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Coral mortality following extreme low tides and high solar radiation

K. R. N. Anthony · A. P. Kerswell

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Abstract Extreme tidal events are one of the most predictable natural disturbances in marine benthic habitats and are important determinants of zonation patterns in intertidal benthic communities. On coral reefs, spring low tides are recurrent disturbances, but are rarely reported to cause mass mortality. However, in years when extremely low tides coincide with high noon irradiances, they have the potential to cause widespread damage. Here, we report on such an event on a fringing coral reef in the central Great Barrier Reef (Australia) in September 2005. Visual surveys of colony mortality and bleaching status of more than 13,000 corals at 14 reef sites indicated that most coral taxa at wave-protected sites were severely affected by the event. Between 40 and 75% of colonies in the major coral taxa (*Acropora*, *Porites*, Faviidae, Mussidae and Pocilloporidae) were either bleached or suffered partial mortality. In contrast, corals at wave-exposed sites were largely unaffected (<1% of the corals were bleached), as periodic washing by waves prevented desiccation. Surveys along a 1–9 m depth gradient indicated that high coral mortality was confined to the tidal zone. However, 20–30% of faviid colonies were bleached throughout the depth range, suggesting that the increase in benthic irradiances during extreme

low tides caused light stress in deeper water. Analyses of an 8-year dataset of tidal records for the area indicated that the combination of extended periods of aerial exposure and high irradiances occurs during May–September in most years, but that the event in September 2005 was the most severe. We argue that extreme low-tide, high-irradiance events are important structuring forces of intertidal coral reef communities, and can be as damaging as thermal stress events. Importantly, they occur at a time of year when risks from thermal stress, cyclones and monsoon-associated river run-off are minimal.

Introduction

The tidal zone is one of the most physically challenging habitats in marine benthic habitats (Paine and Levin 1981; Menge and Branch 2001). It is an area of periodic aerial exposure (Brown et al. 1994b; Stapel et al. 1997), frequent strong wave action (Dollar 1982; Denny 1994) and large temperature fluctuations (Helmuth 1998). The intertidal zone is also an area of high solar irradiance and potential UV stress; both of these factors may have deleterious effects on photosynthetic organisms such as corals (Brown et al. 1994a; Shick et al. 1996). Nevertheless, the tidal zone, and in particular the growing reef margin (i.e. the reef crest), is the most productive zone on coral reefs (Barnes and Chalker 1990; Chisholm 2003) and accounts for more than half the species richness on coral reefs (Karlson et al. 2004). Such richness indicates that the range of conditions in the tidal zone is generally within the dynamic tolerance range of corals.

The stress effects of aerial exposure on reef-flat organisms during extreme low tides are well documented,

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K. R. N. Anthony · A. P. Kerswell
School of Marine Biology and Aquaculture,
James Cook University, Townsville, QLD 4811, Australia

K. R. N. Anthony (✉)
Centre for Marine Studies, The University of Queensland,
Brisbane, QLD 4072, Australia
e-mail: k.anthony@uq.edu.au

although mainly in early studies (Glynn 1968; Fishelson 1973). High levels of mortality have been observed in low-diversity coral communities following extreme low tide events (Loya 1976) and extensive coral bleaching has resulted after the coincidence of low tides and unusually cold winter weather (Hoegh-Guldberg et al. 2005). However, the timing, predictability and coral-community consequences of potentially destructive events are less obvious. In situations where lowest astronomical tides occur around noon and coincide with minimal cloud cover, prolonged aerial exposure and elevated or reduced temperatures in combination with high irradiance may exceed the tolerance limit of most corals and lead to widespread damage. Extreme low tides occur twice annually, autumn and spring (vernal and autumnal equinoxes, Allen 1997). Yet, the lowest astronomical tides do not occur every year, do not necessarily occur around noon and may occur under significant cloud cover. Thus, the alignment of prolonged aerial exposure and supra-optimal irradiance constitutes a rare physical disturbance. Analogous to cyclones, extreme low-tide, high-irradiance events may represent a cyclical disturbance pattern that helps maintain high species diversity by periodic exclusion of competitively dominant taxa (Connell 1978; Rogers 1993).

Here, we document the effects of an extreme low-tide, high-irradiance event on a coastal coral reef in the central Great Barrier Reef lagoon during September 2005. We examine the spatial extent of the event along gradients of wave-exposure and depth and the temporal periodicity of similar events using historical tidal data and simulated irradiance regimes for the region. This combined approach allows us to evaluate the implications of destructive tidal and irradiance regimes for the dynamics of shallow-water coral communities.

Methods

Study area

Surveys were conducted at 14 sites on reefs surrounding Orpheus and Pelorous Islands (18.38°S, 146.30°E) (Fig. 1). These islands support extensive fringing reefs, which are representative of inshore reefs of the central region of the Great Barrier Reef. The western, leeward side of the islands is characterized by high turbidity (Anthony and Fabricius 2000), and the eastern side is influenced by waves generated by the prevailing southeasterly trade winds (Larcombe et al. 1995; Pandolfi and Greenstein 1997). Nine sites were chosen along the western, wave-protected side of the islands to achieve

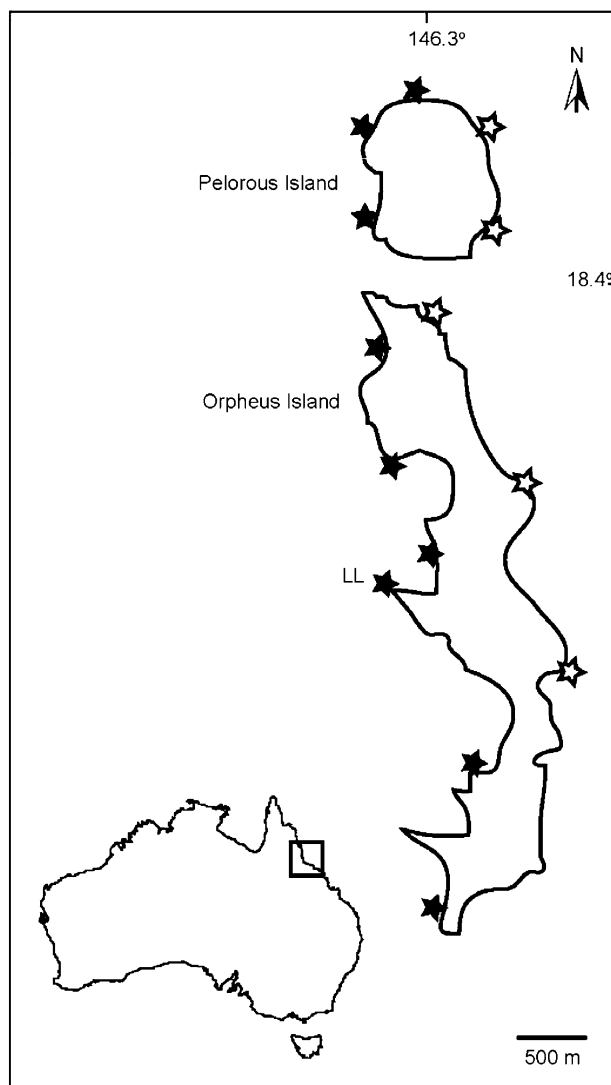


Fig. 1 Map of study sites around Pelorous and Orpheus Islands (Australia). The five eastern (wave exposed) sites are represented by *open stars* and the nine western (wave protected) sites by *closed stars*. The location of the light logger station in Pioneer Bay (Orpheus Island) is marked “LL”

good representation of the varying environmental conditions prevailing in the different bays. Three of those sites were within Pioneer Bay, which has a well-developed reef slope to 6–9 m. Five sites were selected along the eastern, exposed side of the islands to provide good representation of the habitats there. To ensure representation by key coral taxa at all sites (see below), only sites with a coral cover >25% and with a well-developed community composition were selected.

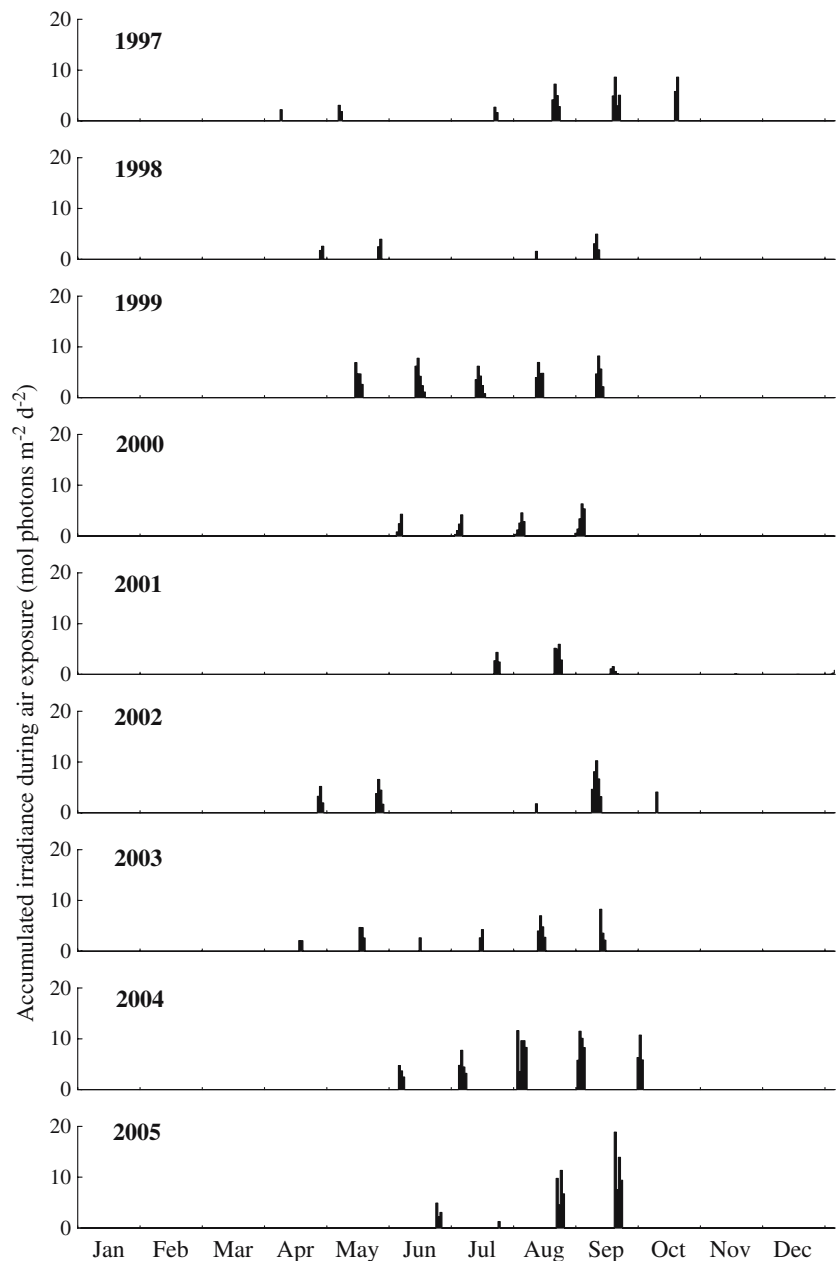
Environmental data

We analysed long-term temporal patterns in the occurrence of extreme low tides as well as reporting in situ point measurements of tidal height and irradiance at

low tide for July–October 2005. Hourly tidal records (observations) were obtained from the Maritime Safety Queensland (Brisbane) for offshore of Lucinda (18°31 S, 146°23 E) between the years 1997 and 2005. Hourly records of surface irradiance for the years 2003–2005 were obtained from the Orpheus Island weather station located in Pioneer Bay. Because long-term irradiance logger data do not exist for the location prior to 2003, surface irradiances for the years 1997–2002 were estimated based on weekly (rolling) noon maxima (E_{\max}) for 2003–2005 (see Anthony et al. 2004). To estimate irradiance as a function of time of day [$E(t)$] we used the relationship $E(t) = E_{\max} \cdot \sin^3(\pi t/12 \text{ h})$ (Marra 1978). By using weekly rolling irradiance maxima (represent-

ing little or no cloud cover) as estimates of irradiance for the period 1997–2003, our comparison of the severity of the low tide, high-light stress event in 2005 with that of events in previous years was highly conservative. To analyse long-term trends in the alignment of low tides with high irradiances, we compiled hourly tidal records and surface irradiances. For every day between 1 January 1997 and 31 December 2005, we calculated the total amount of irradiance accumulated in the intertidal during times of aerial exposure. That is, for every hour that the tidal height was <0.4 m and the benthos air-exposed, the amount of light reaching the intertidal was estimated (Anthony et al. 2004) and each hourly estimate was summed over the entire day.

Fig. 2 Time series of integrated daily irradiances for corals in the intertidal zone (<0.4 m above lowest astronomical tide) around Orpheus and Pelorous Islands. Tidal data are actual tidal heights from the nearby logger station (Fig. 1). Solar irradiance data prior to 2003 are predicted values in the absence of clouds (Anthony et al. 2004) and irradiance values after 2003 are data obtained by the weather station at Orpheus Island Research station



In addition to long-term projections of the tidal-light regime, we obtained detailed patterns of benthic irradiance and turbidity before and during the extreme low tide event in 2005 from in situ light loggers. Specifically, downwelling underwater irradiance was recorded hourly in Pioneer Bay, Orpheus Island from 18 July to 14 October 2005 at two depths: (1) on the reef crest at a depth corresponding to the lowest astronomical tide (LAT) and (2) at the base of the reef slope (14 m below LAT). All irradiance sensors were cosine corrected and designed to record within the photosynthetically active range (PAR, 400–700 nm). The underwater sensors were calibrated underwater against a Li192S sensor (Licor, Nebraska). Both loggers (Dataflow Systems, Christchurch, New Zealand) were equipped with custom-made automated sensor wipers to prevent biofouling. Furthermore, the positioning on the loggers at two depths allowed us to estimate light attenuation (k_D) in Pioneer Bay during this period using Lambert–Beer's law (van Duin 2001; Anthony et al. 2004).

Coral bleaching and mortality surveys

At all 14 sites around Orpheus and Pelorous Islands, we assessed the impact of the extreme low tide event on the coral communities via surveys of the five dominant coral taxa: the genera *Acropora* and *Porities*, and the families Faviidae, Mussidae, and Pocilloporidae. These taxa make up the majority of the coral communities on the Great Barrier Reef (Done 1982; Devantier et al. 2006) including reefs around Orpheus and Pelorus Islands (Baird and Marshall 2002). We also included soft corals of the genera *Lobophyllia* and *Sinullaria* in the surveys as these often constitute >10% of the benthic community in the study area. At all sites, surveys were conducted on the reef crest at a depth of 1 m above to 1 m below lowest astronomical tide (LAT). Furthermore, to assess whether the low tide–high irradiance event impacted corals in deeper water, three sites on the inshore (western) side of the islands were also surveyed at a further four depths between 2 and 9 m below LAT. For all surveys, the status of coral colonies was based on visual assessments and categorized as either healthy, bleached, <50% colony mortality or $\geq 50\%$ colony mortality. Corals were scored as healthy if they had normal colouration over their entire colony surface, and bleached if they were strikingly pale (corresponding to colour categories 3–6 and <3 of the reference chart by Siebeck et al. 2006). Only partial mortalities clearly attributable to the recent event (evidenced by tissue sloughing, visible skeleton and minor algal colonization) were scored. We treated separate colonies as discrete individuals. Because surveys included 400–1,500 (average 648) colonies at each site

and each depth, and covered areas up to 200 m long at a given site, multiple clones of each species were likely to be represented at each site and at each depth.

Results

Analyses of the long-term temporal patterns of extreme low tides (<0.4 m above lowest astronomical tides) coinciding with high noon irradiances indicated that stress from combined air and high-light exposure is most likely to occur during the Austral winter and spring (Fig. 2). Interestingly, the timing and potential severity, here estimated as the accumulated amount of irradiance during periods of air exposure, of such events varied strongly between the years from 1997 to 2005. In 2005, only two significant periods of stress occurred, 17–22 August and 12–18 September (Fig. 2). Despite significant cloud cover on September 15, the integrated amount of irradiance impinging on the air-exposed corals (depths shallower than 0.4 m above LAT) in September 2005 was twice or three times greater than in August and orders of magnitude greater than at any other time of the year (Fig. 2).

During the period 12–18 of September, tidal heights fell to 0.1–0.2 m above LAT in the early afternoon. All coral colonies in the reef-flat and reef-crest assemblages on the western sites were fully emerged and exposed to high irradiances from a clear sky. Although tidal levels on eastern sites were similar to those at the western sites, intertidal colonies on the eastern, wave-exposed sites were only partially air-exposed due to

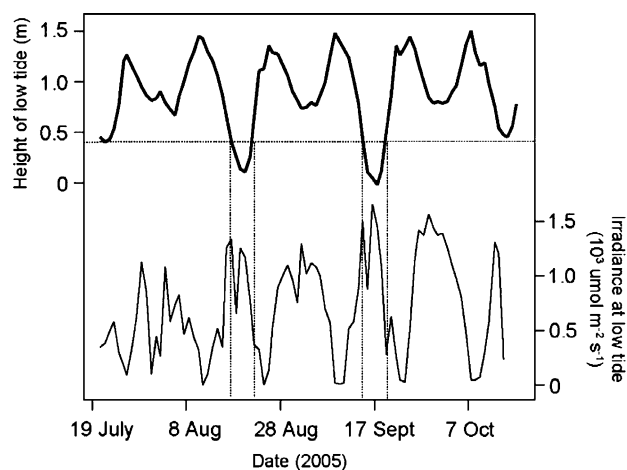


Fig. 3 Temporal patterns of low tides (*upper panel*) and associated solar irradiances (*lower panel*) around Pelorous and Orpheus Islands during Winter–Spring 2005. Vertical lines indicate time periods during which the reef-crest assemblages were air-exposed as well as subject to high solar irradiances. Horizontal lines represent exposure point for inter-tidal corals (~0.4 m above LAT)

washing by the surf. Maximum irradiances on the reef crest, as measured by the in situ light loggers in Pioneer Bay, increased from $\sim 1,000$ to $\sim 1,800 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 3). Light attenuation in Pioneer Bay varied between 0.08 and 0.17 m^{-1} . Based on Lambert–Beer's law (Kirk 1994) this corresponds to between 50 and 80% light attenuation over the 9-m depth transect. At the eastern sites, light attenuation was approximately half that at the western sites (Mia Hoogenboom, unpublished). During the study period, temperature increased from 22 to 26°C only, which is significantly lower than the threshold temperature for coral bleaching in this region (Berkelmans 2002), and therefore unlikely to represent a significant stress factor.

Results of the coral surveys in October (15–17) 2005 indicated a dramatic difference in the stress responses of key coral taxa between western (wave-protected)

and eastern (wave-exposed) sides of the islands. On the eastern sites, $<1\%$ of coral colonies was affected by the event, for all coral taxa. In contrast, on the western sites, all hard coral taxa were markedly affected. Corals in the family Pocilloporidae were most severely affected with 79% of colonies displaying some signs of bleaching or mortality, while $\sim 50\%$ of colonies in all other major taxa were in some way affected by the event (Fig. 4). Notably, soft corals did not show any signs of bleaching or mortality at any site. The degree of stress shown by the scleractinian coral colonies was taxon-specific (Fig. 5). While the majority of affected *Acropora* colonies had $>50\%$ colony mortality, faviids appeared more resistant, with the majority of affected colonies displaying signs of bleaching only. Comparisons of stress responses between crest and slope habitats (four zones ranging from ~ 1 to 9 m below LAT)

Fig. 4 Comparison of number of healthy versus affected (stressed) coral colonies between eastern (wave exposed) and western (wave protected) sites for the major coral taxa in shallow water (crest habitat) 2–6 weeks after the low tide, high-irradiance events

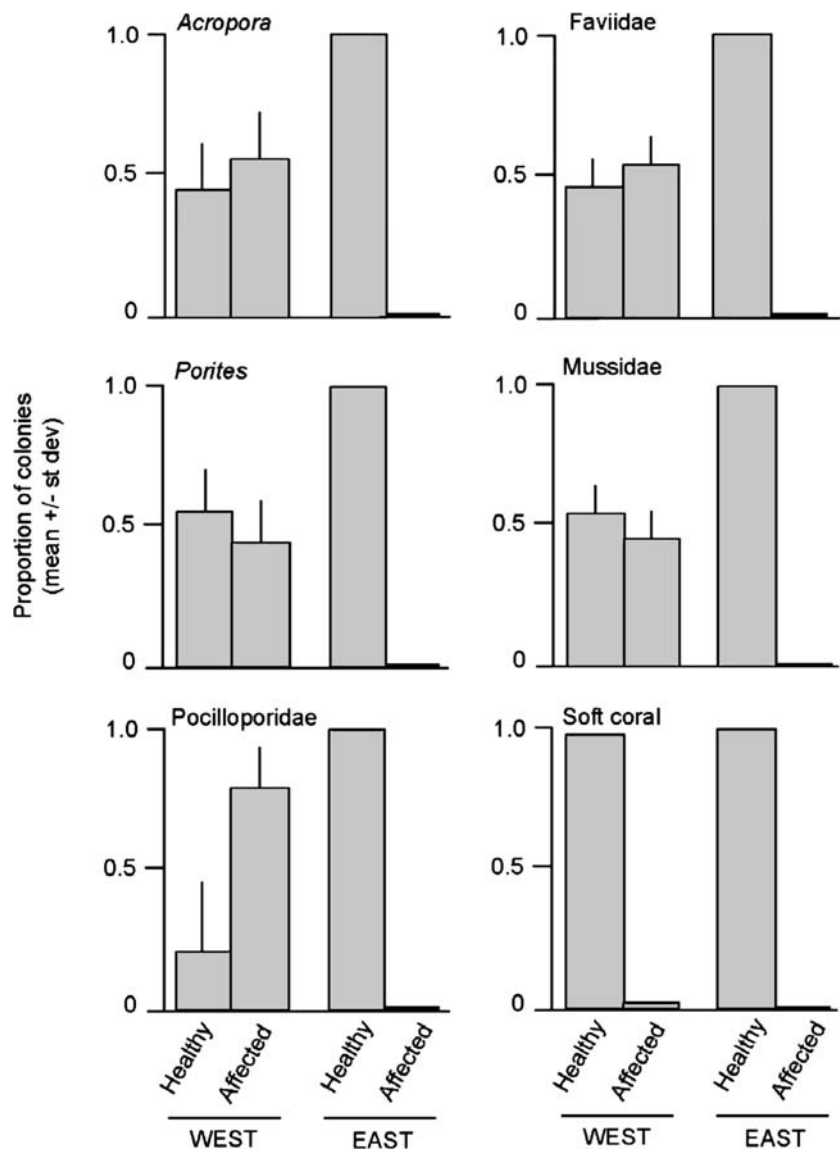
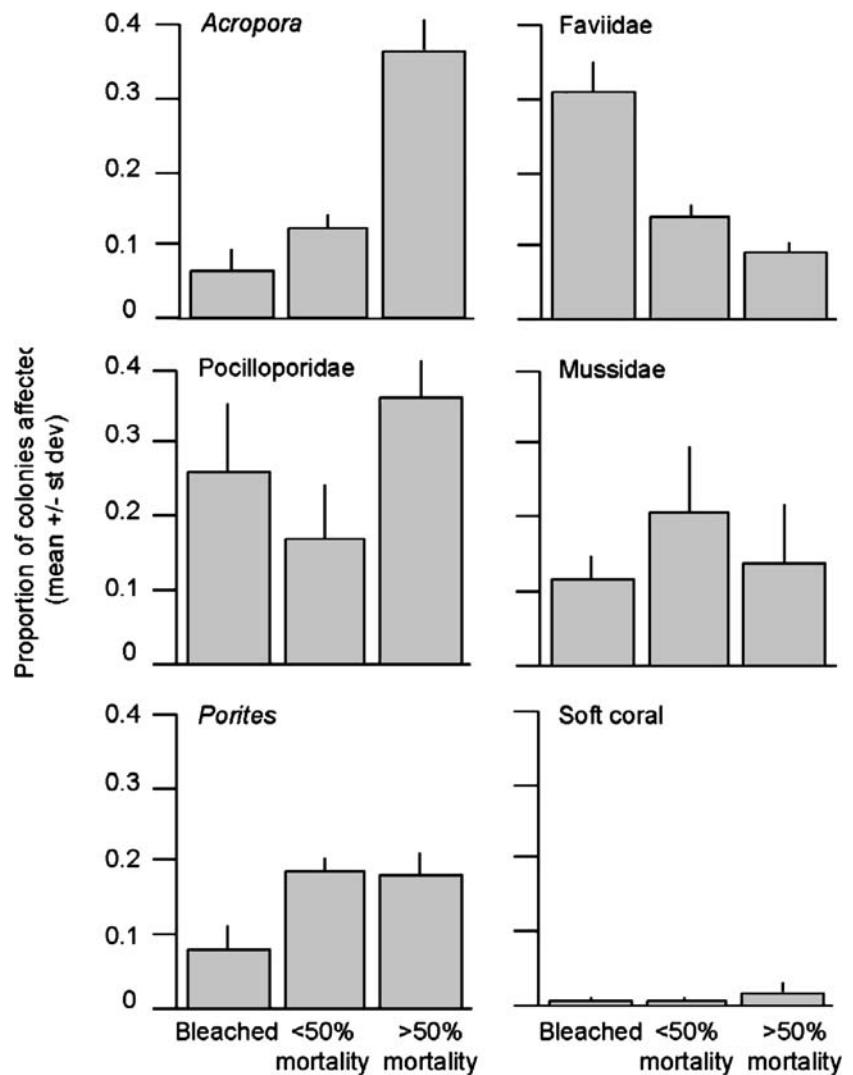


Fig. 5 Detailed comparisons of the severity of stress-response (visual assessments of health status) for all coral taxa for the western sites in shallow water (crest)



for *Acropora*, *Porites*, faviids and mussiids indicated that high mortalities were largely confined to the intertidal crest habitat. However, a large proportion of faviid colonies were also bleached in deep water (Fig. 6). It must be noted that coral surveys were conducted approximately 1 month after the most severe September low tide event. In this short timeframe, recovery from bleaching and mortality are unlikely and the full extent of bleaching may take months to become evident, as many taxa show delayed responses to bleaching stress (Marshall and Baird 2000). Thus, the estimates of bleaching and mortality presented above are likely to be conservative estimates of the magnitude of the low-tide, high-irradiance event.

Discussion

Extreme low tides coinciding with high-midday irradiances are annual events that in some years can cause

widespread damage to intertidal coral communities. Our analyses of an 8-year dataset (1997–2005) of tidal records and surface irradiances indicated that the risk of air exposure coinciding with high light pressure is highest during the period May–October (Austral winter). However, although low noontides are annual seasonal events (Glynn 1968; Fishelson 1973), their timing and severity (hours of exposure to air and high irradiance) vary strongly between years. Based on the calculated, accumulated amount of irradiance during days of air exposure, the event in September 2005 was likely to be the most severe low tide, high-irradiance stress during the 8-year period (Fig. 2). This was despite the fact that irradiance data prior to 2003 were estimated assuming clear skies (Anthony et al. 2004), and thus tended to overestimate historical daily irradiances.

Of the more than 6,000 coral colonies surveyed on the crest at western sites of Orpheus Island, >50% were affected by this tidal event, either in the form of bleaching or partial mortality. This level of damage is

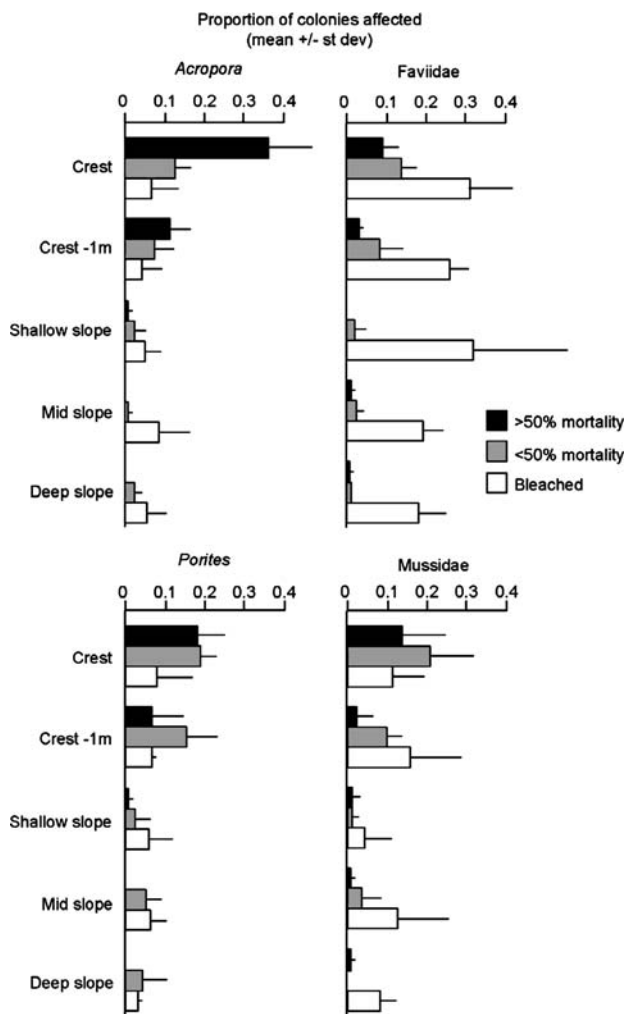


Fig. 6 Severity of stress responses along a 9 m depth gradient for *Acropora*, *Porites*, faviids and mussids at the western sites of Pelorous and Orpheus Islands

comparable to that recorded by Loya (1976) following a similar tidal event in Eilat, Red Sea (1970). Notably, the level of coral mortality resulting from the tidal event at Orpheus Island was greater than the mortality observed at the same reefs following the thermal bleaching event in the summer of 1998 (Baird and Marshall 2002), which was one of the worst on record (Hoegh-Guldberg 1999, 2004). Similar to the pattern for thermal bleaching, members of genus *Acropora* and family Pocilloporidae were most affected by the tidal event, whereas faviids, mussids, *Porites*, and in particular soft corals, were the least affected. Massive scleractinian corals with thick tissue layers, such as faviids and mussids, are able to retract their tissues into the skeleton and thereby withstand long periods of aerial exposure and high solar radiation (Brown et al. 1994a). Importantly, because *Acropora* was the dominant group on the reef crest, and among the most

vulnerable to other stressors such as thermal bleaching (Marshall and Baird 2002) and cyclones (Connell et al. 1997), colonies surviving the winter tidal event are likely to have weakened defences against upcoming summer stressors. Allocation of resources towards tissue repair following the tidal event is likely to impact negatively on energy stores, and thereby increase the risk of starvation following thermal bleaching in summer (Anthony et al. 2007). Furthermore, the timing of extreme low tide, high-irradiance events coincides with key stages of the gametogenic cycle (Babcock et al. 1986). This may, thus cause lowered fecundity as energy stores are diverted to tissue repair or energy acquisition is reduced as a consequence of bleaching (Baird and Marshall 2002; Anthony et al. 2007). As a result, the overall reproductive output of the coral population at Orpheus and Pelorous Islands is likely to have been reduced in 2005 as a result of both mortality removing individuals from the population and reduced fecundity of remaining colonies. Severe tidal events thus have the potential to devastate the intertidal reef community by several means: (1) high mortality of dominant framework builders, (2) physiological stress and reduced energy reserves prior to the onset of subsequent stressors and (3) reductions in the reproductive potential of coral communities.

The primary mechanism likely to be driving the dramatic differences in stress responses between coral communities on western and eastern sites is the contrasting wave regimes. Prevailing southeasterly winds in the Coral Sea and within the Great Barrier Reef lagoon generate sea wave heights of up to 1 m on most days on the eastern side of the islands (personal observation). Specifically, during the periods of extreme low tides in August and September 2005, wind strengths were 10–15 knots from a southeasterly direction, generating significant swells at the eastern sites. As a consequence, intertidal benthic communities at eastern sites were only air-exposed for seconds at a time due to the breaking surf. In contrast, wave-heights at the western protected sites were minimal (less than 0.3 m) and corals on the reef crest were air-exposed at all times during the extreme low tides.

Of secondary importance is the large difference in light attenuation between eastern and western sites. A reduction in water depth due to falling tides causes a much greater relative increase in benthic irradiance in turbid water than in clear water (Anthony et al. 2004). In plants and photo symbioses such as corals, sudden episodes of supraoptimal irradiance can lead to photoinhibition, photodamage and bleaching (Brown et al. 1994a; Hoegh-Guldberg and Jones 1999), often

resulting in mortality (Gleason 1993; Baird and Marshall 2002; McClanahan 2004). In benthic aquatic habitats, the light environment is highly dynamic, driven by at least three variables: tidal regime, cloud cover and turbidity (Anthony et al. 2004). Because corals photoacclimate to average irradiances (analogous to plants and algae, Falkowski and Raven 1997), the extreme low tide, high-irradiance event would have led to greater light stress for the more shade-acclimated corals on the western sites than for the more light-adapted corals at the eastern sites. This is also supported by the observation that 20–30% of faviid and pocilloporid colonies underwent bleaching in shallow as well as deep water on the western side of the islands.

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References

- Allen PA (1997) Earth surface processes. Blackwell Sciences, Oxford, pp 404
- Anthony KRN, Fabricius KE (2000) Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. *J Exp Mar Biol Ecol* 252:221–253
- Anthony KRN, Ridd PV, Orpin A, Larcombe P, Lough JM (2004) Temporal variation in light availability in coastal benthic habitats: effects of clouds, turbidity and tides. *Limnol Oceanogr* 49:2201–2211
- Anthony KRN, Connolly SR, Hoegh-Guldberg O (2007) Bleaching, energetics, and coral mortality risk: effects of temperature, light, and sediment regime. *Limnol Oceanogr* (in press)
- Babcock RC, Bull GD, Harrison PL, Heyward AJ, Oliver JK, Wallace CC, Willis BL (1986) Synchronous spawning of 105 scleractinian coral species on the Great Barrier Reef. *Mar Biol* 90:379–394
- Baird AH, Marshall PA (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Mar Ecol Prog Ser* 237:133–141
- Barnes DJ, Chalker BE (1990) Calcification and photosynthesis in reef-building corals and algae. In: Dubinsky Z (ed) *Ecosystems of the world: coral reefs*. Elsevier, Amsterdam, pp 109–131
- Berkelmans R (2002) Time-integrated thermal bleaching thresholds of reefs and their variation on the Great Barrier Reef. *Mar Ecol Prog Ser* 229:73–82
- Brown BE, Dunne RP, Scoffin TP, Le Tissier MDA (1994a) Solar damage in intertidal corals. *Mar Ecol Prog Ser* 105:219–230
- Brown BE, Le Tissier MDA, Dunne RP (1994b) Tissue retraction in the scleractinian coral *Coeloseris mayeri*, its effect upon coral pigmentation, and preliminary implications for heat balance. *Mar Ecol Prog Ser* 105:209–218
- Chisholm JRM (2003) Primary productivity of reef-building crustose coralline algae. *Limnol Oceanogr* 48:1376–1387
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310
- Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol Monogr* 67:461–488
- Denny MW (1994) Extreme drag forces and the survival of wind- and water-swept organisms. *J Exp Biol* 194:97–115
- Devantier LM, De'ath G, Turak E, Done TJ, Fabricius KE (2006) Species richness and community structure of reef-building corals on the nearshore Great Barrier Reef. *Coral Reefs* 25:329–340
- Dollar SJ (1982) Wave stress and coral community structure in Hawaii. *Coral Reefs* 1:71–81
- Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* 1:95–107
- van Duin EHS (2001) Modeling underwater light climate in relation to sedimentation, resuspension, water quality and autotrophic growth. *Hydrobiologia* 444:25–42
- Falkowski PG, Raven JA (1997) Aquatic photosynthesis. Blackwell Science, Malden, pp 375
- Fishelson L (1973) Ecological and biological phenomena influencing coral-species composition on the reef tables at Eilat (Gulf of Aqaba, Red Sea). *Mar Biol* 19:183–196
- Gleason MG (1993) Effects of disturbance on coral communities: bleaching in Moorea, French Polynesia. *Coral Reefs* 12:193–201
- Glynn PW (1968) Mass mortalities of echinoids and other reef-flat organisms coincident with midday low water exposures in Puerto Rico. *Mar Biol* 1:226–243
- Helmuth BST (1998) Intertidal mussel micro-climates: predicting the body temperature of a sessile invertebrate. *Ecol Monogr* 68:51–74
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshw Res* 50:839–866
- Hoegh-Guldberg O (2004) Coral reefs in a century of rapid environmental change. *Symbiosis* 37:1–31
- Hoegh-Guldberg O, Jones RJ (1999) Photoinhibition and photoprotection in symbiotic dinoflagellates from reef-building corals. *Mar Ecol Prog Ser* 183:73–86
- Hoegh-Guldberg O, Fine M, Skirving W, Johnstone R, Dove S, Strong A (2005) Coral bleaching following wintry weather. *Limnol Oceanogr* 50:265–271
- Karlson RH, Hughes TP, Bellwood DR (2004) Coral communities are regionally enriched along an oceanic biodiversity gradient. *Nature* 429:867–870
- Kirk JTO (1994) Light and photosynthesis in aquatic ecosystems. Cambridge University Press, Cambridge, pp 525
- Larcombe P, Ridd PV, Prytz A, Wilson B (1995) Factors controlling suspended sediment on inner-shelf coral reefs, Townsville, Australia. *Coral Reefs* 14:163–171
- Loya Y (1976) Recolonization of Red Sea corals affected by natural catastrophes and man-made perturbations. *Ecology* 57:278–289
- Marra J (1978) Effect of short-term variations in light intensity on photosynthesis of a marine phytoplankter: a laboratory simulation study. *Mar Biol* 46:191–202
- Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* 19:155–163
- McClanahan TR (2004) The relationship between bleaching and mortality of common corals. *Mar Biol* 144:1239–1245
- Menge BA, Branch GM (2001) Rocky intertidal communities. In: Bertness Mark D, Gaines Steven D, Hay ME (eds) *Marine Community Ecology*. Sinauer Associates, Sunderland, Massachusetts, pp 221–251
- Paine RT, Levin SA (1981) Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol Monogr* 51:145–178

- Pandolfi JM, Greenstein BJ (1997) Taphonomic alteration of reef corals: effects of reef environment and coral growth form: I. The Great Barrier Reef. *Palaios* 12:27–42
- Rogers CS (1993) Hurricanes and coral reefs—the intermediate disturbance hypothesis revisited. *Coral Reefs* 12:127–137
- Shick JM, Lesser MP, Jokiel PL (1996) Effects of ultraviolet radiation on corals and other coral reef organisms. *Glob Change Biol* 2:527–545
- Siebeck UE, Marshall NJ, Kluter A, Hoegh-Guldberg O (2006) Monitoring coral bleaching using a colour reference card. *Coral Reefs* 25:453–460
- Stapel J, Manuntun R, Hemminga MA (1997) Biomass loss and nutrient redistribution in an Indonesian *Thalassia hemprichii* seagrass bed following seasonal low tide exposure during daylight. *Mar Ecol Prog Ser* 148:251–262