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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 α 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 Also, after 72 h these corals had withdrawn their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

1. Introduction

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

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

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

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

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

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

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

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

2. Material and methods

2.1. Study area

Halong Bay

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

2.2. Collection of corals

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

Although several environmental parameters differ between the near- and offshore area, temperature and salinity regimes were almost identical between the areas throughout the year (see Table 1 and Fig. 2a and 2b); and the ambient temperature and salinity during collection was 25.5 °C and 32 psu at all sites. Corals from the two reef areas thus have very similar thermal histories. Within each area, two reef sites were sampled. In the nearshore area, Ba Trai Dao Island (site A, N 20° 47' 20", E 107° 06' 13") and Van Boi Island (site B, N 20° 45' 35", E 107° 04' 24") were selected and in the offshore area, coral specimens were collected from Vung Cay Bang Island (site C, N 20° 37' 27", E 107° 09' 41") and Vung Tau Island (site D, N 20° 37' 21", E 107° 08' 08") (Fig 1). The corals were collected using a hammer and chisel. Two massive species, *Porites lutea* and *Galaxea fascicularis*, were selected and at each of the four sites 10 coral pieces (approximately 85 cm² and 120 cm² for *P. lutea* and *G. fascicularis* respectively) of each species were collected, except for one nearshore site (Van Boi) where no *G. fascicularis* and only 6 pieces of *P. lutea* could be found. Hence, 36 pieces of *P. lutea* and 30 pieces of *G. fascicularis* were collected in total. Immediately after collection, corals were transported to the outdoor laboratory at the Tram Bien Research Station in Do Son under low light condition and continuous aeration. After epiphytes and boring organisms had been carefully removed, the corals were put in aerated aquaria (20 litre each) with filtered and UV-treated seawater. The aquaria were placed in larger water-filled tanks (1 m³) in order to minimise temperature fluctuations (Nyström et al., 2001; Nordemar et al., 2003). The corals were allowed to acclimate to the set control temperature of 25.5 °C and 32 psu (ambient at site of collection) and thereafter kept at that temperature for 48 h before the experiment was started.

2.3. *Experimental setup*

The corals were evenly distributed in eight 20-litre aquaria using a randomized block design. Four of the aquaria were then placed in a heating tank (1 m³) representing temperature “exposure” and the other four were placed in a control tank (1 m³) with ambient water temperature. Aeration pumps mixed the seawater in both the aquaria and the tanks, thus maintaining high oxygen concentrations and distributing water temperature evenly. The water temperature in the exposure tank was increased using heating regulators (ZEBO 300W or FLUVAL Tronic 200W). The temperature was recorded every hour during daytime (between 10 am to 6 pm) and once in the evening as well as once in the early morning (at 9 pm and 6 am respectively) to verify constant temperature throughout a 24 h period before the experiment was started. Throughout the experiment, temperature was measured continuously during the physiological measurements. Between measurements, temperatures were recorded every second hour during daytime and once in the evening as well as once in the early morning (at 9 pm and 6 am respectively). The experiment lasted for 96 h (4 days) during which the temperature was gradually increased for three days, to mimic a natural gradual temperature increase, and then reduced to ambient for a 24-hour recovery period. It is well known that daily temperatures can undergo drastic changes on nearshore reef flats and in coastal lagoons, e.g. 25-33 °C within hours (Semesi et al., 2009). Normal summer temperature in Halong Bay is 30-31.5 °C (Nguyen 2004; Latypov 2005), and studies have shown that large increases (3-4

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

2.4. *Physiological measurements*

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

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

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

2.5. Statistical analysis

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

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

3. Results

3.1. *Galaxea fascicularis*

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

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

3.2. *Porites lutea*

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

4. Discussion

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

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

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

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

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

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

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

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

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

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

5. Conclusion

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

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

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

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

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

The data were acquired from the Giovanni online data system
(http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month;
downloaded 1 November 2010), which was developed and is maintained by the NASA
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Fig 3. *Galaxea fascicularis*. GP/R ratio $\pm$ SE. a) Nearshore corals a) Offshore corals. The
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Fig 4. *Galaxea fascicularis*. Polyp extension. a) Nearshore corals b) Offshore corals when
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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

List of tables

Table 1

	Offshore		Nearshore	
<u>Average (year 2005-2008, n=4)</u>	<i>Dry season^a</i>	<i>Rainy season^b</i>	<i>Dry season^a</i>	<i>Rainy season^b</i>
Salinity (psu)	32	26	32	25
pH	8.13	8.34	8.09	8.32
Sedimentation (g m ⁻² *day ⁻¹)	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 ⁻¹)	86.2±2.5		135.5±11.8	

Numbers show mean±SD. ^aThe dry season lasts from October to May, ^b the rainy season lasts from June to September, * average of 2 measurements March-May 2003.

Table 2

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

Table 3a

	Nearshore		Offshore	
Respiration	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	
	Gross production 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
GP/R	1	3	6.542	0.001
	2	3	1.469	0.243
	3	3	6.161	0.002
	4	3	1.605	0.217
R	1	3	6.911	0.001
	2	3	4.999	0.006
	3	3	3.666	0.023
	4	3	0.771	0.523
GP	1	3	1.536	0.224
	2	3	2.128	0.117
	3	3	3.855	0.018
	4	3	0.803	0.502

Table 5a

	Nearshore		Offshore	
	Respiration 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	
	Gross production 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 2a

Figure 2b

Figure 4a

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Figure 4b

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Figure 5a