

M. Nyström · I. Nordemar · M. Tedengren

Simultaneous and sequential stress from increased temperature and copper on the metabolism of the hermatypic coral *Porites cylindrica*

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Abstract Stressors arising from human activities may interact not only with each other, but also with natural disturbances. However, experimental studies on disturbance complexity and physiological responses of corals to sublethal stresses, especially those due to human activities, are surprisingly few. In this study we investigated the stress response of the scleractinian coral *Porites cylindrica* after 24 h of exposure to copper ($11 \mu\text{g Cu l}^{-1}$) and increased temperature (following a 4°C above-ambient curve), separately and in combination. We also investigated the effect of sequential stress where corals pre-exposed to increased temperature for 24 h were exposed to copper (for 24 h) after a 5-day recovery period. Changes in gross primary production (Pg: per milligram chlorophyll *a* per hour) and respiration (R: per square centimeter per hour) in terms of dissolved oxygen were used as indicators of stress. The results show that heat and the combination of heat and copper significantly reduced production rate. However, corals exposed to elevated temperature displayed a significantly higher production rate following the 5-day recovery period. The combination of the two stressors showed no additive or synergistic effects. Copper alone had no effect on the production rate. However, corals that were pre-exposed to increased temperature and again exposed to copper after 5 days displayed a significant reduction in production rate. The respiration rate was significantly reduced by all treatments, although no significant differences between treatments were detected. The results presented here illustrate how a stressor that does not affect corals when acting in isolation may do so in sequential combination with other stressors.

Introduction

Widespread mass bleaching of coral reefs has been extensively reported around the world over the past 15 years (Brown 2000). Coral bleaching occurs when the coral's white skeleton becomes visible under its transparent tissue as a result of loss of its symbiotic unicellular microalgae (zooxanthellae) and/or microalgal pigment. Bleaching is an ecologically significant response, since the polyp receives a substantial part of its energy from the zooxanthellae (Muller-Parker and D'Elia 1997), and any disruption of this relationship will affect photosynthetic potential, coral growth, and reproductive output and may eventually kill the coral (Szmant and Gassman 1990; Richmond 1997). Coral bleaching has received increasing attention in the literature over the past two decades and has generally been associated with increased seawater temperature and solar radiation (e.g. Glynn 1993; Hoegh-Guldberg 1999; Wilkinson 1999). Corals are not homoiothermic (Hoegh-Guldberg and Smith 1989), and a temperature increase of $2\text{--}4^\circ\text{C}$ is known to cause coral bleaching within days, or within weeks with a temperature increase of $1\text{--}2^\circ\text{C}$ (Brown 1997a; Berkelmans and Willis 1999). However, corals may be able to cope with elevated temperature by micro-adaptive combinations of symbiotic algae (Rowan et al. 1997) and biochemical defense mechanisms, such as the induction of heat-shock proteins (Black et al. 1995; Sharp et al. 1997).

Bleaching is a general stress response in corals exposed to a wide variety of stressors; e.g. heavy metals, pesticides, and increased sedimentation (Harland and Brown 1989; Brown 1997a, 2000). Since the influence of human activities has altered the natural-disturbance regimes of coral reefs (Richmond 1993; Nyström et al. 2000), it has been suggested that global mass-bleaching events will occur more frequently in the future, owing to several local, but widely distributed, causes of disturbance (e.g. Hoegh-Guldberg 1999). In some areas man-made disturbances arrive so frequently that there is little

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M. Nyström (✉) · I. Nordemar · M. Tedengren
Department of Systems Ecology, Stockholm University,
10691 Stockholm, Sweden
E-mail: magnusn@system.ecology.su.se
Fax: +46-8-158417

or no time for recovery; i.e. the disturbances have become chronic background stresses (Connell et al. 1997). Eutrophication, sedimentation, overfishing, and pollution are known examples. This suggests that corals are not only more susceptible to a disturbance superimposed on the existing ones, but also that additive or synergistic effects might be generated. As Brown (1997a) states: "In a world subject to resource exploitation and potential global warming, multiple stresses are more likely to be the norm for the next two decades".

Although the heavy metal copper is an essential element for all organisms (Depledge and Rainbow 1990), it is also known as one of the most common marine pollutants, with coastal run-offs, coastal and offshore mining, anti-fouling paint, and industrial outlets as known sources (Jones 1997a). Since heavy-metal pollution is generally very localized (Brown 2000; but see Guzmán and Jiménez 1992), near-shore coral reefs are more likely to be exposed. Despite increasing human influence on the coral-reef environment, there are relatively few studies that investigate the effects of man-made disturbances on coral reefs (Hatcher 1999). Literature on the effects of heavy metals on the physiology of corals is even more limited (Howard and Brown 1984; Wilkinson 1999), and most studies deal with the incorporation of heavy metals in coral skeleton; e.g. as a proxy of environmental changes (Guzmán and Jiménez 1992; Peters et al. 1997; Bastidas and García 1999; Esslemont 1999).

Although single stresses rarely occur in nature (Brown 1997a, b), most physiological studies investigate single-parameter responses (e.g. Muthiga and Szmant 1987; Coles and Jokiel 1992; Moberg et al. 1997). Surprisingly, there is almost no information on synergistic interaction and the effects of multiple stressors on corals (but see Porter et al. 1999). To our knowledge, ours is the first study to investigate physiological effects on corals of stressors that arrive sequentially, i.e. corals pre-exposed to increased temperature and then exposed to copper, and simultaneously, i.e. corals exposed to copper and increased temperature at once.

In the present study we use changes in levels of dissolved oxygen in production and respiration rates, per chlorophyll *a* and surface area, respectively, as an indicator of stress (Coles and Jokiel 1977; Moberg et al. 1997; Porter et al. 1999). This is a simple and quick method that can be used by researchers in most countries.

Materials and methods

Collection of corals

This study was conducted from November to December 1999 at the MSI (Marine Science Institute, University of the Philippines) field station in Bolinao, northern Philippines. Branches (approximately 10 cm in length) from within and between different coral colonies of the hermatypic coral *Porites cylindrica* were collected from Cuenco Island (N16.21563, E120.03646), within the Hundred Islands archipelago, from approximately 5 m depth. The specimens were transported back to the laboratory under reduced-light conditions.

After epiphytes and boring organisms had been carefully removed, the corals were put in a flow-through tank for 5 days to acclimate to laboratory conditions. During the recovery period the corals were shaded (using layers of fishing net) from natural sunlight to avoid damage by high light intensities.

Exposure of corals

Ten branches of corals were randomly selected and exposed to increased temperature ("pre-exposed" corals) in aerated exposure tanks (72 l, approximately 0.4 m deep) for 24 h. During exposure the corals were shaded using layers of fishing net (see above). The temperature increase followed the diurnal variation in water temperature in the laboratory by approximately 4°C (i.e. maximum 35°C at midday and minimum 31°C at night for exposed corals). Temperature in the field was between 29°C and 30°C at midday (at 4 m depth) which was the same as for the water in the lab at midday. After exposure all corals were put in the flow-through tank for 5 days to recover. After the recovery period the corals were placed in the exposure tanks, where copper was added, together with corals that had not been exposed to increased temperature. Some other previously unexposed corals were exposed to elevated temperature and to the combination of increased temperature and copper. The six treatments were as follows: ambient (previously unexposed), elevated temperature (previously unexposed), copper (11 µg l⁻¹) (previously unexposed), elevated temperature and copper (previously unexposed), ambient (pre-exposed), copper (pre-exposed). Thus, the control corals experienced the same treatment (i.e. being in exposure tanks in ambient water and temperature) as corals being exposed to increased temperature and/or copper. The experimental setting is illustrated in Fig. 1.

Heating regulators (Jäger, TSRH, 300 W) were used to increase the temperature, and readings were made every 5–15 min between 8.00 a.m. and 6.00 p.m. During the night, the readings were made only every 2nd hour since the temperature was more stable.

Corals exposed to copper were incubated for 24 h in 11.0 µg Cu l⁻¹ using a copper sulfate stock solution. The study was repeated after 1 week using new specimens in order to increase the number of replicates.

Production and respiration measurements

To investigate the physiological response of *P. cylindrica* to heat, copper, and a combination of both, changes in levels of dissolved

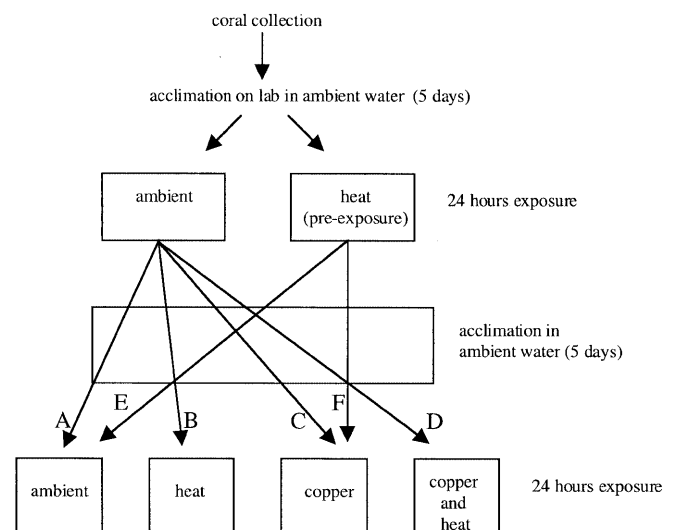


Fig. 1 Experimental set-up. $n = 5$ for all treatments. Repeated sets of data gives $n = 10$ for all treatments. For statistical analysis see below

oxygen in light (net production) and dark (respiration) were used as an indicator of stress (Moberg et al. 1997). The corals were placed in transparent enclosures containing water from the specific treatment and submerged in a cooling bath to limit temperature increase during measurements. Initial production values in light were measured using an oxygen meter (OXI 196), and final values were taken after 1 h. The water was stirred gently before measurement in order to distribute the dissolved oxygen evenly in the water volume. Light intensities were continuously recorded, using a LiCor lightmeter, and were never less than $1500 \mu\text{E m}^{-2}\text{s}^{-1}$, therefore indicating a maximum production rate (Chalker et al. 1983). Temperature showed an average increase of $2\text{--}3^\circ\text{C}$ during measurements. For respiration measurements the corals were kept in darkness for 1 h. As for the production measurements, readings were taken initially and after 1 h. However, before the initial values were taken, the enclosures were kept in darkness for 20 min to avoid a time lag in production (Moberg et al. 1997). No temperature increase was observed. Respiration was added to net production in order to calculate gross primary production, assuming constant respiration over the diurnal cycle (McCloskey et al. 1978).

Surface-area determination

Respiration data were correlated to surface area by weighing the specimens before and after they were immersed in hot wax (Stambler et al. 1991). For production comparisons, measurements were correlated with the chlorophyll-*a* content of the specimens (see below).

Determination of chlorophyll

In the wait for transportation to MSI in Manila and analysis of the chlorophyll content, the corals were stored in a freezer wrapped in aluminum foil. During transportation the samples were kept frozen in foam boxes filled with ice. In the laboratory a tip (of approximately equal size, 1–2 cm) from each coral replicate was taken for chlorophyll analysis. The surface area of the tips was calculated using the Marsh (1970) aluminum-foil method. The reasons for using only the tip were that the coral specimens used in the experiment were too big to be mortared and that chlorophyll could be extracted in one single extraction. We are fully aware that the chlorophyll content and zooxanthella genotypes can vary from one part of the coral to another (e.g. Rowan et al. 1997). However, we argue that this method is appropriate, since we used a part of an outer branch tip (of equal size) for all corals, which gives a relative difference between replicates and treatments. The chlorophyll was extracted in 90% acetone in darkness (at $+8^\circ\text{C}$) for 24 h. Samples were then centrifuged and analyzed for chlorophyll *a* using a Spectronic 21D spectrophotometer. Concentrations were calculated according to the equations of Jeffrey and Humphrey (1975).

Statistical analysis

The data were analyzed for homogeneity of variances (Cochran's test, $P < 0.05$). Two-way ANOVA (Statistica 4.0 software package) was used to compare the different treatments between days. One-way ANOVA was used to compare different treatments. Tukey's Honest Significant Difference Test ($P < 0.05$) was used as a post hoc test.

Results

Statistical analysis of the data from the two separate runs showed that there were no significant differences in gross production in terms of milligrams of oxygen per milligram chlorophyll *a* per hour ($\text{Pg}/\text{chl } a$) or respiration in terms of micrograms of oxygen per square centimeter per hour (R/cm^2) between days and treatment. Thus, the two data sets were pooled.

The effects of elevated temperature and copper on production rate

Visual inspection showed a gradual discoloration of tissue where corals exposed to the combination of copper and heat displayed a greater loss of color, followed by corals exposed to copper and corals exposed to heat. Control corals remained fully colored. There was a significant reduction in the photosynthetic rate when corals were exposed to heat ($P < 0.05$), and to the combination of heat and copper ($P < 0.05$). There was no significant effect of copper alone. Moreover, no significant difference between treatments was detected. Thus, there was no observed synergistic effect of heat and copper (Fig. 2, Table 1).

Corals that were pre-exposed to increased temperature showed a slight loss of coloration. However, after 5 days of recovery, these corals had recovered their colour completely. After the second exposure, this time to copper, the pre-exposed corals were obviously pale. The photosynthetic rate in corals pre-exposed to heat was significantly higher than in control corals ($P < 0.05$). In contrast to the insignificant effect on corals exposed to copper alone, the photosynthetic rate decreased significantly ($P < 0.001$) for corals that were first pre-exposed to increased temperature and subsequently exposed to copper (Fig. 2, Table 1).

The effects of elevated temperature and copper on respiration rate

Respiration rates were significantly reduced by exposure to copper ($P < 0.001$), elevated temperature ($P < 0.001$),

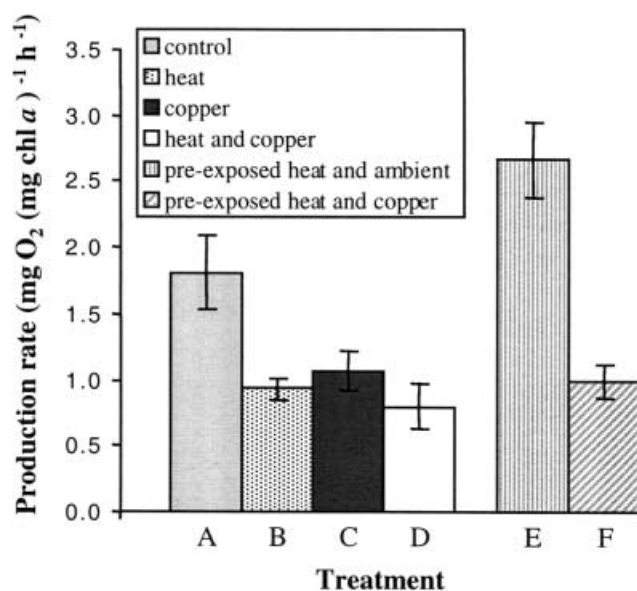


Fig. 2 Effects of copper and elevated temperature (heat) on the gross production rate [$\text{mg O}_2 (\text{mg chl } a)^{-1} \text{h}^{-1}$] \pm SE. There were no significant effects between treatments. $n = 10$ for each treatment. A summary of statistical comparisons is given in Table 1

Table 1 Results of statistical comparisons of the physiological data for *Porites cylindrica* exposed to elevated temperature and to copper and the combination of both. Gross production (*Pg*) per

milligram chlorophyll *a* (*chl a*) per hour; respiration (*R*) per square centimeter per hour. SE of means are in parentheses; *n.s.* not significant; *n* = 10 for each treatment

Treatment	<i>Pg</i> mg O ₂ (mg chl <i>a</i>) ⁻¹ h ⁻¹	<i>R</i> μg O ₂ cm ⁻² h ⁻¹	Treatment interaction					
			(* is <i>P</i> < 0.05, ** is <i>P</i> < 0.01, *** is <i>P</i> < 0.001)					
			A	B	C	D	E	F
A) Control	1.8 (±0.3)		—	*	n.s.	**	*	*
B) Heat	0.9 (±0.1)		*	—	n.s.	n.s.	***	n.s.
C) Copper	1.1 (±0.1)		n.s.	n.s.	—	n.s.	***	n.s.
D) Copper and heat	0.8 (±0.2)		**	n.s.	n.s.	—	***	n.s.
E) Pre-exposed	2.7 (±0.3)		*	***	***	***	—	***
F) Pre-exposed copper	1.0 (±0.1)		*	n.s.	n.s.	n.s.	***	—
A) Control		10.7 (±2.1)	—	**	**	*	n.s.	n.s.
B) Heat		4.6 (±0.5)	**	—	n.s.	n.s.	**	n.s.
C) Copper		4.7 (±0.9)	**	n.s.	—	n.s.	***	n.s.
D) Copper and heat		5.5 (±1.1)	*	n.s.	n.s.	—	***	n.s.
E) Pre-exposed		15.5 (±2.0)	n.s.	***	***	***	—	***
F) Pre-exposed copper		7.0 (±1.4)	n.s.	n.s.	n.s.	n.s.	***	—

and the combination of both (*P* < 0.05), compared to the controls. However, there was no difference in respiration rate between controls and corals pre-exposed to elevated temperature followed by the 5 days of recovery. There was no significant difference between treatments (Fig. 3, Table 1).

Discussion

Increased temperatures and heavy metals are both known to cause physiological stress in corals (e.g. Har-

land and Brown 1989; Glynn 1993). Corals are not homoiothermic (Hoegh-Guldberg and Smith 1989) and short-term temperature stress can cause changes in basal metabolism, such as effects on animal respiration and zooxanthella photosynthesis (Porter et al. 1999). Although *Porites cylindrica* showed a visual gradation of color loss in the different treatments (following the discoloration gradient: heat and copper > heat > copper) no significant difference in chlorophyll-*a* concentration was detected. This result is consistent with observations made by Jones (1997a) on *Acropora formosa* exposed to copper, and could be explained by retraction of coral tissue exposing the white skeleton without any loss of zooxanthellae and/or photosynthetic pigments (Brown et al. 1994). However, retraction of polyps (avoiding contact with the stressor) implies that the zooxanthellae will be less exposed to sunlight, which in turn can lead to a reduced photosynthetic rate. On the other hand, loss of zooxanthellae does not necessarily imply a reduction in photosynthetic pigments, since production of zooxanthellar chlorophyll *a* can increase in the remaining symbionts (Jones 1997b). This could be an alternative explanation to the non-significant difference in chlorophyll-*a* concentration between treatments.

Effects on production rates

Several studies have investigated the effects of temperature on photosynthetic efficiency in isolated zooxanthellae. For example, studies on the zooxanthella *Symbiodinium bermudense* have demonstrated that increased temperature hampers photosynthetic performance (Lesser 1996). Moreover, Iglesias-Pietro et al. (1992) showed that photosynthesis in the symbiotic zooxanthella *Symbiodinium microadriaticum* was impaired at temperatures above 30°C and ceased at 34–36°C. Results obtained from the present study (Figs. 2

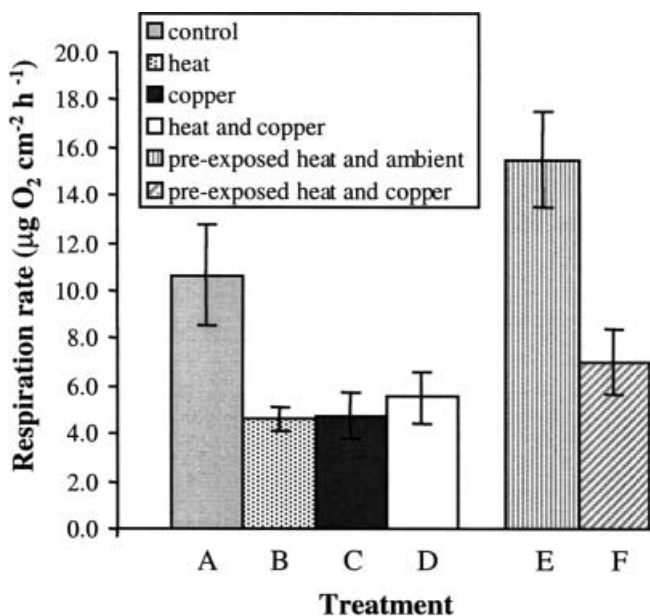


Fig. 3 Effects of copper and elevated temperature (heat) on the respiration rate (μg O₂ cm⁻² h⁻¹) ± SE. There were no significant effects between treatments. *n* = 10 for each treatment. A summary of statistical comparisons is given in Table 1

and 3, and Table 1) support these studies, since photosynthetic rate in corals exposed to increased temperature (B) was significantly reduced by 50%, probably as a consequence of heat damage near or at the centre of photosystem II in the zooxanthellae (Samson et al. 1988). This is in contrast to Coles and Jokiel (1977) who showed a slow increase in production rate in *Montipora annularis* exposed to elevated temperature. However, corals that were allowed to recover for 5 days after being exposed to increased temperature (E) displayed a significantly higher photosynthetic rate (50%) compared to corals that had not been previously exposed (A). A possible explanation for this is a compensation in metabolism in order to repair and/or stabilize impacted physiological processes due to the previously altered environmental condition (see Gates and Edmunds 1999).

Copper is essential to corals in low concentrations, acting as a catalyst of enzyme systems for example (Depledge and Rainbow 1990), but higher concentrations may interfere with coral metabolism (Depledge and Rainbow 1990; Nyström et al. 1997). For example, copper has been suggested as inhibiting electron transport on the oxidizing side of photosystem II (Samson et al. 1988). The copper level in this study ($11 \mu\text{g l}^{-1}$) did not significantly affect the photosynthetic rate when occurring as a single parameter (C). It has been speculated that corals may to some extent be able to regulate heavy-metal uptake by regulation of zooxanthella density (Harland and Brown 1989). This possible mechanism cannot be explained by our results, since no analysis of number of zooxanthellae was conducted. However, the corals in this study were subjected to a static and relatively short-term (24 h) exposure to copper, and length of exposure is often critical to the signs of stress (Porter et al. 1999). Thus, it is possible (or even likely) that production will be affected in the long term even at lower concentrations than used here when corals are exposed to continuous pollution in their natural environment. The combination of heat and copper (D) reduced the production rate significantly by 56%. Our results show no significant difference in production rate between heat, copper and the combination of heat and copper (i.e. B versus D), thus indicating no additive or synergistic effects. It was interesting, however, that corals pre-exposed to increased temperature and then to copper (F) displayed a significant reduction (44%) in the photosynthetic rate. The results presented here illustrate how a stressor that does not affect corals in isolation may do so in sequential combination with other stressors. One might have expected corals pre-exposed to elevated temperature to be more tolerant to copper when arriving sequentially, since relatively recent studies have shown that a heat shock increases heavy-metal tolerance in crustaceans (Bond and Bradley 1995) and bivalves (Tedengren et al. 1999) by induction of heat-shock proteins (hsp). Induction of hsp has also been demonstrated in symbiotic sea anemones (Sharp et al. 1994) and corals (e.g. Sharp et al. 1994; Black et al. 1995) when exposed to increased temperatures. However, the sig-

nificance of the protection from copper offered by such defenses in corals is still unknown (Brown 1997b).

Effects on respiration rates

Elevated temperatures (for hours) are known to cause increased respiration (Porter et al. 1999). For example, Coles and Jokiel (1977) demonstrated an increased measured respiration rate when *Montipora* sp. was exposed to elevated temperature. In this study, however (Figs. 2, 3, Table 1), respiration was highly significantly reduced (57%) by increased temperature (B). Porter et al. (1989) showed that prolonged elevated temperature (several days) reduced the respiration rate in *Montastrea annularis*, but this is less pronounced than the reduction in production rate. Our results showed no significant difference between the decreased rates of production and respiration under exposure to increased temperature. However, in contrast to the primary production, respiration rates did not differ in corals pre-exposed to elevated temperature after the 5-day recovery period (E) compared to the controls (A). Corals exposed to copper (C) alone showed a highly significant decrease (56%) in respiration rate. In contrast, corals that had first been exposed to elevated temperature and then copper (F) did not show a significant response in respiration.

Thus, although no additive or synergistic effects were demonstrated, our results illustrate how human modification of the coral-reef environment (i.e. contribution to chronic background stress) may change the corals' tolerance to future disturbances.

Future concerns

Long-term stress will most likely have negative impacts on growth and reproduction and increase the chance of bacterial infections (Howard and Brown 1984; Loya 1990; Szmant and Gassman 1990; Brown 1997c). Moreover, heavy metals are known not only to affect coral metabolism, but also to reduce fertilization (Reichelt-Brushett and Harrison 1999) and interfere with chemically mediated signals that are involved in synchronizing reproduction, metamorphosis, and coral-larva settlement (Richmond 1997). This is of particular concern, since reproduction often occurs during the rainy season when coastal pollution reaches its peak owing to heavy land run-off (Richmond 1993). Moreover, corals in their larval stage have been shown to be more sensitive to copper than adult corals (e.g. Reichelt-Brushett and Harrison 1999). This suggests that although coral reefs are not directly exposed, pollution barriers may inhibit new recruitment by affecting coral-larva survival. This will most likely have implications for the re-establishment of corals after reef degradation and for managers dealing with coastal-zone management planning.

This raises questions such as: What impacts may be superimposed by increased man-made pollution in the

face of future altered disturbance regimes, such as increased seawater temperature, increased frequency of storms etc. (Nyström et al. 2000)? To what extent is the potential for re-establishment and reorganization threatened?

Combinations of stressors are frequently discussed in the literature and have often been blamed for causing additive or synergistic effects on corals and coral communities, but few studies have experimentally demonstrated these "facts". For example, in the short-term elevated temperature and salinity have shown mitigating effects on coral metabolism (Porter et al. 1999; our unpublished data). Thus, it is likely that the response to multiple-stressor exposure is combination-specific, where some have antagonistic effects and others additive or synergistic effects. This calls for long-term investigations on low-level stresses, and for studies dealing with the complexity by which disturbances may interact, and how this may influence recovery and reorganization following coral-reef degradation.

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References

- Bastidas C, García E (1999) Metal content on the reef coral *Porites asteroides*: an evaluation of river influence and 35 years of chronology. *Mar Pollut Bull* 38:899–907
- Berkelmans R, Willis BL (1999) Seasonal and local spatial patterns in the upper thermal limits of corals on the inshore central Great Barrier Reef. *Coral Reefs* 18:219–228
- Black NA, Voellmy R, Szmant AM (1995) Heat shock protein induction in *Montastrea faveolata* and *Aiptasia pallida* exposed to elevated temperature. *Biol Bull* 188:234–240
- Bond JA, Bradley BP (1995) Heat shock reduces the toxicity of malathion in *Daphnia magna*. *Mar Environ Res* 39:209–212
- Brown BE (1997a) Disturbance to reefs in recent times. In: Birkeland C (ed) *Life and death of coral reefs*. Chapman and Hall, New York, pp 354–379
- Brown BE (1997b) Coral bleaching: causes and consequences. *Coral Reefs* 16:129–138
- Brown BE (1997c) Adaptation of reef corals to physical environmental stress. *Adv Mar Biol* 31:221–229
- Brown BE (2000) The significance of pollution in eliciting the 'bleaching' response in symbiotic cnidarians. *Int J Environ Pollut* 13:392–415
- Brown BE, Le Tissier MDA, Dunne RP (1994) Tissue retraction in the scleractinian coral *Coeloseris mayeri*, its effects upon coral pigmentation, and preliminary implications for heat balance. *Mar Ecol Prog Ser* 105:209–218
- Chalker BE, Dunlap WC, Oliver JK (1983) Bathymetric adaptation of reef-building corals at Davies Reef, Great Barrier Reef, Australia. *J Exp Mar Biol Ecol* 73:37–56
- Coles SL, Jokiel PL (1977) Effects of temperature on photosynthesis and respiration in hermatypic corals. *Mar Biol* 43:209–216
- Coles SL, Jokiel PL (1992) Effects of salinity on coral reefs. In: Connell DW, Hawker DW (eds) *Pollution in tropical aquatic systems*. CRC Press, London
- Connell JH, Hughes TP, Wallace CC (1997) A 30-years study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol Monogr* 67:461–488
- Depledge MH, Rainbow PS (1990) Models of regulation and accumulation of trace metals in marine invertebrates. *Comp Biochem Physiol* 97:1–7
- Esslemont G (1999) Heavy metals in corals from Heron Island and Darwin Harbor, Australia. *Mar Pollut Bull* 38:1051–1054
- Gates RD, Edmunds PJ (1999) The physiological mechanisms of acclimatization in tropical corals. *Am Zool* 39:30–43
- Glynn PW (1993) Coral reef bleaching ecological perspective. *Coral Reefs* 12:1–17
- Guzmán HM, Jiménez CE (1992) Contamination of coral reefs by heavy metals along the Caribbean coast of Central America. *Mar Pollut Bull* 24:554–561
- Harland AD, Brown BE (1989) Metal tolerance in the scleractinian coral *Porites lutea*. *Mar Pollut Bull* 20:353–357
- Hatcher BG (1999) Varieties of science for coral reef management. *Coral Reefs* 18:305–306
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshw Res* 8: 839–866
- Hoegh-Guldberg O, Smith GJ (1989) The effect of sudden changes in temperature, light, and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana. *J Exp Mar Biol Ecol* 129:279–300
- Howard LS, Brown BE (1984) Heavy metals and reef corals. *Oceanogr Mar Biol Annu Rev* 22:195–210
- Iglesias-Pietro R, Matta JL, Robins WA, Trench RK (1992) Photosynthetic response to elevated temperature in the symbiotic dinoflagellate *Symbiodinium microadriaticum* in culture. *Proc Natl Acad Sci USA* 89:10302–10305
- Jeffrey SW, Humphrey GF (1975) New spectrophotometric equations for determining chlorophylls *a*, *b*, *c*₁ and *c*₂ in higher plants, algae and natural phytoplankton. *Biochem Physiol Pflanzen* 167:191–194
- Jones RJ (1997a) Zooxanthellae loss as a bioassay for assessing stress in corals. *Mar Ecol Prog Ser* 149:163–171
- Jones RJ (1997b) Changes in zooxanthellar densities and chlorophyll concentrations in corals during and after a bleaching event. *Mar Ecol Prog Ser* 158:51–59
- Lesser MP (1996) Elevated temperatures and ultraviolet radiation cause oxidative stress and inhibit photosynthesis in symbiotic dinoflagellates. *Limnol Oceanogr* 41:271–283
- Loya Y (1990) Changes in a Red Sea coral community structure: a long-term case history study. In: Woodwell GM (ed) *The Earth in transition: patterns and processes of biotic impoverishment*. Cambridge University Press, Cambridge, pp 369–384
- Marsh JA (1970) Primary productivity of reef-building calcareous algae. *Ecology* 51:255–263
- McCloskey LR, Wethey DS, Porter JW (1978) Measurement and interpretation of photosynthesis and respiration in reef corals. In: Stoddart DR, Johannes RE (eds) *Coral reefs: research methods*. Monographs on oceanographic methodology, vol 5. UNESCO, Paris, pp 379–396
- Moberg F, Nyström M, Tedengren M, Kautsky N, Jarayabhand P (1997) Effects of reduced salinity on the rates of photosynthesis and respiration in the hermatypic corals *Porites lutea* and *Pocillopora damicornis*. *Mar Ecol Prog Ser* 157:53–59
- Muller-Parker G, D'Elia CF (1997) Interactions between corals and their symbiotic algae. In: Birkeland C (ed) *Life and death of coral reefs*. Chapman and Hall, New York, pp 96–113
- Muthiga NA, Szmant AM (1987) The effects of salinity stress on the rates of aerobic respiration and photosynthesis in the hermatypic coral *Siderastrea siderea*. *Biol Bull* 173:539–551
- Nyström M, Moberg F, Tedengren M (1997) Natural and anthropogenic disturbance on reef corals in the inner Gulf of

- Thailand: physiological effects of reduced salinity, copper and siltation. Proceedings of the 8th International Coral Reef Symposium 2:1893–1898. Smithsonian Tropical Research Institute, Balboa, Panama
- Nyström M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol Evol* 15:413–417
- Peters EC, Gassman NJ, Firman JC, Richmond RH, Power EA (1997) Ecotoxicology of tropical ecosystems. *Environ Toxicol Chem* 16:12–40
- Porter JW, Fitt WK, Spero HJ, Rogers CS, White MW (1989) Bleaching in reef corals: physiological and stable isotopic responses. *Proc Natl Acad Sci USA* 86:9342–9346
- Porter JW, Lewis SK, Porter KG (1999) The effect of multiple stressors on the Florida Keys coral reef ecosystem: a landscape hypothesis and a physiological test. *Limnol Oceanogr* 44:941–949
- Reichelt-Brushett AJ, Harrison PL (1999) The effect of copper, zinc and cadmium on fertilization success of gametes from scleractinian reef corals. *Mar Pollut Bull* 38:182–187
- Richmond RH (1993) Coral reefs: present problems and future concerns resulting from anthropogenic disturbance. *Am Zool* 33:524–536
- Richmond RH (1997) Reproduction and recruitment in corals. In: Birkeland C (ed) *Life and death of coral reefs*. Chapman and Hall, New York, pp 175–197
- Rowan R, Knowlton N, Baker A, Jara J (1997) Landscape ecology of algal symbionts creates variation in episodes of bleaching. *Nature* 388:265–269
- Samson G, Morissette J, Popovic R (1988) Copper quenching of the variable fluorescence in *Dunaliella tertiolecta*. New evidence for a copper inhibition effect on PSII photochemistry. *Photochem Photobiol* 48:329–332
- Sharp VA, Miller D, Bythell JC, Brown BE (1994) Expression of low molecular weight hsp-70 related polypeptides from the symbiotic sea-anemone *Anemonia viridis* Forskall in response to heat-shock. *J Exp Mar Biol Ecol* 179:179–193
- Sharp VAB, Brown BE, Miller D (1997) Heat shock protein (hsp 70) expression in the tropical reef coral *Goniopora djiboutiensis*. *J Therm Biol* 22:11–19
- Stambler N, Popper N, Dubinsky ZVY, Stimson J (1991) Effects of nutrient enrichment and water motion on the coral *Pocillopora damicornis*. *Pac Sci* 45:299–307
- Szmant AM, Gassman NJ (1990) The effects of prolonged 'bleaching', on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. *Coral Reefs* 8:217–224
- Tedengren M, Olsson B, Reimer O, Brown DC, Bradley BP (1999) Heat pretreatment increases cadmium resistance and HSP 70 levels in Baltic Sea mussels. *Aquat Toxicol* 48:1–12
- Wilkinson CR (1999) Global and local threats to coral reef functioning and existence: review and predictions. *Mar Freshw Res* 50:867–878