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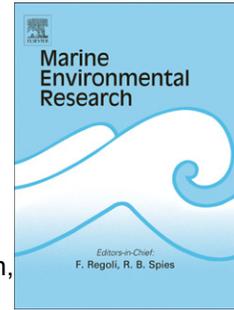
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# Differences in physiological response to increased seawater temperature in nearshore and offshore corals in northern Vietnam

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## 1 ABSTRACT

2 Effects of elevated seawater temperature show high spatial heterogeneity and variation  
3 within and among coral species. The objective of this study was to investigate how two  
4 coral species, *Porites lutea* and *Galaxea fascicularis*, from two high latitude reefs  
5 differently exposed to chronic disturbance, respond to elevated seawater temperatures.  
6 Corals were collected from reefs nearshore, (i.e. subjected to high sediment load, higher  
7 chlorophyll  $\alpha$  concentrations, turbidity etc.) and offshore, (i.e. less exposed). The corals  
8 were exposed in the lab to gradually increasing temperatures (25.5 – 33.5 °C) for 72 h  
9 after which they were allowed to recover to ambient temperature (25.5 °C) for 24 h.  
10 Production and respiration were measured after 24, 48, 72 and 96 hours. The results show  
11 that *P. lutea* from nearshore reefs suffered an initial decrease in gross primary  
12 production/respiration (GP/R) ratio after 24 h, after only a moderate temperature increase  
13 (+ 2 °C, from 25.5 to 27.5 °C), while there was no difference in GP/R ratio between heat-  
14 exposed and controls the other days, indicating that the chronic disturbance in the  
15 nearshore reef had no effect on their thermotolerance. Furthermore, *P. lutea* from the  
16 offshore reef showed a decrease in GP/R ratio both after 24 h and 72 h (33.5 °C) of  
17 exposure.  
18 In comparison, *G. fascicularis* showed a decrease in GP/R ratio after 48 h, 72 h and 96 h  
19 of exposure for the nearshore corals. Also, after 72 h these corals had withdrawn their  
20 polyps. There were no differences between heat-treated and controls for the offshore *G.*  
21 *fascicularis*. This implies that the chronically disturbed *G. fascicularis* had lower  
22 thermotolerance when exposed to a temperature increase.

23           This study, hence, shows that the response of corals to elevated seawater  
24 temperature varies with species and environmental background history.

25

26   Keywords: Increased water temperature, *Galaxea fascicularis*, *Porites lutea*, Disturbance,  
27 Physiological responses, High latitude reefs, Vietnam

28

29

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## 30 **1. Introduction**

31

32 Coral reefs have shown a remarkable persistence, despite reoccurring natural disturbance  
33 events (Wood, 1995). However, reef-building corals have a very restricted thermal  
34 tolerance (Hoegh-Guldberg, 1999). If temperature exceeds a given thermal limit corals  
35 may lose their colour, i.e. they “bleach”. This decolouration is due to the expulsion of the  
36 endosymbiotic microalgae (zooxanthellae) found in the polyp tissue, making the white  
37 calcium carbonate skeleton underneath visible (Douglas, 2003). Since corals receive up to  
38 95% of their energy from their zooxanthellae via photosynthesis (Muscatine, 1990)  
39 bleaching may cause significant mortality, unless the coral host is repopulated with  
40 symbionts, in due time (species specific) to allow recovery (Glynn, 1996; Diaz-Pulido  
41 and McCook, 2002). Hence, in the face of climatic changes and increased sea surface  
42 temperatures (IPCC, 2007) there is great concern for the future health of coral reefs  
43 (Hughes et al., 2003; Sheppard and Rioja-Nieto, 2005; Hoegh-Guldberg et al., 2007). In  
44 tandem coral reefs are exposed to direct human impacts, such as increased sedimentation,  
45 increased nutrient loading, pollution etc., which may reduce their capacity to respond to  
46 environmental changes caused by changes in climate.

47       Extensive coral mortality due to climate-induced bleaching events (i.e. mass coral  
48 bleaching) has occurred repeatedly over the past decades across all oceans (Wilkinson,  
49 2006). These events are predicted to increase in frequency and magnitude in the future  
50 (Hoegh-Guldberg, 1999; Donner et al., 2005). The observed patterns of bleaching,  
51 however, show great spatial variability (e.g. McClanahan et al., 2007). A multitude of  
52 variables may explain different thermal tolerances, including coral morphology

53 (McClanahan, 2000; Spencer et al., 2000; Edwards et al., 2001), taxa (McClanahan,  
54 2004; McClanahan et al., 2004; Ulstrup et al., 2006), depth (Brown, 1997; Warner et al.,  
55 1999; Spencer et al., 2000; Craig et al., 2001), distribution of zooxanthellae clades (i.e.  
56 genotypes) (Glynn et al., 2001; Baker et al., 2004; Rowan, 2004), and local temperature  
57 variations due to local current regimes (McClanahan et al., 2005). Furthermore, it has  
58 also been suggested that reduced water quality can amplify the impacts of elevated  
59 seawater temperature (Hughes et al., 2003; Pandolfi et al., 2007; Mora, 2008). For  
60 example, experimental studies suggest that thermal tolerance in corals can be reduced by  
61 exposure to heavy metals (Nyström et al., 2001), increased nutrients (Nordemar et al.,  
62 2003) sedimentation (Lambo and Ormond, 2006) and decreased salinity (Faxneld et al.,  
63 2010).

64 Besides climate change, increase in sediment load due to human activities, is  
65 considered a major threat to coral reefs (Bryant et al., 1998; Hughes et al., 2003;  
66 Wilkinson, 2004). Sedimentation can lead to reduced coral species diversity and  
67 increased mortality, reduced calcification- and growth rates, decreased net production and  
68 increased respiration (Rogers, 1990; Crabbe, 2005; Fabricius, 2005; Jupiter et al., 2008).

69 Approximately 50% of the reefs in Vietnam are threatened by sedimentation  
70 (Burke et al., 2002). Tuan (2000) reported that the proportion of reefs with less than 25%  
71 live coral cover increased from 25% before 1998 to 50% of the reefs by 1999 in the  
72 Halong Bay and Cat Ba Island (the study area). This has mainly been attributed to  
73 sedimentation (Chou et al., 2002). During that time, *Acropora* spp. suffered significant  
74 mortality on many reefs while *Galaxea fascicularis* was basically unaffected. In 2002 *G.*  
75 *fascicularis* was still the dominating species on many reefs in Halong Bay with up to 40%

76 of the benthic cover (Nguyen D Ngai unpubl. data), thus indicating that tolerance to  
77 sedimentation varies among coral species.

78 The aim of this study was to investigate potential differences in physiological  
79 responses to elevated temperature depending on exposure to earlier disturbance regimes.  
80 For this purpose two common coral species, *Porites lutea* and *Galaxea fascicularis* were  
81 used. Corals were collected from two nearshore reefs, more exposed to sedimentation,  
82 high chlorophyll  $\alpha$  concentrations and nutrients etc. (Fig. 2a and Table 1) and two  
83 offshore (less disturbed) reefs (Fig.1). Two opposite outcomes were predicted  
84 beforehand: (1) corals exposed to chronic disturbance will have reduced capacity to  
85 withstand further thermal stress, since these corals may already be close to their  
86 physiological tolerance limit or (2) corals exposed to chronic disturbance will have  
87 enhanced capacity to withstand further stress, due to a more developed acclimatory  
88 ability.

89 Differences in physiological responses within and between species from different  
90 disturbance regimes can be relevant for identifying sensitive and tolerant coral species  
91 when exposed to additional stress and may have implications when deciding future  
92 establishment of marine protected areas.

93

## 94 **2. Material and methods**

95

### 96 *2.1. Study area*

97

#### 98 *Halong Bay*

99 Halong Bay is a relatively shallow turbid bay exposed to high nutrient loading (Latypov,  
100 2005). Most coral reefs in Halong Bay are also affected by sedimentation and coastal  
101 pollution, especially nearshore reefs (Lang et al., 2004). Furthermore, shipping in and out  
102 of the bay stirs up the sediments from the bottom thus affecting the reefs, more so in the  
103 nearshore sites (Tran et al., 2004). Due to the high turbidity in the bay corals are  
104 restricted to shallow waters and their maximum depth distribution is limited to 3-4 m on  
105 nearshore- and to 5-7 m on offshore reefs (Lang et al., 2004). Water temperature  
106 fluctuates dramatically over the year with a winter (December-February) minimum of 16  
107 °C and normal summer (June-August) maximum around 31.5 °C. Halong Bay is a  
108 relatively species-poor coral community, and it is dominated by massive coral species,  
109 such as *Galaxea fascicularis* and *Porites lutea*. Branching genera, such as *Acropora* and  
110 *Pocillopora* are relatively scarce (Latypov, 2005; Nguyen D Ngai unpubl.).

111

## 112 2.2. Collection of corals

113

114 Pieces of corals were collected at 2-3 m depth from two reef areas in May 2007 (Fig. 1).  
115 The disturbed (i.e. nearshore) reef area (Cat Ba Island National Park) (including site A  
116 and B) is situated close to the coast, in a semi-enclosed area with limited water exchange  
117 and receives run-off water from several rivers, whereas the offshore area (Long Chau  
118 Islands) (including site C and D) is located approximately 20 km south of the nearshore  
119 reef area. The latter location is an open area with good water exchange and it is less  
120 affected by land run-off water (e.g. less sediments, nutrients and lower chlorophyll  $\alpha$   
121 concentrations (a proxy for water clarity, see LaJeunesse et al., 2010a and 2010b).

122 Although several environmental parameters differ between the near- and offshore area,  
123 temperature and salinity regimes were almost identical between the areas throughout the  
124 year (see Table 1 and Fig. 2a and 2b); and the ambient temperature and salinity during  
125 collection was 25.5 °C and 32 psu at all sites. Corals from the two reef areas thus have  
126 very similar thermal histories. Within each area, two reef sites were sampled. In the  
127 nearshore area, Ba Trai Dao Island (site A, N 20° 47' 20", E 107° 06' 13") and Van Boi  
128 Island (site B, N 20° 45' 35", E 107° 04' 24") were selected and in the offshore area, coral  
129 specimens were collected from Vung Cay Bang Island (site C, N 20° 37' 27", E 107° 09'  
130 41") and Vung Tau Island (site D, N 20° 37' 21", E 107° 08' 08") (Fig 1). The corals were  
131 collected using a hammer and chisel. Two massive species, *Porites lutea* and *Galaxea*  
132 *fascicularis*, were selected and at each of the four sites 10 coral pieces (approximately 85  
133 cm<sup>2</sup> and 120 cm<sup>2</sup> for *P. lutea* and *G. fascicularis* respectively) of each species were  
134 collected, except for one nearshore site (Van Boi) where no *G. fascicularis* and only 6  
135 pieces of *P. lutea* could be found. Hence, 36 pieces of *P. lutea* and 30 pieces of *G.*  
136 *fascicularis* were collected in total. Immediately after collection, corals were transported  
137 to the outdoor laboratory at the Tram Bien Research Station in Do Son under low light  
138 condition and continuous aeration. After epiphytes and boring organisms had been  
139 carefully removed, the corals were put in aerated aquaria (20 litre each) with filtered and  
140 UV-treated seawater. The aquaria were placed in larger water-filled tanks (1 m<sup>3</sup>) in order  
141 to minimise temperature fluctuations (Nyström et al., 2001; Nordemar et al., 2003). The  
142 corals were allowed to acclimate to the set control temperature of 25.5 °C and 32 psu  
143 (ambient at site of collection) and thereafter kept at that temperature for 48 h before the  
144 experiment was started.

145

146 2.3. *Experimental setup*

147

148 The corals were evenly distributed in eight 20-litre aquaria using a randomized block  
149 design. Four of the aquaria were then placed in a heating tank (1 m<sup>3</sup>) representing  
150 temperature “exposure” and the other four were placed in a control tank (1 m<sup>3</sup>) with  
151 ambient water temperature. Aeration pumps mixed the seawater in both the aquaria and  
152 the tanks, thus maintaining high oxygen concentrations and distributing water  
153 temperature evenly. The water temperature in the exposure tank was increased using  
154 heating regulators (ZEBO 300W or FLUVAL Tronic 200W). The temperature was  
155 recorded every hour during daytime (between 10 am to 6 pm) and once in the evening as  
156 well as once in the early morning (at 9 pm and 6 am respectively) to verify constant  
157 temperature throughout a 24 h period before the experiment was started. Throughout the  
158 experiment, temperature was measured continuously during the physiological  
159 measurements. Between measurements, temperatures were recorded every second hour  
160 during daytime and once in the evening as well as once in the early morning (at 9 pm and  
161 6 am respectively). The experiment lasted for 96 h (4 days) during which the temperature  
162 was gradually increased for three days, to mimic a natural gradual temperature increase,  
163 and then reduced to ambient for a 24-hour recovery period. It is well known that daily  
164 temperatures can undergo drastic changes on nearshore reef flats and in coastal lagoons,  
165 e.g. 25-33 °C within hours (Semesi et al., 2009). Normal summer temperature in Halong  
166 Bay is 30-31.5 °C (Nguyen 2004; Latypov 2005), and studies have shown that large  
167 increases (3-4

168 °C above normal summer maximum) over a few days can bleach corals (Glynn and  
169 D’Croz 1990; Jokiel and Coles 1990). The temperature treatment in the exposure tank  
170 was set to: day 1: (27.5 °C), day 2: (30.5 °C), day 3: (33.5 °C) and day 4: (25.5 °C). The  
171 maximum exposure temperature of 33.5 °C in the present study was chosen since 2 °C  
172 above expected summer maximum is known to induce physiological stress in most coral  
173 species. It took approximately four hours before the new temperature was reached.  
174 Hence, the corals were exposed in each temperature for 20 hours before the production  
175 and respiration were measured. Temperature in the control tank was maintained at 25.5  
176 °C throughout the study. Due to effective heaters and stirring we were able to keep the  
177 temperatures very constant (deviation < 0.2 °C from set temperature) throughout the  
178 experiment. The experiment was conducted outdoors in natural sunlight, under low light  
179 conditions (414-529  $\mu\text{E m}^{-2} \text{s}^{-1}$ ), corresponding to recorded light levels on shallow reefs  
180 (e.g. Semesi et al., 2009). Production and respiration measurements were conducted each  
181 day for both exposed and control corals.

182

#### 183 2.4. *Physiological measurements*

184

185 Before net primary production and respiration were measured, each coral was put in a 1.5  
186 litre transparent plastic jar with a tight-fitting lid, without extra supplies of oxygen. Each  
187 jar contained water with a temperature identical to the treatment temperature. During the  
188 measurements, the temperatures also in the measurement jars were constant (set temp.  $\pm$   
189 0.2 °C). Changes in dissolved oxygen concentration in light (net primary production) and  
190 darkness (respiration) were measured according to Moberg et al. (1997) using an

191 oximeter (WTW OXI 330). An earlier pilot test showed that the most stable and reliable  
192 values were obtained after a 30 minutes and 2.5 hours acclimation period in light and  
193 darkness for production and respiration, respectively. Dissolved oxygen concentration  
194 was initially measured in light and then again after 30 minutes. Corals were then placed  
195 in darkness and after 2.5 h the oxygen concentration was measured once more and  
196 respiration rates calculated. Before the statistical analyses, production and respiration  
197 rates were converted to 1-hour values. Four water controls (jars containing only water)  
198 were used for each measurement, two with control water temperature and two with a  
199 temperature that corresponded to that of the exposed corals. Net primary production was  
200 always measured during mid-day, at 1 pm. During the measurements, the oxygen  
201 saturation levels never dropped below 75%. To compensate for volume dependent  
202 differences in dissolved oxygen concentration, the volumes of the corals were measured  
203 by submerging the coral into a graded beaker filled with a known volume of water. Live  
204 coral surface area was determined using the aluminium foil method (March, 1970). Net  
205 production- and respiration rates were expressed per hour and coral surface area ( $\text{cm}^2$ ).  
206 Respiration rate (R) was added to the net production value in order to achieve gross  
207 primary production rate (GP). Gross primary production rates were then corrected for  
208 temporal differences in light intensities between measurements. This was done to  
209 compensate for light dependent differences between measurements, since measurements  
210 were performed for four consecutive days. In order to do this, the production values were  
211 divided by the light intensity during measurement, and then multiplied with the average  
212 light intensity during all measurements, assuming a linear relationship between light  
213 intensity and primary production in the narrow light interval in this study. Due to lack of

214 laboratory facilities, data on coral biomass, zooxanthellae density and chlorophyll  
215 concentration could not be obtained. Consequently gross primary production and  
216 respiration rates are expressed as per  $\text{cm}^2$  coral surface area according to Moberg et al.  
217 (1997). Gross primary production/respiration (GP/R) ratios were also calculated to get a  
218 dimensionless estimate of the physiological status of the corals.

219

### 220 2.5. Statistical analysis

221

222 A two-way ANOVA was used to analyse the effect of site (i.e. nearshore site A vs. B and  
223 offshore site C vs. D) and treatment (i.e. heat vs. control) on the gross primary production  
224 rate, respiration rate and GP/R ratio of both species. Since there were no differences  
225 between the two offshore or nearshore sites (the data from site A and B, and the data  
226 from site C and D) the data were pooled into one offshore and one nearshore group for  
227 each species. A General Linear Model (GLM) univariate one-way ANOVA was used to  
228 analyse the effects of the four different treatments (i.e. offshore / heat, nearshore / heat,  
229 offshore / control and nearshore / control) on gross primary production rate, respiration  
230 rate and GP/R ratio for *G. fascicularis* and *P. lutea* respectively. The analyses were  
231 carried out separately for each day and species. Where the one-way ANOVA showed  
232 differences, Tukey HSD was used as a post hoc test ( $p < 0.05$ ). All data were tested for  
233 homogeneity of variances using Levene's test ( $p < 0.05$ ) before the ANOVA was carried  
234 out. When necessary, the data were log transformed. When Levene's test showed  
235 differences in variance and no transformations proved efficient, the non-parametric

236 Kruskal-Wallis and Mann-Whitney  $U$  test was used. For the statistical analyses SPSS  
237 17.0 for Mac OS X was used.

238

### 239 **3. Results**

240

#### 241 *3.1. Galaxea fascicularis*

242

243 There were significant differences when comparing heat-treated corals and controls in  
244 nearshore and offshore areas (Table 2). Corals from the nearshore area showed a  
245 significant decrease in GP/R ratio on day 2, 3 and 4 when exposed to elevated  
246 temperature compared to the controls ( $p < 0.05$  Tukey HSD, Fig. 3a), whereas no  
247 significant differences were observed for heat-treated and controls for the offshore corals  
248 (Fig. 3b). The differences in GP/R ratio for the nearshore corals were mainly caused by  
249 an increase in respiration rates compared to the control (Table 3a). However, on day 3 the  
250 difference was also explained by a decrease in gross primary production rates compared  
251 to the control (Table 3b).

252 Sixty percent of the heat-treated *Galaxea fascicularis* from the nearshore area had  
253 withdrawn their polyps (Fig. 4a) after exposure to 33.5 °C, i.e. on the third day of  
254 exposure. Heat-treated offshore- and control corals showed no such response (Fig. 4b).

255

#### 256 *3.2. Porites lutea*

257

258 For *P. lutea* there were significant differences between heat-treated and control corals  
259 from nearshore and offshore areas (Table 4). The GP/R ratio was significantly lower on  
260 day 1 for nearshore heat-treated corals compared to the controls ( $p < 0.05$  Tukey HSD,  
261 Fig. 5a). This was explained by a significant increase in respiration rates that day ( $p <$   
262  $0.01$  Tukey HSD, Table 5a). Furthermore, the offshore heat-treated corals displayed a  
263 significant decrease in GP/R ratio both on day 1 and day 3 ( $p < 0.05$  Tukey HSD, Fig.  
264 5b). This decrease in GP/R ratio was mainly explained by an increase in respiration rates  
265 (Table 5a). There were no differences in gross primary production rates between  
266 treatments (Table 5b).

267

#### 268 **4. Discussion**

269

270 For *Galaxea fascicularis* the GP/R ratio differed between the offshore and nearshore area,  
271 except for day 1. Heat-treated corals from nearshore reefs showed a decrease in GP/R  
272 ratio throughout the study. On day 3 the corals had also withdrawn their polyps, which  
273 might explain the large decrease in gross primary production rate observed that day. A  
274 direct effect on zooxanthellae cannot be excluded although no counting of zooxanthellae  
275 could be done. Other studies have shown that withdrawal of polyps is a stress response in  
276 corals (Coyer et al., 1993; Brown et al., 1994; Jones et al., 2000).

277 The difference in response between nearshore and offshore *G. fascicularis*  
278 suggests that corals pre-exposed to other stressors (i.e. nearshore corals) are more  
279 sensitive to heat stress compared to the offshore (less disturbed) reefs. Similar findings  
280 have been reported by Carilli et al. (2009), who investigated skeletal growth rates in  
281 *Montastrea faveolata* before and after the 1998 bleaching event in reefs exposed to

282 different levels of local stress (e.g. sedimentation and nutrients). The authors found that  
283 the growth rate was suppressed for longer time after the bleaching event at the reefs  
284 exposed to higher levels of stress, thus they were less resilient to coral bleaching.

285         There were no significant differences in physiological response between *Porites*  
286 *lutea* from offshore and nearshore reefs on any day of exposure (Fig. 5a and 5b). There  
287 were only significant differences between heat-treated and control corals for the  
288 nearshore *P. lutea* at day 1 of exposure (Fig. 5a) even though the temperature increase  
289 was higher, with a maximum of 8 °C above ambient temperature on day 3. This indicates  
290 that even a small increase in temperature can affect *P. lutea* initially, but that they are  
291 able to “maintain” their physiological status (GP/R ratios indicating maintained  
292 autotrophy) over the temperature range tested in the present study. Although all heat-  
293 treated *Porites* showed a relative decrease in GP/R ratio compared to the corresponding  
294 controls, anthropogenic disturbances (e.g. land run-off, sedimentation) seem not to affect  
295 their thermotolerance during heat stress. One possible explanation of this could be a more  
296 rapid induction of cellular defence mechanisms (e.g. HSP 70 – see Brown, 1997) in these  
297 chronically exposed specimens, something that has been demonstrated in marine mussels  
298 exposed to heavy metal pollution followed by thermal stress (Veldhuizen-Tsoerkan et al.,  
299 1990).

300 Another explanation could be that the coral clades differ between *P. lutea* and *G.*  
301 *fascicularis* and/or differ between the two areas, since it has been shown that different  
302 corals may host different clades of *Symbiodinium* (LaJeunesse, 2002) and clades can also  
303 differ between regions (Baker and Rowan, 1997; Garren et al., 2006). *G. fascicularis*  
304 have been found to harbour both clade C and D (LaJeunesse et al., 2004; Done et al.,

305 2009), while *P. lutea* is only hosted by clade C (Chen et al., 2005; Apprill et al., 2007;  
306 Hennige et al., 2010), which generally is not associated with corals located in areas  
307 exposed to high temperatures (e.g. Baker et al., 2004). Since no analyses of the clades  
308 were conducted in this study, further research comparing clades between nearshore and  
309 offshore reefs in the area would be of scientific interest. A further explanation to the  
310 different responses between the two species and areas could be that the coral hosts are  
311 genetically adapted to the local environmental conditions on these reefs, since the  
312 environmental quality do differ between nearshore- and offshore reefs, although the  
313 thermal history are identical between the areas in the study presented here.

314       Reduction of GP/R ratio has been recognized as a common stress response in  
315 corals when exposed to elevated seawater temperature (Coles and Jokiel, 1977; Hoegh-  
316 Guldberg and Smith, 1989; Fitt and Warner, 1995; Porter et al., 1999). The observed  
317 decrease in GP/R ratio for both *P. lutea* and *G. fascicularis* was primarily a result of an  
318 increase in respiration rate, which has been demonstrated by other authors (Hoegh-  
319 Guldberg and Smith, 1989; Faxneld et al., 2010). However, for nearshore *G. fascicularis*  
320 on day 3 the decrease in GP/R ratio was also explained by a decrease in primary  
321 production rates, which also has been shown by other authors (Fitt and Warner, 1995;  
322 Porter et al., 1999; Nyström et al., 2001). The higher respiration- and production rates,  
323 observed for offshore *G. fascicularis*, controls and heat-treated, is likely to be attributed  
324 to the fact that the offshore colonies were generally smaller – presumably younger  
325 colonies – that do have higher metabolic activity.

326       None of the coral species showed signs of bleaching in our study, which supports  
327 others studies showing that both *G. fascicularis* (Marshall and Baird, 2000; McClanahan

328 et al., 2004) and *P. lutea* (e.g. Riegl, 1999; Loya et al., 2001; Obura, 2001) are relatively  
329 tolerant to elevated seawater temperatures, and suggests that the corals in the present  
330 study were not exposed to lethal temperatures, although an increase by 2-3 °C in 4 hours  
331 is in the upper range of what can be expected on shallow reefs in the study area.

332 It should be emphasized that of the temperatures tested here, the 27.5 and 30.5 °C  
333 treatments are well below the thermotolerance threshold for most coral species and only  
334 the 33.5 °C treatment is above the normal summer maximum.

335

## 336 **5. Conclusion**

337

338 This study shows that the response of corals to elevated seawater temperature varies with  
339 species and environmental background history. The study suggests that the physiological  
340 response in *G. fascicularis* was more pronounced in more disturbed nearshore areas  
341 compared to their conspecifics from less disturbed environments, thus supporting the  
342 hypothesis that corals in stressful environments (e.g. subjected to land-based pollution  
343 and sedimentation) are less tolerant to elevated water temperature. An explanation for this  
344 could be that nearshore corals are already closer to their physiological tolerance limit and  
345 therefore more sensitive to additional disturbances (Paine et al., 1998). On the other hand,  
346 the acclimatory ability may very well differ between coral species. For example, *P. lutea*  
347 from nearshore reefs were not more physiologically affected by the temperature increase  
348 than corals from offshore reefs. Consequently, it is difficult to predict general effects on  
349 coral reefs if episodes of elevated seawater temperatures become more frequent in the  
350 future, since these effects may be area and species specific. One likely consequence,

351 however, is that due to differences in acclimatory capability among coral species, reefs  
352 may suffer losses in biodiversity (Loya et al., 2001), which in turn may impact the  
353 resilience of coral reefs (Nyström et al., 2000; Bellwood et al., 2004).

354

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359 Research Station. We also thank the anonymous reviewers for their pertinent and helpful  
360 comments.

361

### 362 **List of figures**

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364 Fig 1. Map showing the collection sites. The nearshore, more disturbed reefs (Ba Trai  
365 Dao and Van Boi) are situated in the north and the offshore less disturbed reefs (Vung  
366 Tau and Vung Cay Bang) ~ 20 km to the south.

367

368 Fig 2. a) Monthly averages of chlorophyll  $\alpha$  concentrations (a proxy for water clarity)  
369 from September 1997 to August 2010. The solid line shows the nearshore area and the  
370 dotted line shows the offshore area.

371 b) Monthly averages of temperature ( $^{\circ}\text{C}$ ) from July 2002 to July 2010. The solid line is  
372 showing data for both the nearshore and the offshore areas, since the average  
373 temperatures were identical.

374 The data were acquired from the Giovanni online data system  
375 ([http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance\\_id=ocean\\_month](http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month);  
376 downloaded 1 November 2010), which was developed and is maintained by the NASA  
377 Goddard Earth Sciences (GES) Data and Information Services Center (DISC).

378

379 Fig 3. *Galaxea fascicularis*. GP/R ratio  $\pm$  SE. a) Nearshore corals a) Offshore corals. The  
380 dark bars show the controls (exposed to 25.5 °C during the whole study) and the light  
381 bars are the heat-exposed corals (heat-exposure: day 1=27.5 °C, day 2=30.5 °C, day  
382 3=33.5 °C, day 4=25.5 °C). \*  $p < 0.05$ .

383

384 Fig 4. *Galaxea fascicularis*. Polyp extension. a) Nearshore corals b) Offshore corals when  
385 exposed to 33.5 °C on day 3.

386

387 Fig 5. *Porites lutea*. GP/R ratio  $\pm$  SE. a) Nearshore corals b) Offshore corals. The dark  
388 bars show the controls (exposed to 25.5 °C during the whole study) and the light bars are  
389 the heat-exposed corals (heat-exposure: day 1=27.5 °C, day 2=30.5 °C, day 3=33.5 °C,  
390 day 4=25.5 °C). \*  $p < 0.05$ .

391

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394 Table 1. Environmental data from the offshore (Long Chau Islands) and the nearshore  
395 (Cat Ba) sites used in this study. Data from biannual surveys provided by The Institute of  
396 Marine Environment and Resources, Hai Phong, Vietnam.

397

398 Table 2. *Galaxea fascicularis*. Results from the ANOVA where all nearshore and  
399 offshore corals have been compared to the controls. P-values < 0.05 demonstrate  
400 significant differences between heat-treated and controls. + depicts cases when Kruskal-  
401 Wallis was used.

402

403 Table 3. *Galaxea fascicularis*. Mean  $\pm$  SE for heat-treated and controls from nearshore  
404 and offshore reefs. a) Respiration rates b) Gross primary production rates.

405

406 Table 4. *Porites lutea*. Results from the ANOVA where all nearshore and offshore corals  
407 have been compared to the controls. P-values < 0.05 demonstrate significant differences  
408 between heat-treated and controls.

409

410 Table 5. *Porites lutea*. Mean  $\pm$  SE for heat-treated and controls from nearshore and  
411 offshore reefs. a) Respiration rates b) Gross primary production rates. \*\* p < 0.01.

412

413

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Chronically disturbed *Galaxea fascicularis* respond negatively to temperature increase

*Porites lutea* not more affected by elevated temperature when chronically stressed

Temperature increase affects even coral species from the same area differently

ACCEPTED MANUSCRIPT

## List of tables

Table 1

	Offshore		Nearshore	
	Dry season <sup>a</sup>	Rainy season <sup>b</sup>	Dry season <sup>a</sup>	Rainy season <sup>b</sup>
<b>Average (year 2005-2008, n=4)</b>				
Salinity (psu)	32	26	32	25
pH	8.13	8.34	8.09	8.32
Sedimentation (g m <sup>-2</sup> *day <sup>-1</sup> )	1.99±0.39	0.38±0.17	3.42±0.14	4.19±0.21
Visibility (m)	3.0	3.0	5.5	4.0
Nitrate* (µg*l <sup>-1</sup> )	86.2±2.5		135.5±11.8	

Numbers show mean±SD. <sup>a</sup>The dry season lasts from October to May, <sup>b</sup> the rainy season lasts from June to September, \* average of 2 measurements March-May 2003.

Table 2

	Day	df	F	p
<b>GP/R</b>	1	3	4.835 +	0.184
	2	3	8.677	<b>0.000</b>
	3	3	15.417 +	<b>0.001</b>
	4	3	8.305 +	<b>0.040</b>
<b>R</b>	1	3	7.947	<b>0.001</b>
	2	3	21.149	<b>0.000</b>
	3	3	22.454 +	<b>0.000</b>
	4	3	11.150	<b>0.000</b>
<b>GP</b>	1	3	4.459	<b>0.012</b>
	2	3	7.812	<b>0.001</b>
	3	3	6.357	<b>0.002</b>
	4	3	6.354	<b>0.002</b>

Table 3a

Respiration	Nearshore		Offshore	
	Control	Heat-treated	Control	Heat-treated
Day 1	5.21±1.47	7.88±0.35	11.95±1.30	17.0±2.15
Day 2	4.44±1.29	7.16±0.56	11.49±1.13	20.3±2.21
Day 3	2.78±1.25	8.85±1.42	8.29±0.76	21.9±2.10
Day 4	2.06±0.97	7.68±0.89	6.06±1.03	15.7±2.30

Table 3b

	Nearshore		Offshore	
	Control	Heat-treated	Control	Heat-treated
Day 1	19.9±7.35	20.7±1.93	25.8±3.02	43.3±6.34
Day 2	28.2±18.7	21.5±2.43	27.1±3.06	54.9±6.49
Day 3	29.1±1.35	15.1±4.87	34.1±4.51	59.7±6.47
Day 4	26.8±1.00	28.8±1.99	39.2±5.91	73.2±1.05

Table 4

	Day	df	F	p
<b>GP/R</b>	1	3	6.542	<b>0.001</b>
	2	3	1.469	0.243
	3	3	6.161	<b>0.002</b>
	4	3	1.605	0.217
<b>R</b>	1	3	6.911	<b>0.001</b>
	2	3	4.999	<b>0.006</b>
	3	3	3.666	<b>0.023</b>
	4	3	0.771	0.523
<b>GP</b>	1	3	1.536	0.224
	2	3	2.128	0.117
	3	3	3.855	<b>0.018</b>
	4	3	0.803	0.502

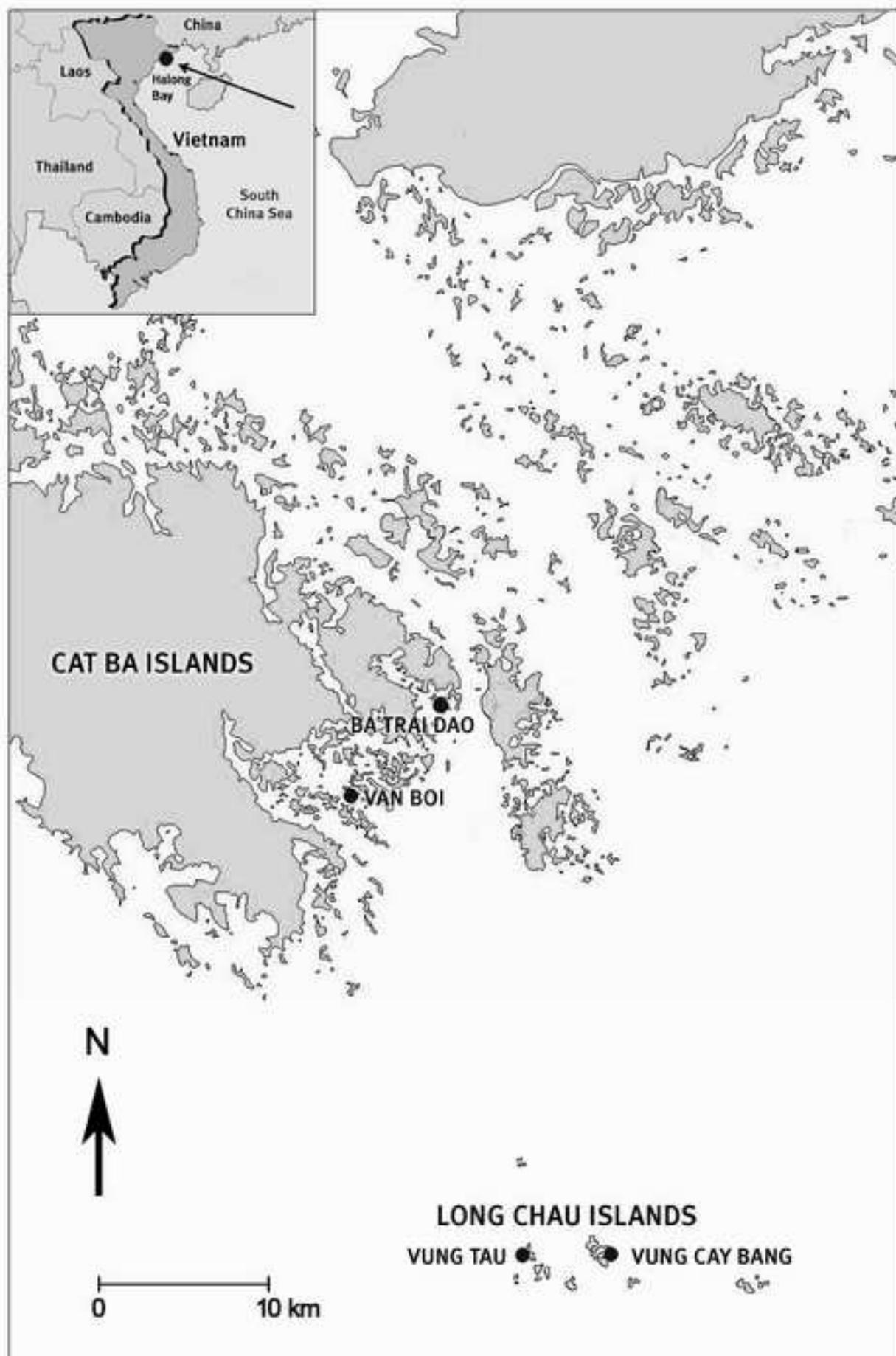
Table 5a

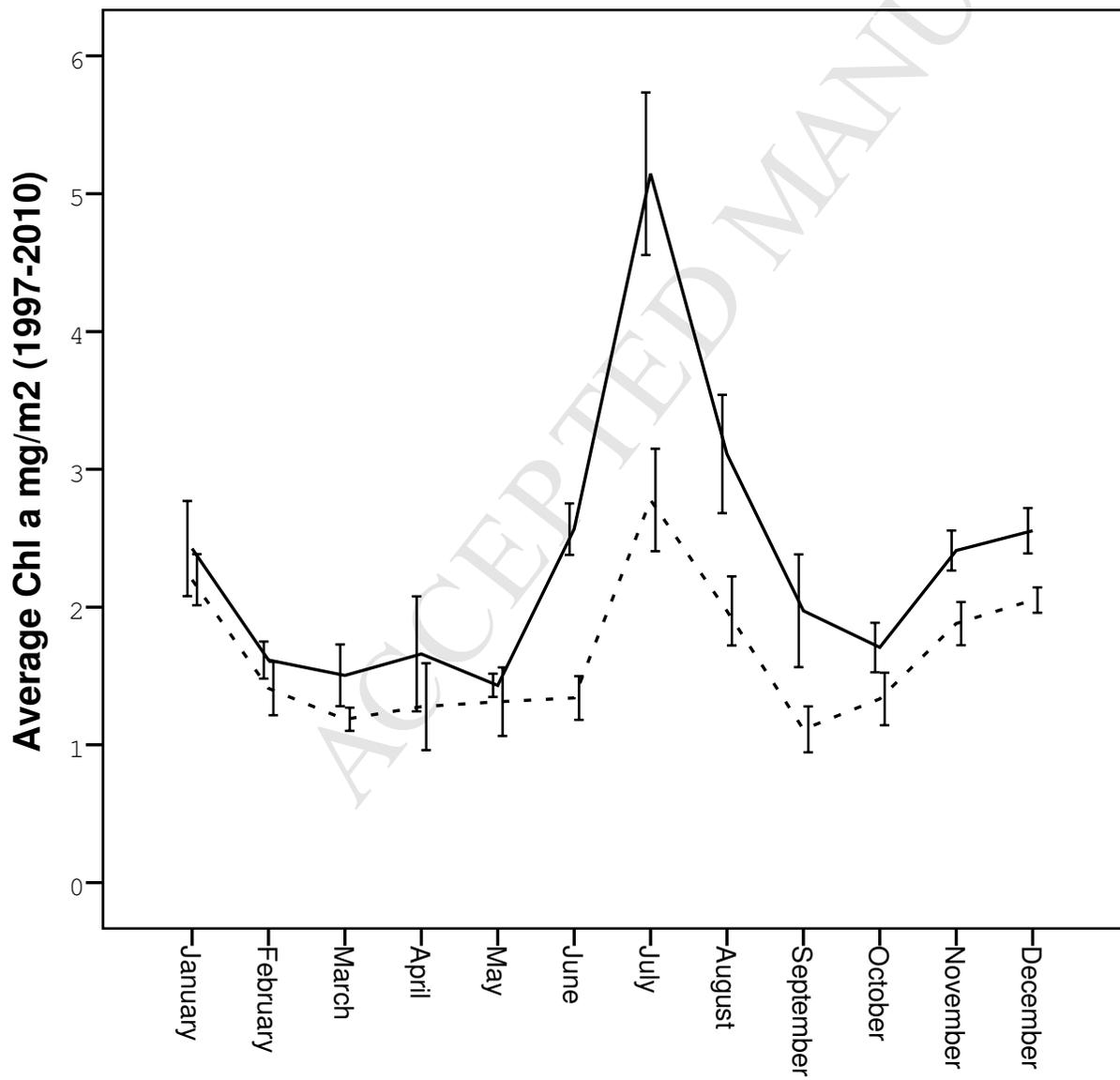
	Nearshore		Offshore	
	Control	Heat-treated	Control	Heat-treated
Day 1	6.29±0.79	15.9±2.16 **	5.99±0.92	9.61±2.39
Day 2	5.74±0.49	14.3±1.14	6.09±0.76	7.75±2.77
Day 3	4.69±0.98	9.08±1.56	3.21±0.79	5.84±1.50
Day 4	3.63±0.51	4.81±1.08	2.29±0.54	2.94±0.53

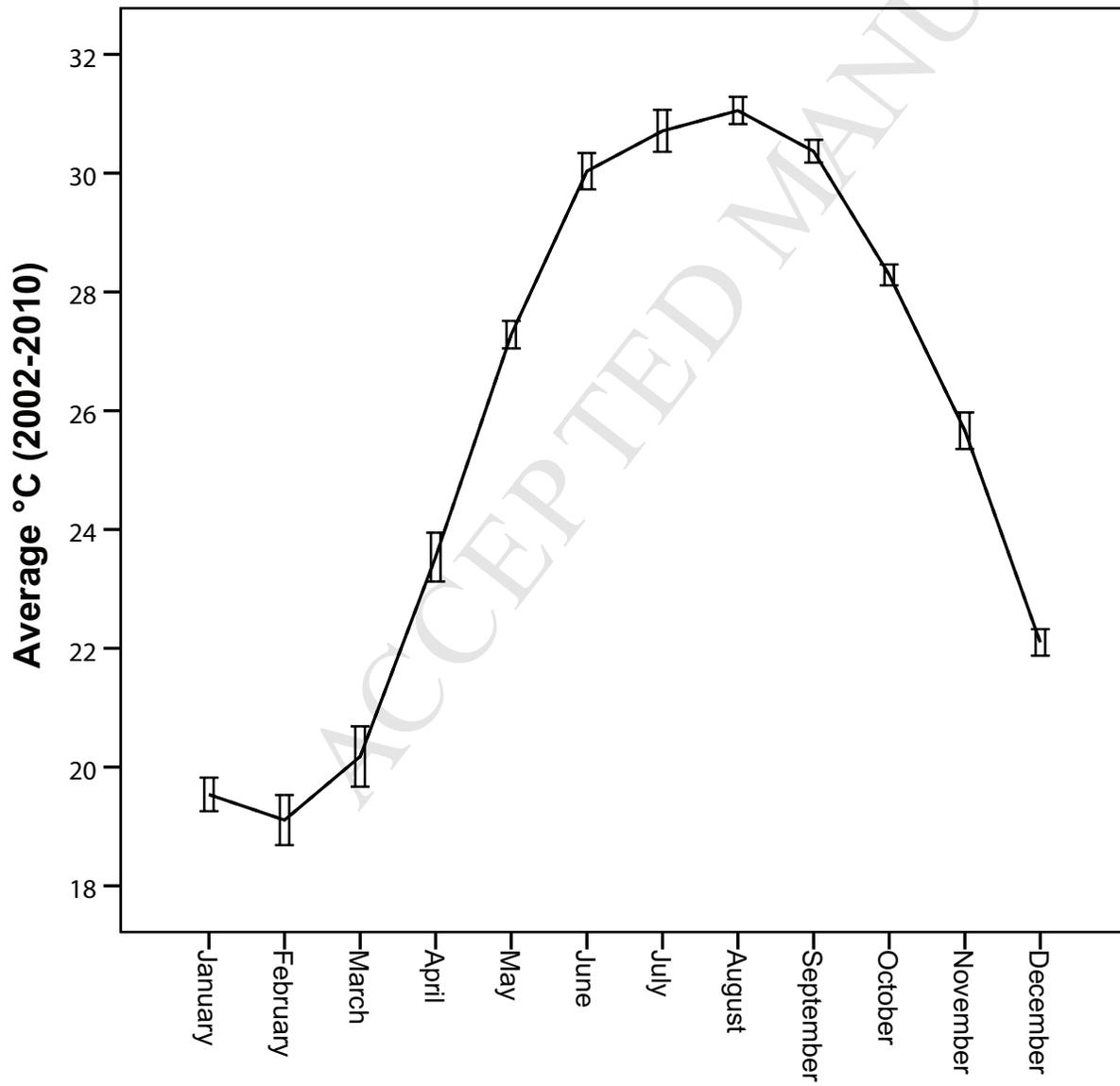
Table 5b

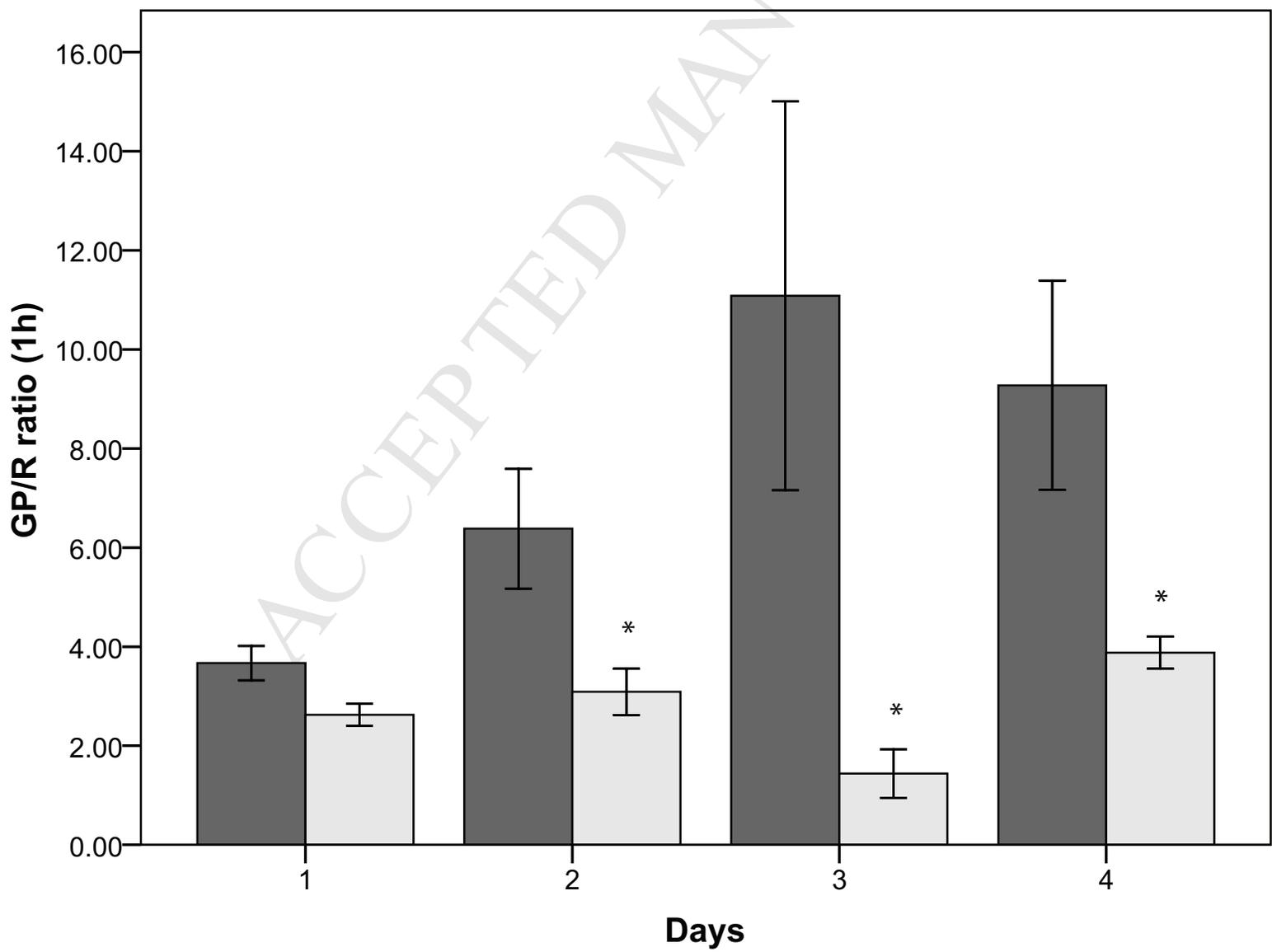
	Nearshore		Offshore	
	Control	Heat-treated	Control	Heat-treated
Day 1	21.7±3.97	31.3±4.62	19.9±2.12	22.6±4.79
Day 2	24.2±3.06	41.3±4.27	23.7±2.56	26.0±1.04
Day 3	32.5±5.31	48.2±7.12	21.8±3.15	22.6±7.85
Day 4	31.9±4.36	35.8±5.62	25.8±2.48	25.7±7.88

Figure 1









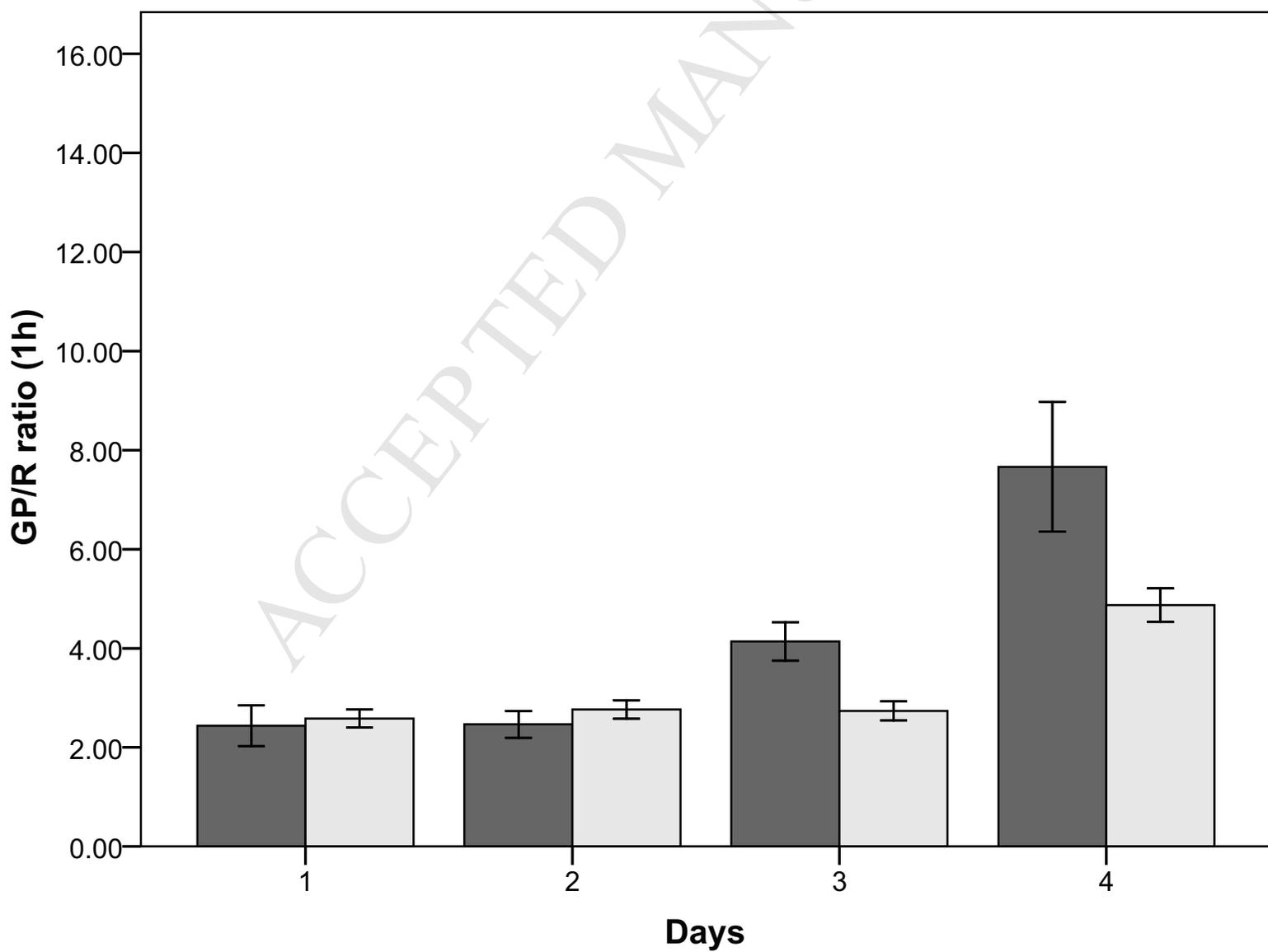


Figure 4a

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Figure 4b  
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