



RESEARCH ARTICLE

REVISED Depth-dependent mortality of reef corals following a severe bleaching event: implications for thermal refuges and population recovery [v3; ref status: indexed, <http://f1000r.es/2zg>]

Tom C. L. Bridge^{1,2}, Andrew S Hoey¹, Stuart J Campbell³, Efin Muttaqin³, Edi Rudi⁴⁺, Nur Fadli⁴, Andrew H Baird¹

¹ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811, Australia

²Australian Institute of Marine Science, Townsville, Queensland 4810, Australia

³Wildlife Conservation Society, Indonesia Marine Program, Bogor, Indonesia

⁴Centre for Marine and Fisheries Studies, Syiah Kuala University, Banda Aceh, Indonesia

+ Deceased author

v3 First published: 16 Sep 2013, 2:187 (doi: [10.12688/f1000research.2-187.v1](https://doi.org/10.12688/f1000research.2-187.v1))
 Second version: 31 Oct 2013, 2:187 (doi: [10.12688/f1000research.2-187.v2](https://doi.org/10.12688/f1000research.2-187.v2))
 Latest published: 19 Feb 2014, 2:187 (doi: [10.12688/f1000research.2-187.v3](https://doi.org/10.12688/f1000research.2-187.v3))

Abstract

Coral bleaching caused by rising sea temperature is a primary cause of coral reef degradation. However, bleaching patterns often show significant spatial variability, therefore identifying locations where local conditions may provide thermal refuges is a high conservation priority. Coral bleaching mortality often diminishes with increasing depth, but clear depth zonation of coral communities and putative limited overlap in species composition between deep and shallow reef habitats has led to the conclusion that deeper reef habitats will provide limited refuge from bleaching for most species. Here, we show that coral mortality following a severe bleaching event diminished sharply with depth. Bleaching-induced mortality of *Acropora* was approximately 90% at 0-2m, 60% at 3-4 m, yet at 6-8m there was negligible mortality. Importantly, at least two-thirds of the shallow-water (2-3 m) *Acropora* assemblage had a depth range that straddled the transition from high to low mortality. Cold-water upwelling may have contributed to the lower mortality observed in all but the shallowest depths. Our results demonstrate that, in this instance, depth provided a refuge for individuals from a high proportion of species in this *Acropora*-dominated assemblage. The persistence of deeper populations may provide a critical source of propagules to assist recovery of adjacent shallow-water reefs.

Open Peer Review

Referee Status:

	Invited Referees		
	1	2	3
REVISED version 3 published 19 Feb 2014			
UPDATED version 2 published 31 Oct 2013		 report	 report
version 1 published 16 Sep 2013	 report	 report	

- 1 **Tyler Smith**, University of the Virgin Islands Virgin Islands, U.S.
- 2 **John Rooney**, National Oceanic and Atmospheric Administration USA
- 3 **Bert Hoeksema**, Netherlands Centre for Biodiversity Naturalis Netherlands

Discuss this article

Comments (0)

Corresponding author: Tom C. L. Bridge (thomas.bridge@jcu.edu.au)

How to cite this article: Bridge TCL, Hoey AS, Campbell SJ *et al.* **Depth-dependent mortality of reef corals following a severe bleaching event: implications for thermal refuges and population recovery [v3; ref status: indexed, <http://f1000r.es/2zg>]** *F1000Research* 2014, **2**:187 (doi: [10.12688/f1000research.2-187.v3](https://doi.org/10.12688/f1000research.2-187.v3))

Copyright: © 2014 Bridge TCL *et al.* This is an open access article distributed under the terms of the [Creative Commons Attribution Licence](#), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. Data associated with the article are available under the terms of the [Creative Commons Zero "No rights reserved" data waiver](#) (CC0 1.0 Public domain dedication).

Grant information: Funding for this study was provided by the Australian Research Council Centre of Excellence for Coral Reef Studies, the Wildlife Conservation Society Indonesia Marine Program, and the Kerzner Marine Foundation.

The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: No competing interests were disclosed.

First published: 16 Sep 2013, **2**:187 (doi: [10.12688/f1000research.2-187.v1](https://doi.org/10.12688/f1000research.2-187.v1))

First indexed: 24 Jan 2014, **2**:187 (doi: [10.12688/f1000research.2-187.v2](https://doi.org/10.12688/f1000research.2-187.v2))

REVISED Amendments from Version 2

We have responded to each of the reviewers' comments as outlined below. We have amended Figure 2 to show that shallow corals may have been observed anywhere from 0–2 m depth. We have also clarified the sentence in the discussion regarding the importance of surveying multiple depths to accurately quantify the effects of a bleaching event.

See referee reports

Introduction

Mass bleaching events causing extensive mortality of reef-building corals have become more frequent and widespread in recent decades and have affected almost all coral reef regions^{1–3}. Coral bleaching is a generalised stress response resulting from numerous causes including sedimentation, freshwater exposure or disease⁴; however, the most geographically extensive and severe events are correlated with sustained periods of elevated sea water temperatures and high light irradiance⁵. The bleaching response is caused by the expulsion of a symbiotic dinoflagellate *Symbiodinium* that occur within the coral tissue and allow corals to harness energy from sunlight, thus providing a significant portion of the energy requirements. The sensitivity of this symbiosis to elevated sea temperature is well-documented^{5,6}, suggesting that many coral species will be highly vulnerable to the effects of global warming^{7,8}.

Despite this apparent sensitivity, reef corals have persisted through numerous large-magnitude and sometimes rapid changes in sea surface temperatures over the past 240 million years^{3,9}. One mechanism by which a species can cope with changing local climate is to move to a more favourable area, and tropical reef corals have repeatedly shifted their distribution to higher latitudes in response to past climate warming^{10,11}. Alternatively, populations may persist in microrefugia, defined as small areas of suitable habitat within regionally unfavourable environmental conditions^{12,13}. Despite increasing recognition of their importance for conservation planning in terrestrial ecosystems^{14–16}, microrefugia are less considered in the marine realm.

The severity of coral bleaching is often spatially heterogeneous due to both historical^{17,18} and environmental^{19–21} factors. Coral bleaching is caused by a synergistic effect between heat and light, and therefore microrefugia from bleaching are likely to occur in regions where oceanographic or atmospheric conditions reduce water temperatures or light irradiance relative to surrounding areas²². Light irradiance declines with depth and ambient temperatures are often lower in deeper waters, therefore the incidence of bleaching and/or subsequent mortality is likely to be lower at greater water depths^{1,5,22}. Warm-water coral bleaching is occasionally reported to depths of 50 m, however, such observations are rarely followed up in order to estimate bleaching-induced mortality. Typically the incidence of bleaching is substantially lower at greater depths and in the few cases it has been measured, so is bleaching-induced mortality^{23–25}. For example, mortality rates of corals at a depth of 6 m were only a third of those in 2 m across several turbid inshore reefs on the Great Barrier Reef (GBR)²⁴. A transition from high to low mortality with increasing depth was observed at numerous sites in the western Indian Ocean during 1998,

the most severe and widespread bleaching event on record²⁶. This transition often occurred across a fairly sharp depth boundary at intermediate depths of 10–15 m²⁶, therefore species with depth ranges that straddle this transition from high to low bleaching mortality will have a refuge from bleaching in deeper water. However, most assessments of coral reefs consider only shallow habitats, and reductions in mortality with increasing depth may go unnoticed. Furthermore, recent studies of deep-water reefs have indicated that many corals may occur over a wider depth range than currently thought^{27,28}.

In May–June 2010, a sustained increase in seawater temperatures in the Andaman and South China Seas resulted in extensive coral bleaching and caused high mortality of many coral species²⁹. Six weeks after the peak seawater temperatures, 45% of all corals and 94% of *Acropora* colonies were dead in shallow waters (1–2 m) around Pulau Weh, Sumatra, Indonesia²⁹. Here, we assess the effects of this severe thermal bleaching event at Pulau Weh over a depth gradient from 2–27 m to investigate 1) whether severe mortality of reef corals observed in shallow water (0–2 m) extended into deeper habitats; and 2) whether depth provided a refuge from bleaching mortality. We concentrate on the corals of the genus *Acropora* because they are the most diverse and abundant genus in the Indo-Pacific, and are important ecosystem engineers on most Indo-Pacific coral reefs. They are also often amongst the most susceptible taxa to bleaching-induced mortality, and bleaching events often result in shifts from *Acropora* – dominated communities towards communities dominated by more bleaching resistant taxa (e.g. *Porites* and the family Merulinidae)^{26,30}. Change in *Acropora* cover before and after a bleaching event is therefore a useful indicator of bleaching severity.

Materials and methods

Pulau Weh (5° 50'N, 95° 20'E) is located in the province of Aceh off the northwest coast of Sumatra, Indonesia. The region's reefs have received little attention from scientists, but support similarly diverse coral communities to the rest of the Indo-Australian Archipelago³¹. Northwest Sumatra was the epicentre of the December 2004 Indian Ocean tsunami, and although Pulau Weh's coral communities were relatively unaffected by this event³², they suffered substantial mortality in the 2010 Andaman Sea bleaching²⁹. To examine the influence of depth on bleaching mortality, we compared both total coral cover and *Acropora* cover collected before (November 2009 to February 2010) and after (July 2011) the bleaching event at three depths (0–2 m, 3–4 m and 6–8 m) at four sites on the northern and western sides of Pulau Weh (Batee Gla, Ba Kopra, Rubiah Sea Garden, Rubiah Channel – Figure S1). Coral cover was estimated along 6–10 replicate 10 m line intercept transects, which were haphazardly placed at 0–2 m, and 3–6 replicate 50 m point intercept transects at 3–4 m and 6–8 m (see Data File). Any live hard coral (i.e. scleractinian or hydrozoan coral) underlying each survey point was recorded to genus level. Changes in total live coral cover and *Acropora* cover between 2009 and 2011 were compared using two-factor ANOVA's. Assumptions of the ANOVA's were examined using residual analysis and no transformation was necessary. The analyses were based on the proportion of total coral or *Acropora* cover per 50 m transect.

To determine the proportion of the *Acropora* assemblage afforded a depth refuge from this bleaching event, we conducted species-level

surveys of *Acropora* assemblages in 0 to 2 m and then at 5 m intervals from 3–27 m in February 2012 at five sites on the northern and western sides of Pulau Weh (Batee Gla, Ba Kopra, Rubiah Sea Garden, Rubiah Channel and Tokong - Figure S1). Sites were chosen based on their bathymetry profiles, with accessible deep sites only present on the steeply-sloping, ocean-facing northern and western coasts. Data were collected at 5 m depth intervals using replicate 10-minute timed swims, where the species identity of every living *Acropora* colony was recorded. Post-bleaching surveys were compared to shallow-water (0–2 m) surveys conducted in November 2009 before the bleaching event using 40 min timed swims³¹ at these same sites. Corals were identified using taxonomic references provided in “Staghorn Corals of the World” by Wallace CC and “Corals of the World”, by Veron JEN^{33,34}. Analysis of Similarities (ANOSIM), a multivariate approximation of ANOVA³⁵, was performed on a square root-transformed Bray-Curtis similarity matrix to determine any significant difference in the *Acropora* assemblage among sites.

Total hard coral cover and *Acropora* cover for each transect pre-bleaching (2009) and post-bleaching (2011)

1 Data File

<http://dx.doi.org/10.6084/m9.figshare.777781>

Results and discussion

A total of 40 *Acropora* species were observed during the study, confirming the high diversity previously reported on Acehnese reefs³¹. ANOSIM revealed no significant difference in assemblage structure among sites, which were therefore pooled for further analysis. Bleaching mortality was very high in the shallows, however, mortality diminished rapidly with increasing depth (Figure 1). Total coral cover declined by 75% at 0–2 m but only 20% at 3–4 m, while there was no significant change at 6–8 m (Figure 1a; 2-way ANOVA depth by year interaction; $F_{2,123} = 21.2$, $p < 0.001$). The decline in mortality was even more pronounced in the *Acropora*, with cover declining by approximately 90% at 0–2 m and 60% at 3–4 m, with

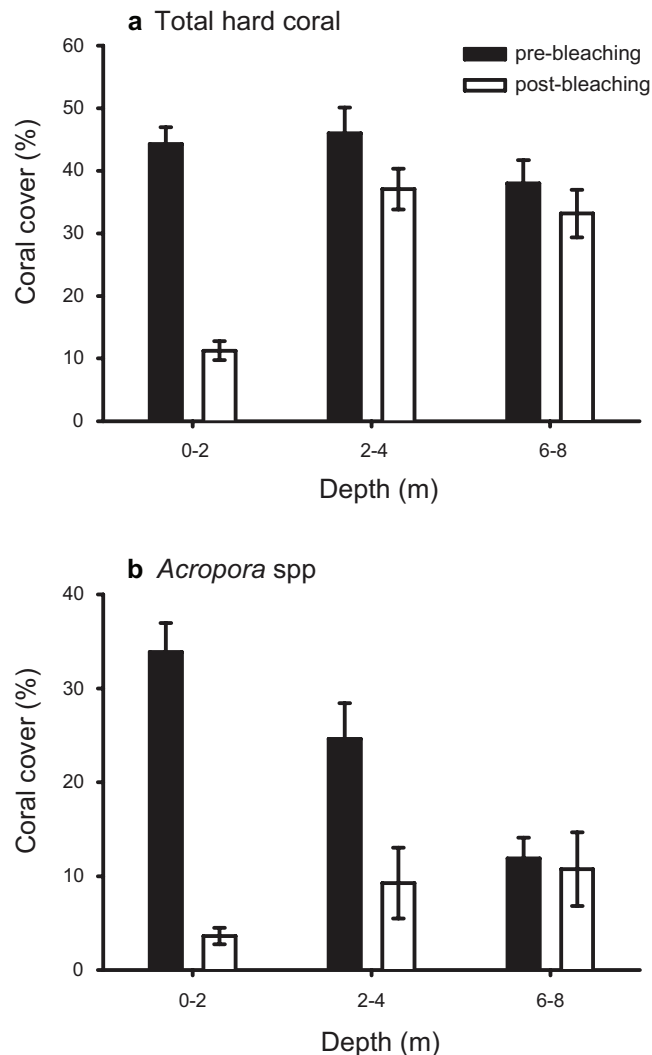


Figure 1. Change in live coral cover on Pulau Weh following the 2010 bleaching event at depths of 0–2, 2–4, and 6–8 metres. (a) total live coral cover; and (b) live *Acropora* cover.

no change detected at 6–8 m (Figure 1b; 2-way ANOVA depth x year; $F_{2,123} = 17.9, p < 0.001$).

A high proportion of this diverse *Acropora* assemblage was afforded a refuge from bleaching mortality in deeper water. Of the 29 *Acropora* species occurring in shallow waters < 7 m, 19 (66%) also occurred below the approximate depth of transition from high to low mortality (Figure 2). However, the refuge effect would be diminished if mortality had reached into deeper waters. If, for example, the transition between high and low bleaching mortality had occurred at 12 m, 14 (48%) of the species affected would have had a refuge in depth. Similarly, if bleaching mortality extended to 22 m, only 6 species from the shallow assemblage (21%) would have had colonies persisting below the transition depth.

Doubts regarding the potential significance of depth as a refuge for corals from warm-water bleaching have previously been raised

because (1) bleaching has been observed in the deeper areas of reefs, (2) there is limited overlap of species between deep and shallow reef areas, and (3) genetic partitioning within species among depths suggests that deeper population cannot provide an effective source of recruits for shallow populations^{36,37}. Firstly, while *bleaching* often extends to the lower depth limits of some shallow water species, both bleaching frequency and, most importantly, *mortality*, is often strongly depth dependent (Figure 3)^{24,26,38}. Indeed, a transition from high to low mortality occurred at depths of ≤ 15 m ~50% of sites surveyed in the Indian Ocean in 1998²⁶ – see Table 1). Secondly, our results indicate that even with a pronounced depth zonation in the *Acropora* assemblage, two-thirds of species occurring in shallow depths had a depth range that straddled the transition in bleaching mortality. The depth zonation of coral assemblages is one of the most consistent and predictable patterns in nature^{39,40} and therefore our results are not an anomaly. Thirdly, the genetic divergence between populations above and below the transition in mortality at between 4 and 8 m is unlikely

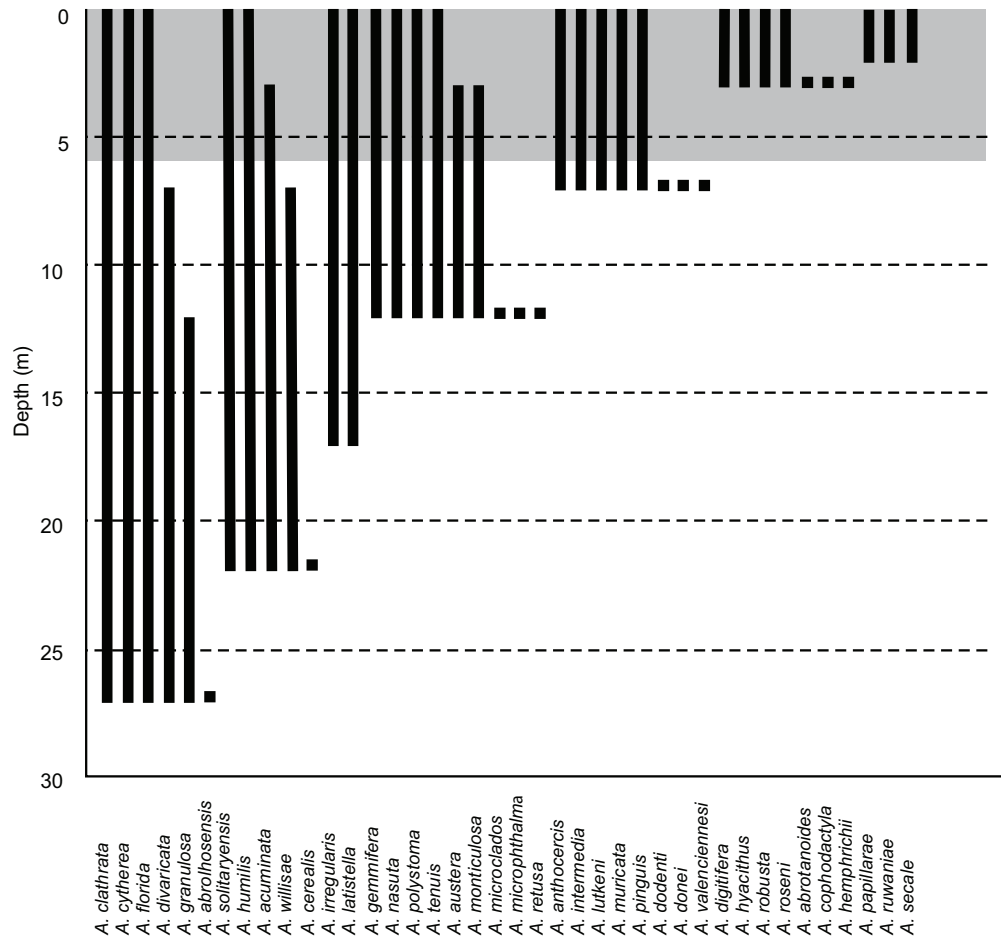


Figure 2. Depth distribution of 40 *Acropora* species observed at Pulau Weh following the bleaching event. Shaded (grey) panel indicates the depth range where bleaching mortality was high. Of the 29 species occurring in 0–7 m depth, 19 (66%) also occurred below 7 m.

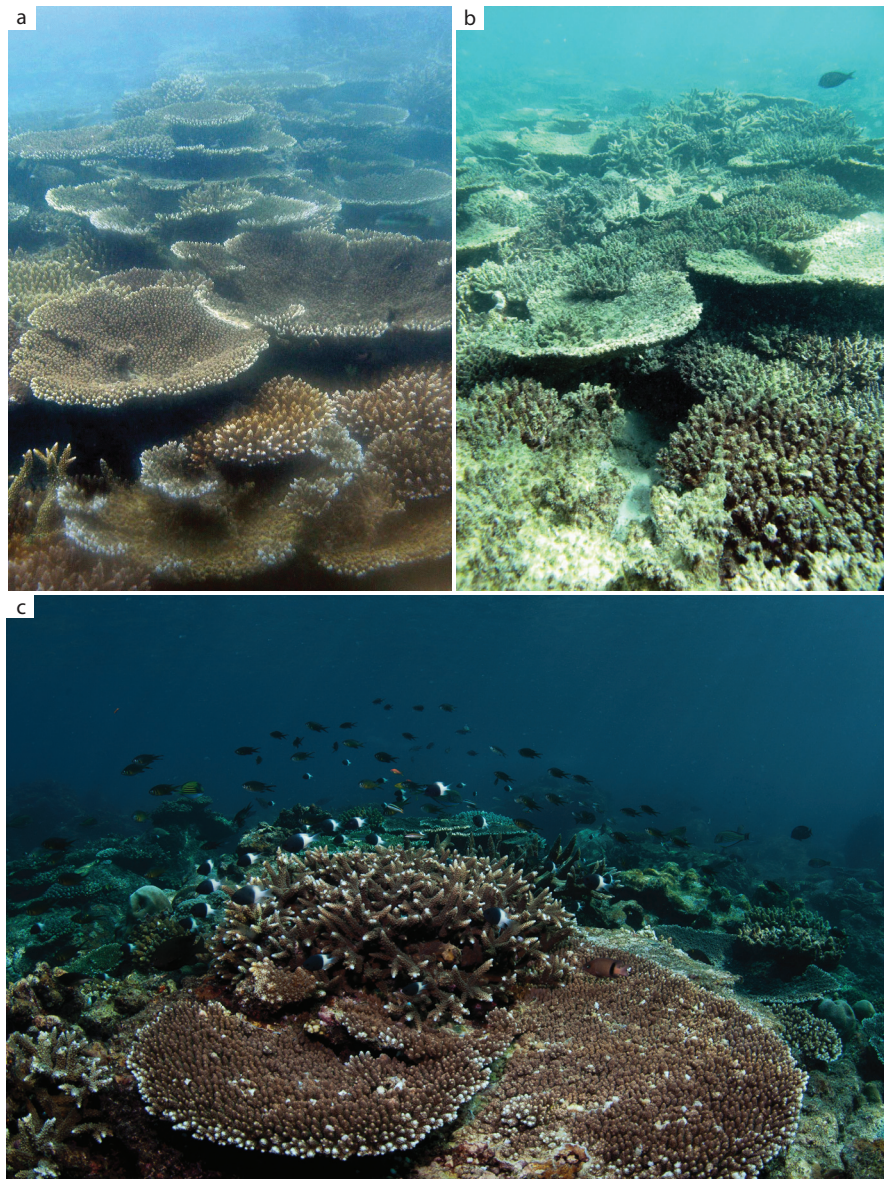


Figure 3. *Acropora*-dominated communities at Pulau Weh. (a) Reef crest at 2 m depth prior to bleaching (16 November 2009); (b) the same reef crest six weeks after the peak of bleaching (26 July 2010); (c) upper reef slope community at 6 m depth largely unaffected by the bleaching event, 25 February 2012.

to be sufficient to prevent larval migration in either direction. For example, larvae of the coral *Seriatopota hystrix* migrate among sub-populations over a 30 m depth range⁴¹. Furthermore, connectivity modelling in two Caribbean coral species indicates demographically significant larval subsidy from deep to shallow reef habitats over a much greater depth range (5–40 m) even when deep-water fertilisation rates and post-settlement survival are greatly reduced⁴².

Our results, and those of previous studies^{24,26,38}, indicate that bleaching mortality can vary considerably over a small depth range. Consequently, surveys conducted at a single depth may greatly misrepresent the proportion of coral populations killed by coral bleaching³⁹. For example, long-term, large-scale monitoring of

coral cover on reef slopes (6–9 m depth) on the GBR suggests that bleaching has been a comparatively minor source of coral mortality over the last few decades^{43,44}, despite two mass bleaching events in 1998 and 2002⁴⁵. However, in the 1998 bleaching event on the inshore GBR, bleaching mortality was on average 3-times higher at 2–4 m when compared to 5–8 m²⁴. Clearly, ecosystem assessments considering only a single depth may provide a biased view of the relative importance of the many different agents of coral mortality, and should therefore be conducted over a range of depths to accurately assess the relative importance of multiple stressors.

Identifying areas or conditions that consistently provide refuges for corals from thermal stress is critically important for coral reef

conservation under future climate change. In 1998, lower mortality and a shallower transition depth was often associated with sites that experienced episodic upwelling of cold water^{26,46,47}. Although environmental data are not available from Pulau Weh, pulses of cold water were regularly experienced during data collection, and rapid upwelling-driven temperature plunges of up to 10°C are recorded from the west coast of the nearby Similan Islands⁴⁸. Interestingly, Acehnese reefs appeared unaffected by the 1998 bleaching event²⁹, despite the coral bleaching extending across virtually the entire Indian Ocean from east Africa and north-western Australia^{26,49,50}. These cold-water upwelling events may explain the lack of mortality in 1998 and the shallow transition depth during 2010 despite very high sea surface temperatures. Depth-dependent mortality was most evident at Ba Kopra, on the western side of Pulau Weh (Figure S1), supporting the hypothesis that these upwelling events may create small-scale refugia from thermal anomalies. If so, this region may provide a consistent refuge for many corals against rising sea temperatures. In summary, our results show that coral bleaching mortality can diminish rapidly even where shallow-water corals experience severe mortality, and modest depths can provide a refuge for a significant proportion of coral species. Identifying sites where oceanographic conditions reduce the effects of thermal anomalies should be a priority for coral reef conservation.

Author contributions

TCLB and AHB conceived the study. TCLB, AHB and ASH designed the study. All authors were involved in data collection.

TCLB, AHB and ASH analysed these data. TCLB, AHB and ASH wrote the manuscript with additional contributions from all other authors.

Competing interests

No competing interests were disclosed.

Grant information

Funding for this study was provided by the Australian Research Council Centre of Excellence for Coral Reef Studies, the Wildlife Conservation Society Indonesia Marine Program, and the Kerzner Marine Foundation.

The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Acknowledgements

The activities for this study were conducted under a Memorandum of Understanding (MoU) between the Wildlife Conservation Society (WCS) and the Indonesian Ministry of Forestry, and a MoU between the ARC Centre of Excellence for Coral Reef Studies, James Cook University, Australia and Syiah Kuala University, Banda Aceh, Indonesia. No flora or fauna were collected or manipulated during this research and all surveys were conducted on public land. We thank Ismayudi Dodent and Rubiah Tirtah Divers for their field support.

This paper is dedicated to the late Dr Edi Rudi, a pioneer of coral research in Aceh and a great friend.

Supplementary material

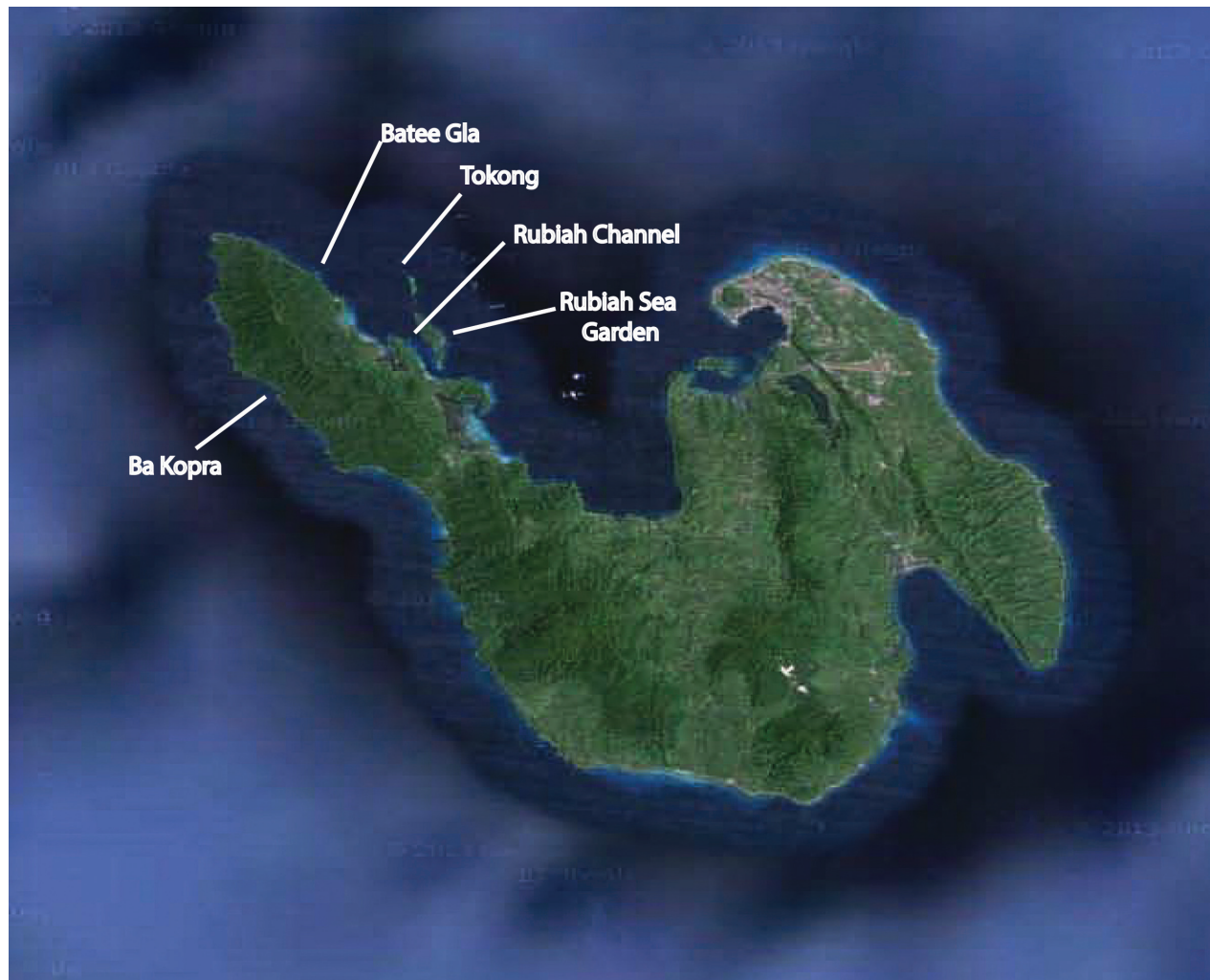


Figure S1. Map of Pulau Weh showing location of study sites.

References

- Hughes TP, Baird AH, Bellwood DR, *et al.*: **Climate change, human impacts, and the resilience of Coral Reefs.** *Science*. 2003; **301**(5635): 929–933.
[PubMed Abstract](#) | [Publisher Full Text](#)
- Baker AC, Glynn PW, Riegl B: **Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends, and future outlook.** *Estuar Coast Shelf Sci*. 2008; **80**: 435–471.
[Publisher Full Text](#)
- Pandolfi JM, Connolly SR, Marshall DJ, *et al.*: **Projecting coral reef futures under global warming and ocean acidification.** *Science*. 2011; **333**(6041): 418–422.
[PubMed Abstract](#) | [Publisher Full Text](#)
- Baird AH, Bhagooli R, Ralph PJ, *et al.*: **Coral bleaching: The role of the host.** *Trends Ecol Evol*. 2009; **24**(1): 16–20.
[PubMed Abstract](#) | [Publisher Full Text](#)
- Glynn PW: **Coral reef bleaching: facts, hypotheses and implications.** *Glob Chang Biol*. 1996; **2**: 495–509.
[Publisher Full Text](#)
- Brown BE: **Coral bleaching: causes and consequences.** *Coral Reefs*. 1997; **16**: 129–138.
[Publisher Full Text](#)
- Carpenter KE, Abrar M, Aeby G, *et al.*: **One-third of reef-building corals face elevated extinction risk from climate change and local impacts.** *Science*. 2008; **321**(5888): 560–563.
[PubMed Abstract](#) | [Publisher Full Text](#)
- Foden WB, Butchart SHM, Stuart SN, *et al.*: **Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals.** *PLoS One*. 2013; **8**(6): e65427.
[PubMed Abstract](#) | [Publisher Full Text](#)
- Veron JEN: **Corals in space and time: the biogeography and evolution of the**

- Scleractinia.** Comstock/Cornell University Press, Ithaca, NY. 1995; 321pp.
[Reference Source](#)
10. Wallace CC, Rosen BR: **Diverse staghorn corals (Acropora) in high-latitude Eocene assemblages: implications for the evolution of modern diversity patterns of reef corals.** *Proc Biol Sci.* 2006; **273**(1589): 975–982.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 11. Greenstein BJ, Pandolfi JM: **Escaping the heat: range shifts of reef coral taxa in coastal Western Australia.** *Glob Chang Biol.* 2008; **14**: 513–528.
[Publisher Full Text](#)
 12. Rull V: **Microrefugia.** *J Biogeogr.* 2009; **36**: 481–484.
[Publisher Full Text](#)
 13. Dobrowski SZ: **A climatic basis for microrefugia: the influence of terrain on climate.** *Glob Chang Biol.* 2011; **17**: 1022–1035.
[Publisher Full Text](#)
 14. Ashcroft MB: **Identifying refugia from climate change.** *J Biogeogr.* 2010; **37**: 1407–1413.
[Publisher Full Text](#)
 15. Keppel G, Van Niel KP, Wardell-Johnson GW, *et al.*: **Refugia: identifying and understanding safe havens for biodiversity under climate change.** *Global Ecol Biogeogr.* 2012; **21**: 393–404.
[Publisher Full Text](#)
 16. Groves CR, Game ET, Anderson MG, *et al.*: **Incorporating climate change into systematic conservation planning.** *Biodivers Conserv.* 2012; **21**: 1651–1671.
[Publisher Full Text](#)
 17. Thompson DM, van Woessik R: **Corals escape bleaching in regions that recently and historically experienced frequent thermal stress.** *Proc Biol Sci.* 2009; **276**(1669): 2893–2901.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 18. Oliver TA, Palumbi SR: **Many corals host thermally resistant symbionts in high-temperature habitat.** *Coral Reefs.* 2011; **30**: 241–250.
[Publisher Full Text](#)
 19. Dunne RP, Brown BE: **The influence of solar radiation on bleaching of shallow water reef corals in the Andaman Sea 1993–1998.** *Coral Reefs.* 2001; **20**: 201–210.
[Publisher Full Text](#)
 20. Kleypas JA, Danabasoglu G, Lough JM: **Potential role of the ocean thermostat in determining regional differences in coral reef bleaching events.** *Geophys Res Lett.* 2008; **35**: L03613.
[Publisher Full Text](#)
 21. Woessik R, Houk P, Isechal AL, *et al.*: **Climate-change refugia in the sheltered bays of Palau: analogs of future reefs.** *Ecol Evol.* 2012; **2**(10): 2474–2484.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 22. Riegl B, Piller WE: **Possible refugia for reefs in times of environmental stress.** *Int J Earth Sci.* 2003; **92**: 520–531.
[Publisher Full Text](#)
 23. Rowan R, Knowlton N, Baker AC, *et al.*: **Landscape ecology of algal symbionts creates variation in episodes of coral bleaching.** *Nature.* 1997; **388**(6639): 265–269.
[PubMed Abstract](#)
 24. Marshall PA, Baird AH: **Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa.** *Coral Reefs.* 2000; **19**: 155–163.
[Publisher Full Text](#)
 25. Glynn PW, Mate JL, Baker AC, *et al.*: **Coral bleaching and mortality in Panama and Ecuador during the 1997–1998 El Niño-Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982–1983 event.** *Bull Mar Sci.* 2001; **69**: 79–109.
[Reference Source](#)
 26. Sheppard CRC, Obura D: **Corals and reefs of the Cosmoledo and Aldabra atolls: Extent of damage, assemblage shifts and recovery following the severe mortality of 1998.** *J Nat Hist.* 2005; **39**: 103–121.
[Publisher Full Text](#)
 27. Bridge TCL, Fabricius KE, Bongaerts P, *et al.*: **Diversity of Scleractinia and Octocorallia in the mesophotic zone of the Great Barrier Reef, Australia.** *Coral Reefs.* 2012; **31**: 179–189.
[Publisher Full Text](#)
 28. Bridge TCL, Hughes TP, Guinotte JM, *et al.*: **Call to protect all coral reefs.** *Nat Clim Chang.* 2013; **3**: 528–529.
[Publisher Full Text](#)
 29. Guest JR, Baird AH, Maynard JA, *et al.*: **Contrasting patterns of coral bleaching susceptibility in 2010 suggest adaptive response to the thermal stress.** *PLoS One.* 2012; **7**(3): e33353.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 30. Loya Y, Sakai K, Yamazato K, *et al.*: **Coral bleaching: the winners and losers.** *Ecol Lett.* 2001; **4**: 122–131.
[Publisher Full Text](#)
 31. Rudi E, Campbell SJ, Hoey AS, *et al.*: **The Coral Triangle Initiative: What are we missing? A case study from Aceh, Indonesia.** *Oryx.* 2012; **46**: 482–485.
[Publisher Full Text](#)
 32. Baird AH, Campbell SJ, Anggoro AW, *et al.*: **Acehnese reefs in the wake of the Asian tsunami.** *Curr Biol.* 2005; **15**(21): 1926–1930.
[PubMed Abstract](#) | [Publisher Full Text](#)
 33. Wallace CC: **Staghorn corals of the world.** CSIRO Publishing, Collingwood, Victoria. 1999.
[Reference Source](#)
 34. Veron JEN: **Corals of the world.** Australian Institute of Marine Science, Townsville. 2006.
[Reference Source](#)
 35. Clarke KR, Gorley RN: **PRIMER v6: user manual/tutorial.** PRIMER-E: Plymouth. 2006.
[Reference Source](#)
 36. Bongaerts P, Riginos C, Ridgway T, *et al.*: **Genetic divergence across habitats in the widespread coral *Seriatopora hystrix* and its associated Symbiodinium.** *PLoS One.* 2010; **5**(5): e10871.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 37. Brazeau DA, Lesser MP, Slattery M: **Genetic Structure in the Coral, *Montastraea cavernosa*: Assessing Genetic Differentiation among and within Mesophotic Reefs.** *PLoS One.* 2013; **8**(5): e65845.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 38. Hoeksema BW: **Control of bleaching in mushroom coral populations (Scleractinia: Fungiidae) in the Java Sea: stress tolerance and interference by life history strategy.** *Mar Ecol Prog Ser.* 1991; **74**: 225–237.
[Publisher Full Text](#)
 39. Done TJ: **Coral zonation: its nature and significance** *Perspectives on Coral Reefs.* Brian Clouston, Manuka, A.C.T. 1983; pp95–147.
[Reference Source](#)
 40. Hughes TP, Baird AH, Dinsdale EA, *et al.*: **Assembly rules of reef corals are flexible along a steep climatic gradient.** *Curr Biol.* 2012; **22**(8): 736–741.
[PubMed Abstract](#) | [Publisher Full Text](#)
 41. van Oppen MJ, Bongaerts P, Underwood JN, *et al.*: **The role of deep reefs in shallow reef recovery: an assessment of vertical connectivity in a brooding coral from west and east Australia.** *Mol Ecol.* 2011; **20**(8): 1647–1660.
[PubMed Abstract](#) | [Publisher Full Text](#)
 42. Holstein DM: **Vertical connectivity in mesophotic coral ecosystems.** Open Access Dissertations. Paper 1064. 2013.
[Reference Source](#)
 43. Osborne K, Dolman AM, Burgess SC, *et al.*: **Disturbance and the dynamics of coral cover on the Great Barrier Reef (1995–2009).** *PLoS One.* 2009; **6**(3): e17516.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 44. De'ath G, Fabricius KE, Sweatman H, *et al.*: **The 27-year decline of coral cover on the Great Barrier Reef and its causes.** *Proc Natl Acad Sci U S A.* 2012; **109**(44): 17995–9.
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
 45. Berkelmans R, De'ath G, Kininmonth S, *et al.*: **A comparison of the 1998 and 2002 coral bleaching events on the Great Barrier Reef: spatial correlation, patterns and predictions.** *Coral Reefs.* 2004; **23**: 74–83.
[Publisher Full Text](#)
 46. Teleki KA, Spencer T: **Reef systems of the islands of the southern Seychelles.** In: Souter D, Obura D, Linden O, editors. *Coral Reef Degradation in the Indian Ocean.* Kalmar, Sweden: CORDIO. 2000; p 87–93.
[Reference Source](#)
 47. Goreau T, McClanahan T, Hayes R, *et al.*: **Conservation of coral reefs after the 1998 global bleaching event.** *Conserv Biol.* 2000; **14**: 5–15.
[Publisher Full Text](#)
 48. Schmidt GM, Phongsuwan N, Jantzen C, *et al.*: **Coral community composition and reef development at the Similan Islands, Andaman Sea in response to strong environmental variations.** *Marine Ecology Progress Series.* 2012; **456**: 113–126.
[Publisher Full Text](#)
 49. Sheppard CR: **Predicted recurrences of mass coral mortality in the Indian Ocean.** *Nature.* 2003; **425**(6955): 294–297.
[PubMed Abstract](#) | [Publisher Full Text](#)
 50. Gilmour JP, Smith LD, Heyward AJ, *et al.*: **Recovery of an isolated coral reef system following severe disturbance.** *Science.* 2013; **340**(6128): 69–71.
[PubMed Abstract](#) | [Publisher Full Text](#)

Open Peer Review

Current Referee Status:



Version 3

Referee Report 22 May 2014

doi:10.5256/f1000research.3868.r4852



Bert Hoeksema

Netherlands Centre for Biodiversity Naturalis, Leiden, Netherlands

I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

Competing Interests: No competing interests were disclosed.

Version 2

Referee Report 24 January 2014

doi:10.5256/f1000research.2830.r3294



Bert Hoeksema

Netherlands Centre for Biodiversity Naturalis, Leiden, Netherlands

This article presents information on the depth-related occurrence of bleaching among 40 *Acropora* species around Pulau Weh, off North Sumatra. The article is providing important data. It is written in a concise way but I suggest that the authors add a bit more nuance to their argumentation.

Title: The authors could be more specific regarding mentioning the selection of coral species in the title. The contents of the paper is not about a representative selection of "reef corals" mainly about staghorn corals, *Acropora* species, which according to the authors "are also often amongst the most susceptible taxa to bleaching-induced mortality".

Figure 2: The caption is confusing. It mentions the bathymetrical distribution of 41 *Acropora* species, and the depth range where mortality as a result of bleaching was reported to be high. The main text mentions 40 *Acropora* species. Does bleaching mortality in 0-2 m refer to all corals or just *Acropora* corals, because it seems that (almost) no *Acropora* corals were found here. The authors should explain that this figure represents a mix of data from 2009-2011 (0-8 m: i.e. 0-2, 3-4, 6-8 m) and from 2012 (2-27 m: i.e. 2, 7, 12, 17, 22, 27 m).

Results and discussion: The sentence "Doubts regarding the potential significance of depth as a refuge

for corals from warm-water bleaching have previously been raised because...” seems to overlook various papers that do agree with depth-related coral bleaching (e.g. [Hoeksema 1991](#), [Marshall & Baird 2000](#), [Craig et al. 2001](#), [Furby et al. 2013](#)).

The sentences “Our results indicate that bleaching mortality can vary considerably over a small depth range. Consequently, surveys conducted only in shallow waters may greatly overestimate the proportion of coral populations killed by coral bleaching” overlook the fact that some coral species show less bleaching on sun-exposed reef flats, suggesting that they are pre-adapted to high water temperatures (e.g. [Hoeksema 1991](#), [Ware et al. 1996](#), [Craig et al. 2001](#), [Hoeksema & Matthews 2011](#)).

Since *Acropora* corals were identified at species level in 2012, is there a way to tell whether the species showed interspecific differences in bleaching (see [Hoeksema 1991](#), [Craig et al. 2001](#), [Hoeksema & Matthews 2011](#))?

I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

Competing Interests: No competing interests were disclosed.

Author Response 21 Feb 2014

Tom Bridge, James Cook University, Australia

- *“The authors could be more specific regarding mentioning the selection of coral species in the title. The contents of the paper is not about a representative selection of “reef corals” mainly about staghorn corals, Acropora species, which according to the authors “are also often amongst the most susceptible taxa to bleaching-induced mortality”*

We do assess depth-dependent mortality for all corals, but focus on depth distributions of *Acropora* because they were the dominant group at these sites. Therefore, we believe the title accurately reflects the nature of the research.

- *“Does bleaching mortality in 0-2 m refer to all corals or just Acropora corals, because it seems that (almost) no Acropora corals were found here. The authors should explain that this figure represents a mix of data from 2009-2011 (0-8 m: i.e. 0-2, 3-4, 6-8 m) and from 2012 (2-27 m: i.e. 2, 7, 12, 17, 22, 27 m).”*

All of the data presented in Figure 2 is from 2012 (post-bleaching), as stated in the Methods. In Figure 2, the bars on the species encountered in the shallowest depth range (0-2 m) have been extended to 0 m to indicate that they could have occurred anywhere from 0-2 m depth.

- *“The sentence “Doubts regarding the potential significance of depth as a refuge for corals from warm-water bleaching have previously been raised because...” seems to overlook various papers that do agree with depth-related coral bleaching”*

Our discussion states that various authors have discounted the depth refuge effect by several mechanisms. However, we go on to cite examples ([Marshall & Baird, 2000](#); [Sheppard & Obura, 2005](#)) of studies that report depth-dependent coral bleaching, demonstrating that the depth-dependent bleaching observed in this study is not an isolated

case. We have added a citation to [Hoeksema \(1991\)](#) as a further example of depth-dependent coral bleaching.

- *“The sentences “Our results indicate that bleaching mortality can vary considerably over a small depth range. Consequently, surveys conducted only in shallow waters may greatly overestimate the proportion of coral populations killed by coral bleaching” overlook the fact that some coral species show less bleaching on sun-exposed reef flats, suggesting that they are pre-adapted to high water temperatures”*

To clarify, we have altered the text to state that “Our results, and those of previous, indicate that bleaching mortality can vary considerably over a small depth range. Consequently, surveys conducted at a single depth may greatly misrepresent the proportion of coral populations killed by bleaching”.

- *“Since Acropora corals were identified at species level in 2012, is there a way to tell whether the species showed interspecific differences in bleaching?”*

We could test for interspecific differences in mortality among some of the more abundant species; however, this is beyond the scope of the current manuscript, which focuses on depth-dependent mortality.

Competing Interests: No competing interests were disclosed.

Referee Report 05 December 2013

doi:[10.5256/f1000research.2830.r2275](https://doi.org/10.5256/f1000research.2830.r2275)



John Rooney

Coral Reef Ecosystem Division, National Oceanic and Atmospheric Administration, Washington, DC, USA

The authors report that coral bleaching at their study site declined dramatically with increasing depth and they hypothesize that the mitigation of bleaching was caused by localized decreases in temperature caused by cold water upwelling. Although they are continuing their research at the site, including monitoring temperature, at the time they wrote this article no data were available to discuss the magnitude and temporal characteristics of temperature differences between heavily and lightly or unbleached sites. However, the manuscript would be improved with a brief discussion of the magnitude and duration of temperature differences that have been reported in the scientific literature (e.g. [Hoegh-Guldberg, 1999](#)) that have been found to induce bleaching.

I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

Competing Interests: No competing interests were disclosed.

Author Response 21 Feb 2014

Tom Bridge, James Cook University, Australia

In the literature, there is a large range of temperatures reported as thresholds to induce bleaching, and considerable variation in these thresholds due to geographic location, composition of the assemblage, thermal history etc. It is certainly an interesting question, but we maintain that without any data any attempt to identify thresholds in this case would be overly speculative. As such, we do not believe this is the correct venue to incorporate such discussion.

Competing Interests: No competing interests were disclosed.

Version 1

Referee Report 02 October 2013

doi:[10.5256/f1000research.2162.r1825](https://doi.org/10.5256/f1000research.2162.r1825)



John Rooney

Coral Reef Ecosystem Division, National Oceanic and Atmospheric Administration, Washington, DC, USA

This paper makes a valuable contribution, highlighting the marked differences in bleaching-induced coral mortality associated with changes in depth of just a few meters. It highlights the need to conduct surveys over a range of depths to characterize bleaching events and, in particular, to identify “microrefugia” - sites where oceanographic conditions reduce the effects of thermal anomalies - as a priority for coral reef conservation.

In their introduction the authors mention the importance of both irradiance and temperature, but no further mention of irradiance's possible role in the observed coral bleaching and mortality patterns is made. Additionally, the author's state that “pulses of cold water were regularly experienced during data collection” as evidence that upwelling of cold water was the mechanism responsible for the reduced bleaching-induced coral mortality at their deeper survey sites. Although it may not be possible to reconstruct temperature differences during the 2010 bleaching event at their study sites, even temperature records from the different survey depths on the Acehnese reefs well after the event may provide some insight into the possible magnitude of temperature differences that were sufficient to reduce coral mortality. Some discussion of the specific parameters that might distinguish microrefugia, e.g. the frequency and magnitude of differences in temperature or irradiance relative to surrounding waters, would greatly enhance the paper's utility, and provide an important addition to further work on this topic.

I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

Competing Interests: No competing interests were disclosed.

Author Response 27 Oct 2013

Tom Bridge, James Cook University, Australia

Unfortunately, no data are currently available to quantify the local oceanographic patterns at this time, and to address this question without such data would be overly speculative. However, we plan to collect temperature data at Pulau Weh as part of ongoing monitoring of reefs in the region.

Competing Interests: No competing interests were disclosed.

Referee Report 20 September 2013

doi:10.5256/f1000research.2162.r1823



Tyler Smith

Center for Marine and Environmental Studies, University of the Virgin Islands, St Thomas, Virgin Islands, U.S.

The article is of great interest considering the impact of thermal stress on coral reefs globally, and the pressing need to identify refugia that might support coral diversity in a warming ocean. The article is basic, in that it only attempts to directly answer two questions: (1) did acroporid corals do better at deeper depths (8m) versus shallower depths (2 and 4m), and (2) is there a significant proportion of acroporid diversity that would be protected by the identified depth refuge in 2010 (i.e., how many acroporid species have a sufficiently wide depth range). I believe that they answer these questions well, but I would have liked to see more thorough investigation of the patterns in the data and I think there are some anomalous parts of the data that I cannot explain. For example, while most sites followed a pattern with increasing bleaching mortality at shallower depths, plotting of the data provided in table 1 shows that one site, Ba Kobra at 4m, showed no change or even an increase in total and acroporid cover, respectively. The authors never discuss this site to site variability, which might be important for "Identifying sites where oceanographic conditions reduce the effects of thermal anomalies should be a priority for coral reef conservation".

As for anomalous parts of the data, I can't understand why the absolute cover change of acroporid corals seems to surpass that of total coral cover at some sites. For example, at Rubiah Channel the acroporid cover drops an absolute amount of 38.1%, by my calculation. That is a simple calculation of final cover - initial cover, not standardized to the initial coral cover (which would be relative cover change). Therefore, the total absolute coral cover change has to be at least 38.1%, yet it is only 23.6%. This is not that the total cover is really the total cover excluding acropora, since the prior to bleaching acropora + total cover = 102%. Can the authors explain this?

In the methods it would also be necessary to know if the pre- and post-bleaching transects are the same (i.e., fixed permanent transects) or whether they are randomly placed. In either case, but particularly for the latter, it is also necessary to know the method by which the placement of the transect was determined at a site. How are we to know potential biases in the pre- and post-assessments without this knowledge. There is also no information given on the exact location of monitoring sites, which is important for replication of the study. Perhaps coordinates and a map would be appropriate.

One further addition that would be nice, though an addition to the two primary questions of the manuscript, is what is the relative importance of the depth refuge to the *in situ* shallow coral survival? They mention "recovery" in the title, but this isn't really addressed much in the manuscript, and improving the discussion of potential recovery process would help on that point. I.e., what absolute amount of cover for each species survived deep, and could contribute to shallow water recovery via larval recruitment,

versus the amount that survived shallow and could contribute to direct asexual recovery and larval recruitment? Also, any speculation on the relative importance of the processes in recovery (deep to shallow larval recruitment versus shallow to shallow larval and asexual recruitment) would be a good addition and set up future research.

I have a feeling all these questions are easily answerable and that the conclusions are justified, and I think the manuscript is an important addition to a rather sparse body of knowledge concerning reef refuges and refugia.

I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.

Competing Interests: No competing interests were disclosed.

Author Response 27 Oct 2013

Tom Bridge, James Cook University, Australia

Our response to the issues raised by the reviewer are summarised below:

- We acknowledge some variability among sites in the depth of transition from high to low mortality, but the overall trend of decreasing mortality with increasing depth is consistent among sites.
- The reviewer noted that the 'absolute cover change of Acroporid corals seems to surpass that of total coral cover', and we note three possible reasons for this observation. Firstly, such variations are commonly observed on coral reefs after a disturbance event such as coral bleaching due to 'canopy effects', whereby removal of canopy-forming taxa (in this case *Acropora*) can cause apparent increases in taxa which were concealed underneath the canopy. Canopy effects have been well documented in the coral reef literature (e.g. [Goatley CHR & Bellwood DR, 2011](#)). In Pulau Weh, the increases in encrusting/massive *Porites* and *Faviids* suggest canopy effects were a likely cause of these observations. Secondly, surviving corals will have grown from 2009 to 2011. Thirdly, transects were haphazardly placed and therefore some variability within a site is possible from year to year.
- We have included a map of study sites, and also stated in the text that transects were haphazardly placed within a site.
- Coral cover data from 2009 to 2011 was collected only to genus level, therefore it was not possible to address species-specific changes in abundance before and after the bleaching.

Competing Interests: No competing interests were disclosed.