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Increased seawater temperature and decreased dissolved oxygen triggers fish kill at the Cocos (Keeling) Islands, Indian Ocean

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At the Cocos (Keeling) Islands in the north-eastern Indian Ocean >592 fishes from at least 11 species died in a series of events in December 2007, January and February 2008 and April 2009. The dead fishes were from a wide range of taxonomic families, indicating that conditions exceeded the tolerances of a broad array of species. The 2007–2008 die-off events occurred on the warmest and calmest days of a significantly warmer and calmer summer. Fishes died in the southern inshore areas of the coral atoll lagoon at survey sites where seawater temperature was highest (33–35° C) and dissolved oxygen was lowest (1.4–1.8 mg l⁻¹). The water temperature at these fish-kill survey sites (33–35° C) was significantly warmer than previous years (1997 to 2005, mean ± s.e. = 28.7 ± 0.1° C). Fishes probably died because they were unable to obtain the additional oxygen required for metabolism at higher temperatures. Repeated die-off events over the last 130 years indicate that some fishes have not yet adapted to rises in seawater temperature. This study provides empirical evidence to support suggestions that differences in physiological tolerances to increasing sea temperatures may be important in determining the structure of future coral-reef fish communities with respect to climate change.

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Key words: climate change; coral-reef fishes; fish kill; global warming; hypoxia; physiological tolerance.

INTRODUCTION

Rising sea temperatures associated with global warming are challenging the physiological tolerances of marine organisms, particularly those on coral reefs. Increasing water temperatures have caused extensive coral mortality leading to rapid and broad scale destruction of coral reefs (Wilkinson, 2004; Hoegh-Guldberg *et al.*, 2007). This climate-induced habitat loss has had a significant effect on reef-fish communities, including local extinctions (Bellwood *et al.*, 2006; Graham *et al.*, 2006; Wilson *et al.*, 2006; Munday *et al.*, 2008a; Pratchett *et al.*, 2008). Furthermore, increasing

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sea temperature reduces oxygen solubility and over the last 50 years the amount of hypoxic habitat (low dissolved oxygen) has increased in many regions (Garcia *et al.*, 2005; Brierley & Kingsford, 2009). Relatively little is known, however, on how these direct threats (rising seawater temperature and decreasing oxygen availability) affect reef-fish physiology and how this will affect fish populations and communities (Munday *et al.*, 2008b; Nilsson *et al.*, 2009).

Recent laboratory trials have found that slight increases in seawater temperature can reduce growth and even lead to death in some coral-reef fishes (Munday *et al.*, 2008b; Nilsson *et al.*, 2009). Increases in seawater temperature affect a fish's ability to obtain sufficient oxygen because warmer temperatures increase the amount of oxygen required for metabolism (Nilsson *et al.*, 2007a, 2009). In addition, the solubility of oxygen in sea water decreases with increasing temperature making it more difficult for fishes to obtain the extra oxygen required for respiration in warmer waters (Nilsson *et al.*, 2007a). Although laboratory experiments have shown that seawater temperatures predicted under future global warming conditions can kill some reef fishes (Nilsson *et al.*, 2009), it is not known whether these increases in seawater temperature result in fish mortality in the wild or if there is a potential for acclimation, adaptation or avoidance. Species inhabiting low-latitude reefs appear most at risk due to a limited scope for adaptation to rising sea temperatures because they are unable to receive heat-tolerant offspring from warmer regions (Nilsson *et al.*, 2009).

A series of fish die-off events occurred at the Cocos (Keeling) Islands in the north-eastern Indian Ocean (12° 12' S; 96° 54' E) during the austral summer of 2007–2008 (1 December to 29 February). The aims of this study were to (1) quantify the spatial, temporal and taxonomic extent of the die-off events, (2) determine the seawater temperature and levels of dissolved oxygen during the die-off events and (3) examine climate conditions at the time of the die-off events.

MATERIALS AND METHODS

The Cocos (Keeling) Islands constitute an isolated coral atoll with 26 low-lying islands around the perimeter of a central lagoon (Fig. 1). Due to its equatorial and oceanic position, the air temperature is warm and relatively constant: annual mean temperature range is 24.5–29.0° C (Australian Government Bureau of Meteorology, 2009). The waters surrounding the Cocos (Keeling) Islands support >550 species of fishes (Allen & Smith-Vaniz, 1994), many of which are a staple food source for *c.* 600 people that reside within the islands. The lagoon contains a range of habitats with shallow seagrass beds and sand banks in the south, changing to coral reefs and deeper, sink-hole areas in the north (Williams, 1994). Coral reefs line the outside perimeter of the atoll.

To quantify the spatial, temporal and taxonomic extent of the 2007–2008 summer die-off events, observations during the February 25–26 die off were combined with information on earlier events gained from local people. The local people are subsistence fishers who fish throughout the lagoon and outer reefs and have extensive traditional knowledge of fish species. Seventeen of these local fishers were interviewed at West and Home Island in February and March 2008 and asked about the timing, location, species and quantity of dead fishes that were seen (either floating or on the shore) over the summer period.

To determine the physical–chemical conditions of the water during the die-off events a multimeter [Horiba, Water Checker U10; www.horiba.com (calibrated previously)] was deployed on 26 February 2008, during the last die-off event of the 2007–2008 summer. The multimeter was deployed from a small boat in the shallows, near the shoreline. Water temperature (° C) and dissolved oxygen (mg l⁻¹) were measured over the course of the day from seven different sites (Fig. 1). The multimeter was deployed 0.5 m below the surface

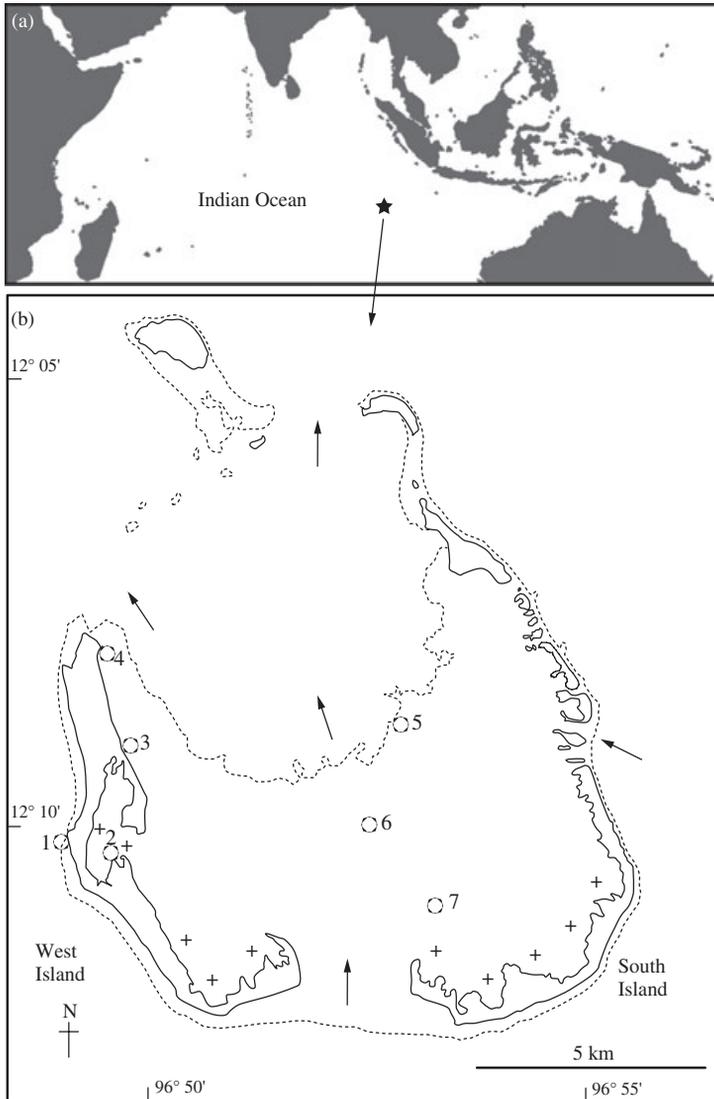


FIG. 1. (a) The location of the Cocos (Keeling) Islands in the north-eastern Indian Ocean (★). (b) The position of the survey sites (1–7) around the southern atoll of the Cocos (Keeling) Islands. Solid arrows indicate the prevailing water circulation on a falling tide (from Kench, 1994). The locations where dead fishes were observed during die-off events in summer 2007–2008 (1 December to 29 February) are indicated (+).

in water 1 m deep at sites where fishes were known to have died in the current or previous events and at control locations where it was known that fishes did not die. A site from the ocean side of the atoll was included to provide a reference for comparing lagoonal waters. Measurements were also taken at night at some of the sites to determine temporal variability in physico-chemical conditions. Water temperatures ($^{\circ}\text{C}$) at sites where fishes died were compared to the long-term average recorded at 11 sites, on 31 days between 1997 and 2005 (Parks Australia, unpubl. data), using one-sample t -tests (Zar, 1999).

To examine the potential role of climate on the die offs, field measurements, information gained from interviews and personal observations were combined with extensive meteorological data recorded at the Cocos Islands Airport Meteorological Office (Australian Government Bureau of Meteorology, 2009). Meteorological data from 1957 to 2007 were used to construct long-term averages of the summer (1 December to 28–29 February) mean maximum air temperature ($^{\circ}\text{C}$) and the summer mean wind speed (km h^{-1}) taken at 1500 hours. Wind is important for flushing the lagoon (Kench, 1994) and it also creates turbulence that increases the amount of oxygen dissolving at the water surface. Data for wind speed were not available for the summer of 1983–1984. To compare the weather conditions during the summer of 2007–2008 with the long-term averages, a one-sample t -test was used (Zar, 1999). The weather conditions on the days of the die-off events were compared to the rest of the 2007–2008 summer using independent samples t -tests (Zar, 1999). Levene's test ($P = 0.05$) was used to check for homogeneity of variance, and where this assumption was not met a t -test that assumed unequal variance was used. All analyses were performed using SPSS version 16 (www.spss.com) and data are presented as the arithmetic mean \pm standard error (S.E.).

RESULTS

Field observations and interviews with the local people revealed that the die-off events occurred four times during the summer months between 22 December 2007 and 26 February 2008. During the die-off events, dead fishes were seen floating, or on the shoreline, for periods of 2–5 days (Fig. 2). Fish kills were restricted to shallow (<1 m depth) inshore areas of the southern and western lagoon (Fig. 1). More than 220 individuals were reported to have died during the events. Individuals of at least six fish species died across a broad range of families: black-tip reef shark *Carcharhinus melanopterus* (Quoy & Gaimard), blacktail snapper *Lutjanus fulvus* (Forster), silverbiddy *Gerres longirostris* (Lacépède), mullet *Crenimugil crenilabis* (Forskål), bonefish *Albula vulpes* (L.) and pufferfish *Arothron hispidus* (L.) (Table I). Many of the dead fishes were small and probably juveniles; however, adult-size individuals were observed for *L. fulvus*, *G. longirostris*, *C. crenilabis* and *A. hispidus*. Organisms other than fishes also died in the southern and western lagoon (*e.g.* octopus and crabs).

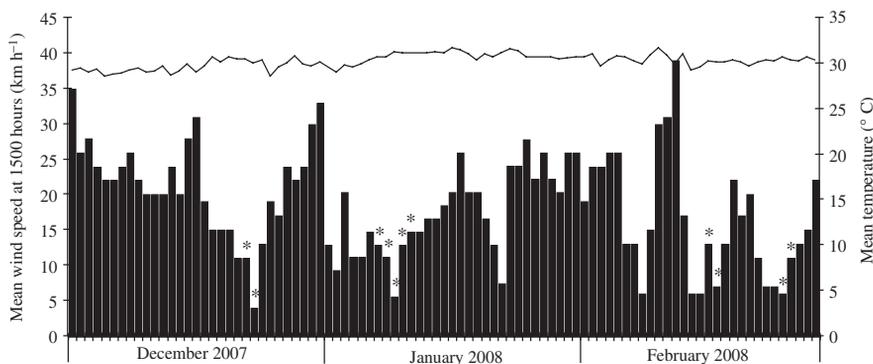


FIG. 2. The daily wind speed at 1500 hours (■) and maximum daily air temperature (—) during summer (1 December to 29 February) 2007–2008 at the Cocos (Keeling) Islands. *, days when dead fishes were observed.

TABLE I. The taxonomic composition of fishes killed at the Cocos (Keeling) Islands during die-off events in summer 2007–2008 and April 2009. The reported number of dead individuals per species is indicative of relative, rather than absolute, numbers because the true magnitude of the die-offs events was underestimated

| Species | Family | Summer 2007–2008 | April 2009 |
|----------------------------------|----------------|------------------|------------|
| <i>Carcharhinus melanopterus</i> | Carcharhinidae | 3 | 1 |
| <i>Lutjanus fulvus</i> | Lutjanidae | >63 | >100 |
| <i>Gerres longirostris</i> | Gerreidae | >55 | 10 |
| <i>Crenimugil crenilabris</i> | Mugilidae | >80 | 18 |
| <i>Albula vulpes</i> | Albulidae | 4 | 0 |
| <i>Arothron hispidus</i> | Tetraodontidae | 15 | >100 |
| <i>Chanos chanos</i> | Chanidae | 0 | 6 |
| <i>Epinephelus ongus</i> | Serranidae | 0 | 12 |
| <i>Epinephelus polyphemadion</i> | Serranidae | 0 | >20 |
| <i>Epinephelus</i> sp. | Serranidae | 0 | 5 |
| Unidentified moray eel | Muraenidae | 0 | >100 |
| Total | | >220 | >372 |

TABLE II. Water temperature and dissolved oxygen readings taken 0.5 m below the water surface at seven sites (Fig. 1) at the Cocos (Keeling) Islands. Measurements were conducted during the die-off event on 26 February 2008 between 1330 and 2330 hours

| Site number | Time (hours) | Temperature (° C) | Dissolved oxygen (mg l ⁻¹) |
|-------------|--------------|-------------------|--|
| 1 | 1330 | 29 | 4.5 |
| 1 | 2300 | 28 | 4.2 |
| 2* | 1400 | 35 | 1.8 |
| 2* | 2330 | 28 | 1.4 |
| 3 | 1430 | 35 | 2.5 |
| 3 | 2315 | 32 | 1.4 |
| 4 | 2100 | 30 | 3.5 |
| 5 | 1630 | 31 | 3.2 |
| 6 | 1500 | 31 | 2.1 |
| 7* | 1530 | 33 | 1.5 |

*Sites where fishes died.

Readings of physical variables taken during the last die-off event on 26 February 2008 revealed that the water temperature was highest (35° C) during the day in inshore areas of the lagoon and lowest on the outside (ocean side) of the atoll (28° C) (Table II). Lagoonal temperatures decreased from 35° C during the day to 28° C at night. The daytime water temperature at sites where dead fishes were seen was 35° C (site 2) and 33° C (site 7), which was significantly higher (one-sample *t*-test, d.f. = 74, *P* < 0.001) than the average water temperature in previous years (mean ± s.e. = 28.7 ± 0.1, *n* = 75 recordings across 11 sites over 31 days from 1997 to 2005). Dissolved oxygen was also lowest in the southern (1.5 mg l⁻¹) and western lagoon (1.4 mg l⁻¹) and highest on the outside of the atoll (4.5 mg l⁻¹) (Table II). Dissolved oxygen was also low at site 3 (2.5 mg l⁻¹ during the day and 1.4 mg l⁻¹

at night) in the western lagoon; however, no dead fishes were seen at this site possibly because fishes could move into nearby deeper water where conditions may have been more favourable.

Die-off events occurred on the warmest and calmest days of an unusually warm and calm summer. The mean maximum air temperature for the summer of 2007–2008 was significantly warmer than the long-term (1957–2007) average summer temperature [one-sample *t*-test, d.f. = 49, $P < 0.001$; Fig. 3(a)] and the mean wind speed was significantly lower than the long-term summer average [one-sample *t*-test,

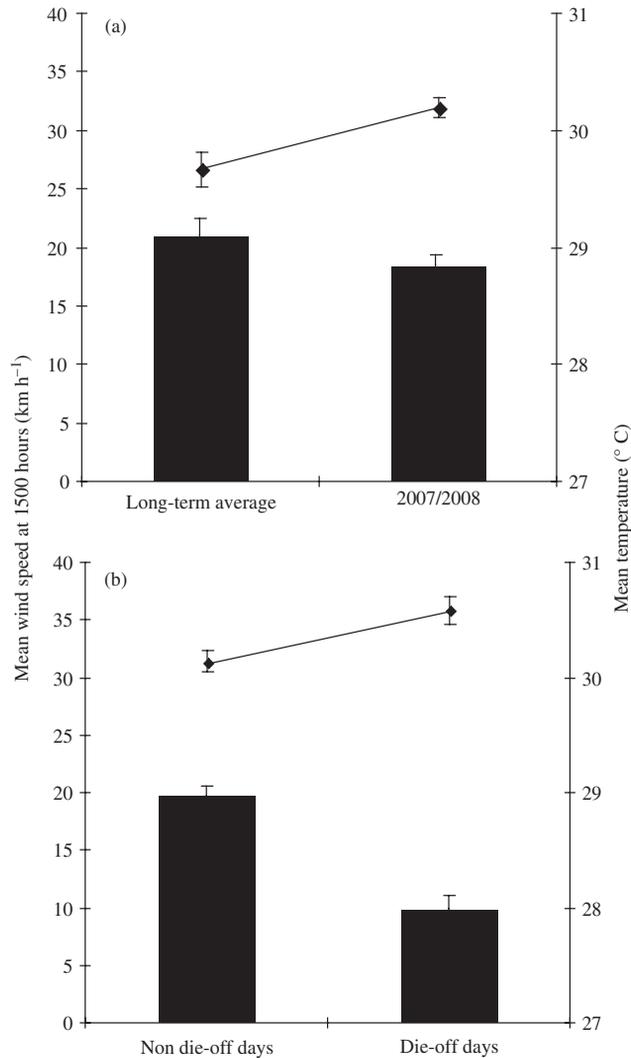


FIG. 3. The mean \pm S.E. wind speed at 1500 hours (■) and the mean \pm S.E. maximum air temperature (—) for (a) the long-term summer average (1957–2007) and 2007–2008 summer average and (b) for days when fishes did not die compared to days when fishes did die during summer (1 December to 29 February) 2007–2008 at the Cocos (Keeling) Islands.

d.f. = 48, $P < 0.001$; Fig. 3(a)]. Compared to the rest of the 2007–2008 summer days, die-off events occurred on days when the air temperature was significantly warmer (t -test, d.f. = 21, $P < 0.01$) and the wind was considerably lighter [t -test, d.f. = 89, $P < 0.001$; Fig. 3(b)].

Following the original study, an additional die-off event was reported on 23 April 2009. Through correspondence with local fishers it was established that the following species were seen floating dead or washed up on the shore: *C. melanopterus*, *L. fulvus*, *G. longirostris*, *C. crenilabis*, *A. hispidus*, milkfish *Chanos chanos* (Forsskål), white-streaked grouper *Epinephelus ongus* (Bloch), camouflage grouper *Epinephelus polyphekadion* (Bleeker), unidentified *Epinephelus* sp. (Serranidae) and an unidentified species of moray eel (Muraenidae) (Table 1). The dead fishes represented a mixture of small and large individuals. In total, >372 individuals died, primarily in the inshore areas of the western lagoon in the vicinity of site 2 (Fig. 1). Examination of weather data revealed that the week of the die off (17–23 April) contained the second and fourth hottest days (1500 hours air temperature) since the last die-off event in February 2008. The week of the April 2009 die off was also very calm with the average weekly wind speed (recorded at 1500 hours) being the second lowest since the last February 2008 die off. The calmest conditions occurred on the day dead fishes were seen (23 April) and the wind speed on this day (7 km h^{-1}) was less than the average wind speed experienced on die-off days in the summer of 2007–2008 ($9.9 \pm 1.1 \text{ km h}^{-1}$). Water temperature and dissolved oxygen levels were not recorded during this die-off event due to an absence of personnel.

DISCUSSION

Die-off events typically occur when environmental conditions exceed the physiological tolerances of the inhabiting organisms. In this case, >592 fishes from at least 11 species, and several other taxa (*e.g.* octopus and crabs), died in the lagoon at the Cocos (Keeling) Islands during a series of die-off events in the summer of 2007–2008 and in April 2009. Many more fishes died, however, they were not all counted and identified, and therefore, the magnitude of the die-off events has been underestimated. This is because it was not possible to thoroughly search the large areas where fishes died using detailed scientific surveys, but rather information was gathered from fishers who saw dead fishes at locations they visited within the fish-kill areas. Despite the underestimate in magnitude, information on the spatial and temporal extent of the die-off events is relatively accurate because every day the local people fish and travel throughout the atoll.

The 2007–2008 die-off events occurred on the warmest and calmest days of a significantly warm and calm summer, with similar conditions triggering a die-off event in April 2009. It is likely that the physico-chemical conditions of the lagoonal waters challenged the physiological tolerances of fishes throughout the 2007–2008 summer period; however, it was only on the hottest and calmest days that these tolerances were exceeded. The short duration of the die-off events (2–5 days) was probably because the changes in the weather conditions that followed these events (reductions in air temperature and increases in wind speed) would have improved water conditions (decreased water temperature and increased dissolved oxygen).

Cocos (Keeling) Islands has had a history of die-off events associated with warm calm weather. Since human colonization in 1826, significant die-off events have reportedly occurred in 1876, 1961 and at least four times between 1958 and 1988, in addition to numerous smaller die-off events (Bunce, 1988). The March 1983 die-off event was particularly severe with thousands of fishes dying, and anecdotal reports of 100% mortality of fishes, corals and algae in the southern lagoon (Bunce, 1988; J. Hender, C. A. McDonald & J. J. Gilligan, unpubl. data). The die off lasted 2 weeks and 'foul water' covered at least a third of the lagoon (Bunce, 1988). The 1983 die-off and previous events have been associated with El Niño weather conditions that have brought unusually hot calm weather to the region (Bunce, 1988; J. Hender, C. A. McDonald & J. J. Gilligan, unpubl. data). Die-off events of corals have also occurred in other Indo-Pacific locations due to increased water temperatures associated with a warmer El Niño climate (Goreau *et al.*, 2000; Wilkinson, 2004). In contrast to previous die-off events at the Cocos (Keeling) Islands, the 2007–2008 summer die-off event occurred during a period of La Niña conditions (Australian Government Bureau of Meteorology, 2009). This indicates that hot calm weather during either El Niño or La Niña periods can trigger die-off events.

The die-off events appear to have resulted from a culmination of factors. Elevated water temperatures challenge the physiological capabilities of fishes because the concentration of oxygen required for basic metabolism increases with temperature (Nilsson *et al.*, 2007a, 2009). The unusually warm 2007–2008 summer heated the waters, particularly in the shallow lagoonal areas where daytime water temperatures rose to 33–35° C, which was considerably higher than previously recorded at the atoll (mean 28.7° C). A rise in water temperature from 29 to 33° C has been shown to kill some coral-reef fishes because they are unable to obtain sufficient oxygen to fuel their basic metabolic needs (Nilsson *et al.*, 2009). At the Cocos (Keeling) Islands, obtaining the additional oxygen required for metabolism at higher temperatures would have been even more difficult for fishes inhabiting waters where dissolved oxygen was low.

As seawater temperature increased, dissolved oxygen would have decreased due to a reduction in oxygen solubility. For example, an increase in seawater temperature from 28.7 to 33.0–35.0° C would have resulted in a decrease in dissolved oxygen of *c.* 0.5 mg l⁻¹ (Ramsing & Gundersen, 2003). Decreased oxygen solubility, however, only partly explains the low dissolved oxygen levels recorded in the lagoon (1.4–1.8 mg l⁻¹) compared to 4.2–4.5 mg l⁻¹ (28–29° C) recorded on the outside of the atoll at the time of the die offs. The calm weather at the time of the die offs would have also reduced dissolved oxygen by limiting the amount of oxygen being dissolved at the water surface through turbulence and the amount of cooler, oxygenated water being flushed into the lagoon from outside of the atoll (Kench, 1994). In addition, the change in physical and chemical conditions may have stressed, or killed, the large amounts of seagrass and algae present in the lagoon (as has occurred in past die-off events; Bunce, 1988; J. Hender, C. A. McDonald & J. J. Gilligan, unpubl. data), thereby reducing the amount of dissolved oxygen produced from these photosynthetic organisms. The increased consumption of oxygen by fishes (and other organisms) during elevated temperatures (Nilsson *et al.*, 2009) would have further reduced the amount of available dissolved oxygen. Finally, the decomposition of dead fishes and other organisms may have stripped oxygen from the water (Rogers & Lockwood, 1990).

Although coral-reef fishes have some tolerance to hypoxic conditions (Nilsson *et al.*, 2007a), the low levels of dissolved oxygen recorded at some lagoonal sites in this study would have presented a physiological challenge. Previous research using closed respirometry on a broad range of coral-reef fishes (48 species) found that fishes were negatively affected when dissolved oxygen concentrations fell below 0.90–2.07 mg l⁻¹ and could not tolerate dissolved oxygen levels <0.02–0.78 mg l⁻¹ (Nilsson *et al.*, 2007a). The fishes in this study died at sites where dissolved oxygen levels were 1.4–1.8 mg l⁻¹. This may indicate that the species in this study are more sensitive to decreases in oxygen levels. It is more likely, however, that fishes died because they were unable to obtain sufficient oxygen to sustain basic metabolic needs due to the combined effect of increased oxygen requirements caused by elevated water temperatures and a decrease in available dissolved oxygen. Indeed, the sites with the highest water temperatures and lowest levels of dissolved oxygen were the same locations where dead fishes were observed.

If reef fishes cannot acclimate or adapt to episodes of elevated water temperature and reduced dissolved oxygen, then occurrences of die-off events will increase with global warming. Some reef fishes are better adapted than others to increased water temperatures and reduced levels of dissolved oxygen (*e.g.* gobiids and blenniids; Nilsson *et al.*, 2007a, b, 2009) while others may be able to obtain the necessary oxygen from the atmosphere (*e.g.* coral-dwelling gobiids and some scorpaenids; Nilsson *et al.*, 2004, 2007b). During the last die-off event, bumphead parrotfish *Bolbometopon muricatum* (Valenciennes) were observed rising to the surface and gulping air in the southern lagoon near site 6 (see Fig. 1). This behaviour has been reported in freshwater fishes as an adaptation to obtaining sufficient oxygen in hypoxic environments (Graham, 1997). Some fishes at the Cocos (Keeling) Islands may be able to avoid hot and hypoxic waters by moving to deeper cooler areas of the lagoon, and no mortalities were reported from these deeper waters during the die-off events. While deeper cooler waters may provide a refuge, the shallow areas are often important nursery areas for juveniles of these species and they may not be able to avoid (and therefore will have to adapt to) periods of hypoxia and increased temperatures.

The repeated occurrence of die-off events at the Cocos (Keeling) Islands for at least the last 130 years, and four times within the 2007–2008 summer and again in April 2009, indicates that many reef fishes have not yet acclimated or adapted sufficiently over short or long-time periods. These repeated die offs support suggestions that some fishes occupying low-latitude coral reefs may have limited scope for adaptation to rising sea temperatures (Nilsson *et al.*, 2009). This is particularly concerning, given that some of the greatest increases in sea temperatures are predicted for low-latitude areas, including the Cocos (Keeling) Islands (Sheppard, 2003). Ultimately, differences in physiological tolerances to increased temperature and reduced oxygen availability may influence the composition of reef-fish communities in the future (Nilsson *et al.*, 2009).

In addition to causing sudden mass mortalities of coral-reef organisms (Bunce, 1988; Simpson *et al.*, 1993; Goreau *et al.*, 2000; Wilkinson, 2004), increased sea temperature can also affect growth, reproduction and larval development of reef fishes (Munday *et al.*, 2008a), which may be critical to long-term persistence. This has important implications for fisheries and conservation at locations (such as the Cocos (Keeling) Islands) where marine resources are relied upon by the local people for subsistence. It is imperative that management strategies in these systems take into

account declines in marine populations affected by rising sea temperatures. While this study demonstrates the serious physiological challenges confronting coral-reef fishes at the Cocos (Keeling) Islands, rising sea temperatures will test the physiological tolerances and adaptive capacity of marine fishes worldwide.

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References

- Allen, G. R. & Smith-Vaniz, W. F. (1994). Fishes of Cocos (Keeling) Islands. *Atoll Research Bulletin* **412**, 1–21.
- Bellwood, D. R., Hoey, A. S., Ackerman, J. L. & Depczynski, M. (2006). Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology* **12**, 1587–1594. doi: 10.1111/j.1365-2486.2006.01204.x
- Brierley, A. S. & Kingsford, M. J. (2009). Impacts of climate change on marine organisms and ecosystems. *Current Biology* **19**, R602–R614.
- Bunce, P. (1988). *The Cocos (Keeling) Islands, Australian Atolls in the Indian Ocean*. Brisbane: The Jacaranda Press.
- Garcia, H. E., Boyer, T. P., Levitus, S., Locarnini, R. A. & Antonov, J. (2005). On the variability of dissolved oxygen and apparent oxygen utilization content for the upper world ocean: 1955 to 1998. *Geophysical Research Letters* **32**, LO9604.
- Goreau, T., McClanahan, T., Hayes, R. & Strong, A. (2000). Conservation of coral reefs after the 1998 global bleaching event. *Conservation Biology* **14**, 5–15. doi: 10.1046/j.1523-1739.2000.00011.x
- Graham, J. B. (1997). *Air-Breathing Fishes: Evolution, Diversity, and Adaptation*. San Diego, CA: Academic Press.
- Graham, N. A. J., Wilson, S. K., Jennings, S., Polunin, N. V. C., Bijoux, J. P. & Robinson, J. (2006). Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Science of the United States of America* **103**, 8425–8429.
- Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., Harvell, C. D., Sale, P. F., Edwards, A. J., Caldeira, K., Knowlton, N., Eakin, C. M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R. H., Dubi, A. & Hatziolos, M. E. (2007). Coral reefs under rapid climate change and ocean acidification. *Science* **318**, 1737–1742.
- Kench, P. (1994). Hydrodynamic observations of the Cocos (Keeling) Islands lagoon. *Atoll Research Bulletin* **408**, 1–21.
- Munday, P. L., Jones, G. P., Pratchett, M. S. & Williams, A. J. (2008a). Climate change and the future for coral reef fishes. *Fish and Fisheries* **9**, 261–285. doi: 10.1111/j.1467-2979.2008.00281.x
- Munday, P. L., Kingsford, M. J., O'Callaghan, M. & Donelson, J. M. (2008b). Elevated temperature restricts growth potential of the coral reef fish *Acanthochromis polyacanthus*. *Coral Reefs* **27**, 927–931.
- Nilsson, G. E., Hobbs, J.-P. A., Munday, P. L. & Ostlund-Nilsson, S. (2004). Coward or braveheart: extreme habitat fidelity through hypoxia tolerance in a coral-dwelling goby. *Journal of Experimental Biology* **207**, 33–39.
- Nilsson, G. E., Hobbs, J.-P. A. & Ostlund-Nilsson, S. (2007a). Tribute to P.L. Lutz: respiratory ecophysiology of coral-reef teleosts. *Journal of Experimental Biology* **210**, 1673–1686.

- Nilsson, G. E., Hobbs, J.-P. A., Ostlund-Nilsson, S. & Munday, P. L. (2007b). Hypoxia tolerance and air-breathing correlate with habitat preference in coral-dwelling fishes. *Coral Reefs* **26**, 241–248.
- Nilsson, G. E., Crawley, N., Lunde, I. G. & Munday, P. L. (2009). Elevated temperature reduces the respiratory scope of coral reef fishes. *Global Change Biology* **15**, 1405–1412. doi: 10.1111/j.1365-2486.2008.01767.x
- Pratchett, M. S., Munday, P. L., Wilson, S. K., Graham, N. A. J., Cinner, J. E., Bellwood, D. R., Jones, G. P., Polunin, N. V. C. & McClanahan, T. R. (2008). Effects of climate-induced coral bleaching on coral-reef fishes: ecological and economic consequences. *Oceanography and Marine Biology: An Annual Review* **46**, 251–296.
- Rogers, S. I. & Lockwood, S. J. (1990). Observations on coastal fish fauna during a spring bloom of *Phaeocystis pouchetii* in the eastern Irish Sea. *Journal of the Marine Biological Association of the United Kingdom* **70**, 249–254.
- Sheppard, C. R. C. (2003). Predicted recurrences of mass coral mortality in the Indian Ocean. *Nature* **425**, 294–297.
- Simpson, C. J., Cary, J. L. & Masini, R. J. (1993). Destruction of corals and other reef animals by coral spawn slicks on Ningaloo Reef, Western Australia. *Coral Reefs* **12**, 185–191.
- Wilkinson, C. (2004). *Status of Coral Reefs of the World*. Townsville: Australian Institute of Marine Science.
- Williams, D. G. (1994). Marine habitats of the Cocos (Keeling) Islands. *Atoll Research Bulletin* **406**, 1–10.
- Wilson, S. K., Graham, N. A. J., Pratchett, M. S., Jones, G. P. & Polunin, N. V. C. (2006). Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology* **12**, 2220–2234. doi: 10.1111/j.1365-2486.2006.01252.x
- Zar, J. H. (1999). *Biostatistical Analysis*. London: Prentice-Hall.

Electronic References

- Australian Government Bureau of Meteorology (2009). *Climate Statistics for Australian Locations: Cocos Islands Airport (Site 200284)*. Available at http://www.bom.gov.au/climate/averages/tables/cw_200284.shtml (accessed 9 August 2009).
- Ramsing, N. & Gundersen, J. (2003). *Seawater and Gases*. Available at <http://www.unisense.com/Default.aspx?ID=1109> (accessed 6 April 2010).