer compared to spring. These

332 seasonal changes are plausibly related to variation in water temperature, as changes in

333 environmental temperature are known to have a direct effect on fish physiology (Angilletta

334 2009; Abram 2017). In ectothermic animals, environmental temperatures departing from the

335 optimum are associated with reductions in aerobic scope, reducing energy for costly activities

336 (i.e. swimming, feeding, chasing, etc.) (Pörtner and Knust, 2007; Pörtner and Farrell 2008;

337 Munday 2012). The reduction in activity observed in *P. trichrourus,* is in line with recent

338 work suggesting that, when exposed to short-term higher than average SSTs, coral reef fish

339 may temporarily mitigate bioenergetic inefficiency through reduction in energetically costly

340 activities, as well as through changes in diet (Nowicki et al. 2012; Johansen et al. 2014; Scott

341 et al. 2017; Chase et al. 2018). However, such strategies may not be sufficient to sustain

342 prolonged periods (i.e. months) of extreme temperature (Rummer et al. 2014; Rodgers et al.

343 2018). For example, reductions in food intake and quality, coupled with low aerobic scope

344 under extreme temperatures, can disrupt an ectothermic organism's energy balance, with

345 substantially less energy available for long-term maintenance, growth and reproduction

346 (Gillooly et al. 2001; Pörtner et al. 2010; Neuheimer et al. 2011), impacting individual fitness

347 and potentially survival (Chase et al. 2018).

348 *Pomacentrus trichrourus's* persistence within the Gulf implies that they have adapted over

349 the long-term to the extreme temperature conditions experienced there (Rummer and Munday

350   2017). Our results hint that the key to their survival may be their ability to undertake seasonal

351   energy recovery in spring, compensating for energy loss during winter while building up

352   energetic stores to endure the upcoming summer season (Armstrong and Bond 2013). Many

353   studies on temperate fishes have highlighted the ability to compensate energetic and growth

354   losses during periods of adverse temperatures or food scarcity through increased feeding rate

355   and feeding activity when conditions become favourable again (Sevgili et al. 2013;

356   Armstrong and Bond 2013; Furey et al. 2016; Peng et al. 2017). For *P. trichrourus* such

357   periods of recovery, where it can access highly nutritious food resources (Shraim et al. 2017)

358   under optimal environmental temperatures (Kaschner et al 2016), may be vital for mitigating

359   energy loss during winter and summer, and hence ultimately permit the persistence of

360   abundant populations within the southern Gulf throughout the year.

361   Our lab experiments are consistent with the idea that the seasonal differences in behaviour

362   observed in the field were the result of changes in temperature. However, other potentially

363   important environmental variables also changed with the seasons, including predators and

364   primary productivity. These variables could plausibly be directly responsible for changes in

365   fish behaviour. For example, predators might have had a negative effect on *P. trichrourus*

366   movement (i.e. reduced distance from refugia) and feeding rate (Dill & Fraser 1984; Beck et

367   al. 2016; Catano et al. 2016), potentially leading to the shift to mixed planktonic and benthic

368   diet observed in summer, when *P. trichrourus* may have to rely more on safer benthic food

369   resources (i.e. live corals), despite the loss of nutritional value (Shraim et al. 2017). On the

370   contrary, we did not observe any correlation between changes in primary productivity and

371   changes in feeding activity, suggesting that shifts in diet may not be related to primary

372   productivity (measured as chlorophyll-a concentration) (Rueda et al. 2015; Zhou et al. 2016)

373   but the result of temperature-related differences in food preference (Shraim et al. 2017).

374   Ultimately, we would need manipulative experiments to confirm the potential for predators or

375   other drivers to produce similar behavioural changes to those seen in our temperature

376   manipulation.

377

378   The Gulf's average SST is increasing twice as fast as the global average (Al-Rashidi et al.

379   2009), with predictions of further increases of 0.5°C – 1.4°C by 2050, associated with hot salt

380   brine discharge derived from local desalinisation plants (AGEDI 2016; Vaughan et al. 2019).

381   As *P. trichrourus* populations live for five months of the year above their predicted thermal

382   optimum (Jun–Oct, mean SST >30°C) (Kaschner et al. 2016), of which two months

383 encompass temperatures above the mortality threshold of low latitude Indo-Pacific
384 damselfish (July and August, mean SST ≥ 33°C) (Nilsson et al. 2009; Munday et al. 2009;
385 Rummer et al. 2014; Rodgers et al., 2018), Gulf populations may already be living close to
386 their upper thermal limits; further increases in temperature are expected to pose a serious
387 threat to population persistence. In addition, *P. trichrourus* populations in the Gulf are
388 already considered endangered, associated with a fragmented distribution and strong
389 dependence to diminishing coral habitat resources (Buchanan et al. 2016; 2019). Indeed,
390 *Pomacentrus trichrourus* are highly associated with live coral colonies, utilising them for
391 recruitment, shelter and as trophic resources (Buchanan et al. 2016; Shraim et al. 2017).
392 Therefore, any increases in SST that pose a serious threat to local coral communities, where
393 bleaching events and consequent coral mortality are already common (Riegl and Purkis 2015;
394 Riegl et al. 2018), may deprive *P. trichrourus* populations of suitable habitat and food
395 resources (Keith et al. 2018; Pratchett et al. 2018).

396

397 The Gulf's marine community encompasses 241 species of coral-associated bony fish, which
398 are considered a biogeographic subset of the Indian Ocean's fauna that re-colonised the
399 region between 6000 and 9000 years ago (Riegl and Purkis 2012). The coral reef fish
400 community richness in the Gulf is thought to be lower than that in the Indian Ocean as a
401 consequence of the Gulf's physical extremes, which fewer Indian Ocean species are able to
402 tolerate (Coles 2003; Feary et al. 2010). There is still little understanding of how tolerance is
403 achieved in Gulf-dwelling species. For *P. trichrourus* this study has shown that populations
404 may be able to behaviourally mitigate the high variance in temperature and temperature
405 extremes which are consistent with predictions for the tropical ocean by the end of the
406 century (ICCP 2014). It appears that by reducing movement from shelter and feeding
407 activities within extreme seasons (summer, winter) and showing metabolic compensatory
408 activity behaviour (including feeding) during the environmentally benign spring season,
409 populations of *P. trichrourus* are able to thrive in one of the most thermally extreme marine
410 environments. Such adaptive behavioural plasticity is consistent with current theory
411 regarding how animals deal with extremes, and may be an important mechanism for how
412 increases in temperature and temperature variability may be mitigated by fishes on Indo-
413 Pacific reefs by the end of the century.

414

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416

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Figure Legends

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651 **Fig. 1**. Study area and sampling locations in the southern part of the Persian Gulf. DHAB:

652 Dhabiya; SAAD: Saadiyat; RASG: Ras Ghanada.

653 **Fig. 2**. Changes in *Pomacentrus trichrourus* behaviour *in situ* among seasons (winter = black,

654 spring = grey, summer = white) and locations (Dhabiya [DHAB], Ras Ghanada [RASG] and

655 Saadiyat [SAAD]): **(a)** mean distance from refugia (cm); **(b)** time spent resting (s/120 s) and

656 **(c)** number of feeding bites in 120 s. Thick horizontal lines show the median, boxes show

657 inter-quartile (IQR). Whiskers indicate the range of data, and dots show outliers that are more

658 than 1.5 IQR above the 75th percentile, or more than 1.5 IQR below the 25th percentile.

659 **Fig. 3**. Changes in *Pomacentrus trichrourus* behaviour ex *situ* among temperature treatment:

660 **(a)** mean time spent far from refugia (s), and **(b)** total distance moved (cm). Colours indicate

661 temperature (black = 21°C, grey = 28°C). Thick horizontal lines show the median, boxes

662 show inter-quartile (IQR). Whiskers indicate the range of data, and dots show outliers that are

663 more than 1.5 IQR above the 75th percentile, or more than 1.5 IQR below the 25th percentile.

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665   **Fig. 1**
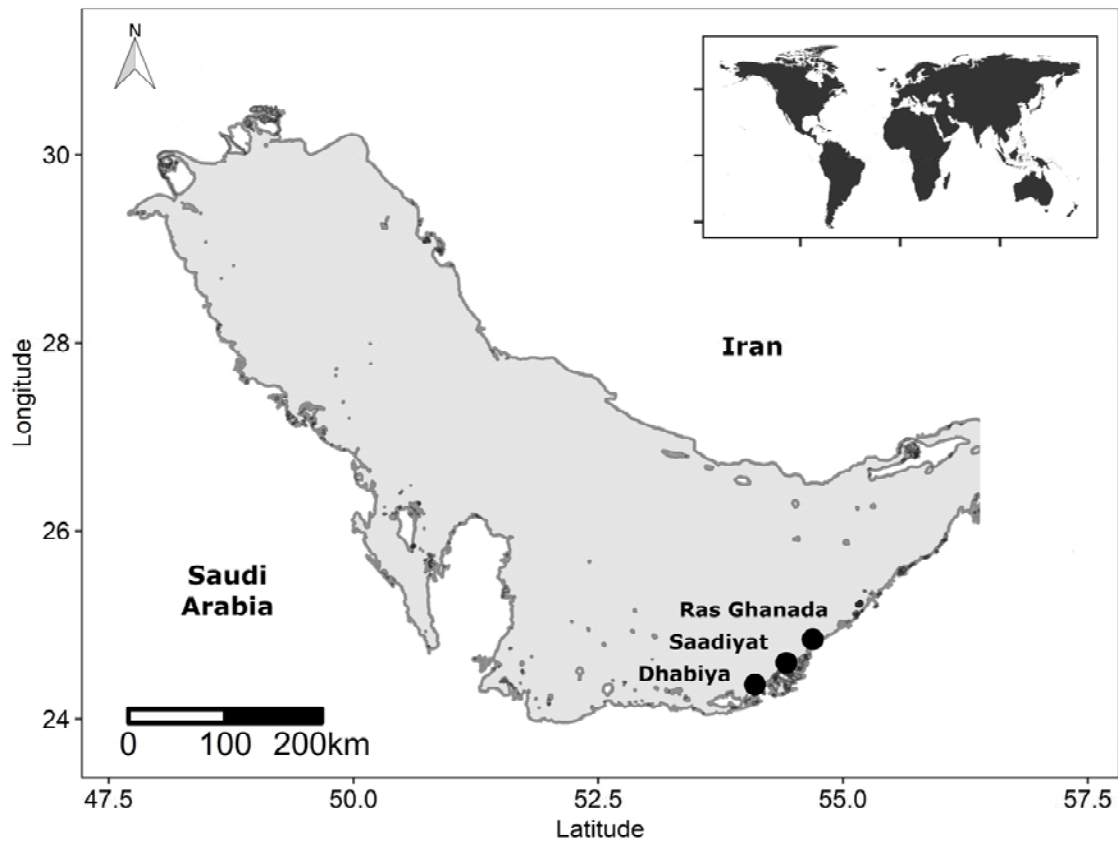
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668   **Fig. 2**
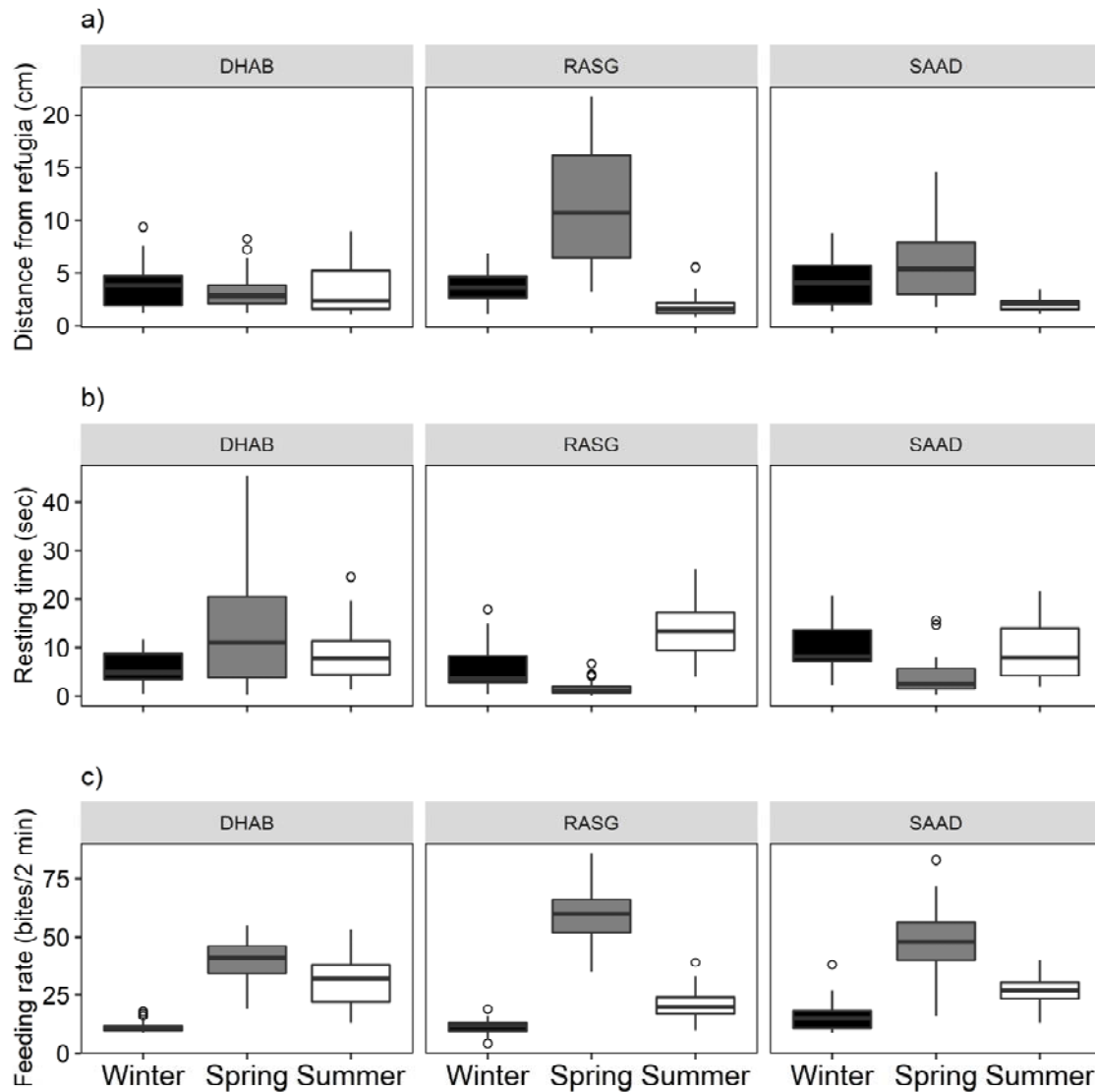
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671 **Fig. 3**

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674 # Tables
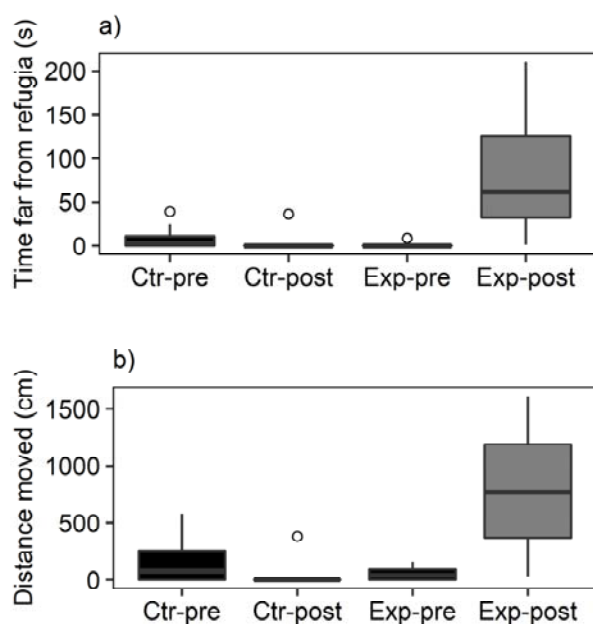
675 **Table 1.** Loadings of each environmental variables on the first three PC axes and the percent

676 variance explained by each axis. The highest loadings on each of the first three PCs are

677 showed in bold.

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Factors	PC1	PC2	PC3
Temperature	**-0.58**	-0.06	-0.04
Dissolved Oxygen	**0.58**	0.11	0.06
Chl-a	**-0.49**	0.25	0.03
Salinity	-0.10	**0.70**	0.14
Wind speed	-0.25	-0.22	-0.26
Water current	0.06	-0.14	**-0.83**
Visibility	-0.08	**-0.60**	**0.47**

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694   **Table 2.** Results of GLMM analysis of effects of biotic/abiotic factors on *Pomacentrus*

695   *trichrourus' in situ* behaviour. Gaussian error structure for distance from refugia and resting

696   time; Poisson error distribution and with log link function for feeding rate. Significant p

697   values are highlighted in bold.

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Response	Predictor	Residual deviance$_{(df)}$	Change in deviance$_{(df)}$	p
Distance from refugia	Season	$8.298_{(5)}$	$10.925_{(2)}$	**0.004**
	Site	$-1.1050_{(5)}$	$1.522_{(2)}$	0.467
	Site : season	$-2.627_{(7)}$	$30.565_{(4)}$	**< 0.001**
	PC1	$-37.767_{(14)}$	$0.430_{(1)}$	0.512
	PC2	$-33.192_{(11)}$	$3.690_{(1)}$	0.055
	PC3	$-37.390_{(13)}$	$0.377_{(1)}$	0.539
	Predators	$-36.882_{(12)}$	$0.508_{(1)}$	0.476
	Competitors	$-38.197_{(15)}$	$0.176_{(1)}$	0.674
Resting time	Season	$89.580_{(5)}$	$4.384_{(2)}$	0.112
	Site	$86.431_{(5)}$	$0.539_{(6)}$	0.539
	Site : season	$85.196_{(7)}$	$29.556_{(4)}$	**< 0.001**
	PC1	$54.937_{(12)}$	$1.013_{(1)}$	0.314
	PC2	$55.640_{(11)}$	$0.703_{(1)}$	0.408
	PC3	$53.924_{(13)}$	$1.324_{(1)}$	0.25
	Predators	$52.042_{(15)}$	$0.015_{(1)}$	0.908
	Competitors	$52.601_{(14)}$	$0.558_{(1)}$	0.455
Feeding rate	Season	$1730.2_{(4)}$	$31.427_{(2)}$	**< 0.001**
	Site	$1700.7_{(4)}$	$1.883_{(2)}$	0.39
	Site : season	$1698.8_{(6)}$	$17.959_{(4)}$	**0.001**
	PC1	$1674.6_{(12)}$	$1.459_{(1)}$	0.227
	PC2	$1680.8_{(10)}$	$3.805_{(1)}$	0.051
	PC3	$1677.0_{(11)}$	$2.487_{(1)}$	0.115
	Predators	$1672.9_{(14)}$	$0.137_{(1)}$	0.137
	Competitors	$1673.1_{(13)}$	$0.165_{(1)}$	0.685

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701 # Electronic Supplementary Material

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703 **Table S1**. Differences in abiotic (a) and biotic (b) environmental variables between seasons.

Environmental factor	Winter	Spring	Summer	Kruskal-Wallis
a) *Abiotic*	n= 4	n = 6	n = 6	
SST	20.60 (0.12)	27.45 (0.19)	33.85 (0.11)	H = 13.294, df = 2, p = **0.001**
DO	6.54 (0.04)	5.61 (0.02)	4.86 (0.01)	H = 13.274, df = 2, p = **0.001**
Chl-a	1.38 (0.05)	1.38 (0.17)	2.97 (0.62)	H = 10.638, df = 2 , p = **0.005**
Salinity	39.93 (0.05)	38.93 (0.03)	39.85 (0.13)	H = 10.770, df = 2, p = **0.005**
Wind speed	5.5 (0.70)	5.91 (0.34)	5.57 (0.56)	H = 2.592, df = 2, p = 0.274
Water current	0.03 (0.02)	0.03 (0.01)	0.03 (0.01)	H = 1.456, df = 2 , p = 0.483
Visibility	6.00 (1.11)	11.95 (1.23)	8.25 (0.66)	H = 6.231, df = 2, p = **0.044**
b) *Biotic*	n = 61	n = 83	n = 83	
Predators	0.22 (0.1)	0.92 (0.2)	6.41 (1)	H = 73.790, df = 2, p < **0.001**
Competitors	0.38 (0.1)	0.75 (0.1)	0.49 (0.1)	H = 7.191, df = 2, p = **0.027**

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706   **Table S2.** Comparison of mean (± SE), maximum and total of predators (**a**) and competitors

707   (**b**) that the focal species *Pomacentrus trichrourus* encountered during the 2 minutes

708   behavioural observation in winter (left), spring (middle) and summer (right). Species ranked

709   by order of abundance at the summer season.

Species	Winter			Spring			Summer		
	Mean	Max	n	Mean	Max	n	Mean	Max	n
(a) Predators									
Lutjanus ehrenbergii	0.08 (0.05)	3	5	0.89 (0.21)	10	74	6.12 (1.00)	59	508
Scolopsis ghanam	0.12 (0.06)	3	7	0.01 (0.01)	1	1	0.17 (0.06)	3	14
Epinephelus spp	0	0	0	0.02 (0.02)	1	1	0.09 (0.05)	1	6
Lutjanus fulviflamma	0	0	0	0.02 (0.02)	1	1	0.09 (0.05)	1	3
Total	**0.22 (0.10)**		12	**0.92 (0.20)**		76	**6.41 (1.00)**		525
(b) Competitors									
Pomacentrus trichrourus	0.35 (0.07)	2	21	0.75 (0.01)	4	62	0.45 (0.06)	2	37
Pomacentrus aquilis (j)	0.05 (0.04)	2	3	0.59 (0.07)	3	49	0.3 (0.05)	2	25
Pomacentrus aquilis	0.03 (0.02)	1	2	0	0	0	0.05 (0.02)	1	4
Total	**0.38 (0.10)**		26	**0.75 (0.10)**		111	**0.49 (0.10)**		66

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712 **Table S3.** Comparison of *in situ* behaviour (median ± SE, max and min) between seasons.

Behaviour	Winter (n = 60)			Spring (n = 83)			Summer (n = 83)		
	Median	Max	Min	Median	Max	Min	Median	Max	Min
Distance from refugia	3.77 (0.3)	9.38	1.08	5.38 (0.5)	21.69	1.15	1.96 (0.2)	9	0.85
Resting	5.62 (0.6)	20.74	0.48	2.48 (1.0)	45.45	0.12	10.37 (0.7)	26.24	10.37
Feeding rate	12 (0.7)	38	4	49 (0.9)	86	16	25 (0.9)	53	25

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715 **Fig. S1**. Changes in abundance of *Pomacentrus trichrourus'* potential predators with seasons
716 (winter = black, spring = grey, summer = white) and locations (Dhabiya [DHAB], Ras
717 Ghanada [RASG] and Saadiyat [SAAD]). Thick horizontal lines show the median, boxes
718 show inter-quartile (IQR). Whiskers indicate the range of data, and dots show outliers that are
719 more than 1.5 IQR above the 75th percentile, or more than 1.5 IQR below the 25th percentile.

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