Published in final edited form as:

Coral Reefs. 2017 June ; 36(2): 395–400. doi:10.1007/s00338-017-1550-4.

Bleaching response of coral species in the context of assemblage response

Timothy D. Swain^{1,2}, Emily DuBois¹, Scott J. Goldberg¹, Vadim Backman³, and Luisa A. Marcelino^{1,2,*}

¹Department of Civil and Environmental Engineering, Northwestern University, 2145 Sheridan Road, Evanston, Illinois, 60208, USA

²Integrative Research Center, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois, 60605, USA

³Department of Biomedical Engineering, Northwestern University, 2145 Sheridan Road, Evanston, Illinois, 60208, USA

Abstract

Caribbean coral reefs are declining due to a mosaic of local and global stresses, including climate change-induced thermal stress. Species and assemblage responses differ due to factors that are not easily identifiable or quantifiable. We calculated a novel species-specific metric of coral bleaching response, taxon- α and - β , which relates the response of a species to that of its assemblages for 16 species over 18 assemblages. By contextualizing species responses within the response of their assemblages, the effects of environmental factors are removed and intrinsic differences among taxa are revealed. Most corals experience either a saturation response, overly-sensitive to weak stress ($\alpha > 0$) but under-responsive compared to assemblage bleaching ($\beta < 1$), or a threshold response, insensitive to weak stress ($\alpha < 0$) but over-responsive compared to assemblage bleaching ($\beta > 1$). This metric may help reveal key factors of bleaching susceptibility and identify species as targets for conservation.

Keywords

Climate change; Coral bleaching; Symbiosis; Thermal stress

Introduction

Anomalously warm water disrupts mutualistic endosymbioses between photosynthetic dinoflagellates (genus *Symbiodinium*) and coral hosts through the bleaching response, eliminating the primary mode of energy acquisition for corals (Muscattine 1990) and leading to the degradation of reef ecosystems globally (Wilkinson 2008). Bleaching responses differ across individuals, taxa, and events (e.g., Wooldridge 2014) through an unknown combination of factors intrinsic to the *coral-Symbiodinium* holobiont (e.g., hosting *Symbiodinium* phylotypes with differential thermotolerance; e.g., Barshis et al. 2013) or

*Corresponding author: Luisa Marcelino, Phone: (847) 491-4035, Fax: (847) 491-4011, l-marcelino@northwestern.edu.

extrinsic to the holobiont (e.g., differential thermal anomalies across reefs; e.g., Ban et al. 2014) with the added complexity of coral acclimation or adaptation to thermal stress (e.g., Guest et al. 2012; Howells et al. 2013).

To isolate the effect of factors intrinsic to the holobiont, we propose a novel metric of bleaching response (taxon- α and $-\beta$) that relates species-specific susceptibility to that of the assemblages where they were surveyed. This metric is contextualized by the responses of the assemblage of corals; if all coral species are equally susceptible the response of each species would mirror its assemblage and react to bleaching stimulus and history of environmental conditions at that site identically. We argue that deviation from the bleaching response of the assemblage should mostly reflect the effects of intrinsic factors on differential bleaching. Parameters α and β were originally derived to model the effect of external and internal factors on differential bleaching susceptibility among corals (Swain et al. 2016a). Here we present taxon- α and $-\beta$ as a species-specific metric of bleaching response calculated using 125 standardized records for 16 taxa at 18 Caribbean sites (Swain et al. 2016a) which experienced thermally induced bleaching events separated by space and time, and were therefore exposed to dissimilar stress events and environmental histories. Using these data, we ask: (1) is the bleaching response of a coral species or assemblage a reflection of the thermal-stress anomalies they are exposed to; and (2) does the bleaching response of species differ from that of the assemblages where they are found (i.e., do species over-react or under-react to similar thermal stress and environmental history)?

Methods

Data collection

Standardized records of bleaching and mortality for Caribbean corals were culled from Swain et al. (2016a). These included 371 bleaching response records (B_{jk} , or bleaching response of taxon j at site k), that are a composite response metric of bleaching and associated mortality that occurred following a thermal event (but not distal effects such as disease or repeated bleaching) standardized across survey methods and bleaching criteria (Swain et al. 2016a), for 39 taxa across 55 Caribbean sites from 1987 to 2006 (Electronic supplementary material, ESM, Table S1). Since bleached corals may either die or recover, and observation timing may bias the data, both bleaching (greater in early surveys) and associated mortality (greater in later surveys) were used to calculate B_{jk} and provide a more accurate assessment. Thermal anomaly records, reported as degree heating weeks (DHW), for matching dates and locations were culled from the U.S. National Oceanic and Atmospheric Administration coral reef watch satellite monitoring database (<http://coralreefwatch.noaa.gov>). DHW is the product of degrees ($^{\circ}\text{C}$) above the highest monthly mean sea surface temperature and its duration in weeks, and bleaching is considered likely at $\text{DHW} > 4$ and mass bleaching and mortality at $\text{DHW} > 8$ (<http://coralreefwatch.noaa.gov>). We used maximum DHW within 6 months prior to survey to capture peak thermal stress. for 42 sites from 1998 to 2006, which included 39 taxa in 287 records.

Data analysis

Coral assemblage-level bleaching response (site-BRI or $SBRI_k$), was calculated as the mean of individual bleaching and mortality responses (B_{jk}) for all taxa j at a given site k (Swain et al. 2016a) as:

$$SBRI_k = \frac{1}{J_k} \sum_{j=1}^{J_k} B_{jk} \quad (1)$$

where J_k is the total number of taxa in site k . $SBRI_k$ was calculated for coral assemblages with 3 taxa (363 B_{jk} records of 39 coral taxa at 49 sites from 1987–2006).

The effect of thermal stress on bleaching response was assessed as the relationship between taxon-specific bleaching responses (B_{jk}) and thermal anomaly (6 month maximum DHW) at sites with 3 taxa (279 B_{jk} records of 39 coral taxa at 36 sites from 1998–2006).

To compare bleaching response of taxon j with that of its coral assemblage without the influence of target taxon j , the response of j was removed from the mean bleaching response of the assemblage (site- B_{jk} or sB_{jk}) (Swain et al. 2016a) as:

$$sB_{jk} = \frac{1}{J_k - 1} \sum_{i=1, i \neq j}^{J_k} B_{ik} \quad (2)$$

where J_k is the total number of taxa in site k . Calculation of sB_{jk} was restricted to sites containing 3 taxa with variable bleaching responses (363 B_{jk} records of 39 taxa at 49 sites from 1987–2006).

Sensitivity of individual taxon-specific bleaching responses, B_{jk} to that of the entire assemblage can be modeled (Swain et al. 2016a) as:

$$B_{jk} = u_{jk} + \beta_j sB_{jk} + \alpha_j, \quad (3)$$

where β_j is the taxon-specific bleaching sensitivity (taxon- β), u_{jk} is variability in estimation of B_{jk} due to error of measurements with $\text{Var}[u_{jk}] = \text{Var}[\delta B_{jk}]$, sB_{jk} is described in Eq. 2, and coefficient α_j is a taxon-specific parameter describing species-specific sensitivity to weak stress (e.g., seasonal *Symbiodinium* density variation; Fitt et al. 2000) in the absence of assemblage response (taxon- α). Taxon- β can be directly measured as the linear regression coefficient in the regression of B_{jk} on sB_{jk} as:

$$\beta_j = \frac{\text{cov}_k(B_{jk}, sB_{jk})}{\text{var}_k(sB_{jk})} = \rho_k(B_{jk}, sB_{jk}) \frac{\sigma_k(B_{jk})}{\sigma_k(sB_{jk})} \quad (4)$$

where Cov and Var are covariance and variance operators, ρ is the correlation coefficient, and σ is standard deviation, all estimated for a given taxon ($j = \text{constant}$). Taxon- $\beta \sim 1$ indicates a rate of change in bleaching response of taxon j that is similar to the assemblages where it is found, taxon- $\beta < 1$ indicates an under-response relative to the rate of change of its assemblages, and taxon- $\beta > 1$ indicates an over-response relative to the rate of change of assemblages. Taxon- β was calculated for taxa surveyed at 3 sites in assemblages with 3 taxa (125 B_{jk} records of 16 taxa at 18 sites from 1987–2006).

Results and discussion

Is bleaching response of a coral species or assemblage a reflection of the thermal-stress anomalies they are exposed to?

Thirty-six Caribbean coral assemblages (sites with 3 taxa; 7.75 ± 4.55 [mean $\pm$ SD] taxa per site, 39 total unique taxa) experienced thermal anomalies ranging 0–15.7 DHW from 1998–2006 (Fig. 1; ESM Table S1). Mean bleaching response of all taxa surveyed in a site (site-BRI, or $SBRI_k$; Eq. 1) varied 19-fold among assemblages ($SBRI_k$ mean $23.0\% \pm 16.34$, range 2.75–52.9%; ESM Table S1; Fig. 1). Bleaching response variability across sites has been used to identify factors affecting that response (e.g., water flow, thermal history, solar irradiance, and acute thermal stress; McClanahan et al. 2005; Howells et al. 2013; Marcelino et al. 2013; Swain et al. 2016a,b).

Although there was a significant positive correlation between DHW and $SBRI_k$, DHW was a poor predictor of $SBRI_k$ (linear regression: $r^2 = 0.21$, $p = 0.005$, $n = 36$ sites; Fig. 1a), which is consistent with other studies of Caribbean corals (e.g., Yee et al. 2008). Similarly, thermal anomalies significantly increased bleaching response of individual taxa, but DHW was a poor predictor of individual bleaching response ($r^2 = 0.10$, $p < 0.001$, $n = 287$, 39 taxa; ESM Fig. S1). These results suggest that differential bleaching among assemblages is only partially explainable by exposure to different thermal anomalies, as indicated by other studies (e.g., McClanahan et al. 2015). We argue that, as a measure of assemblage bleaching response at a site, $SBRI_k$ should reflect the intensity and duration of thermal anomalies, thermal history of the site, chronic and acute environmental stresses that were not directly observed, and capacity of the holobiont to resist thermal stress.

Does the bleaching response of species differ from that of the assemblages where they are found?

Taxon- β , which is the regression coefficient relating bleaching response of a species (B_{jk}) to the response of its assemblages (sB_{jk}) (Eq. 4), was determined for 16 species (limited to taxa surveyed in 3 sites, and sites with 3 taxa; Fig. 2; Table 1). Relative to the bleaching response of its assemblages, species: (1) over-responded, i.e., increased bleaching response at a greater rate than their assemblages (e.g., *Acropora palmata*, taxon- $\beta > 1$); (2) under-responded, i.e., increased bleaching response at a lesser rate than their assemblages (e.g., *Diploria labyrinthiformis*, taxon- $\beta < 1$); or (3) responded similarly (e.g., *Siderastrea siderea*, taxon- $\beta \sim 1$) (Fig. 2; Table 1). Because taxon- β accounts for the bleaching response of a taxon in relation to its assemblages, it removes the effects of environment and history on the response of species and reveals the intrinsic (physiological) differences between taxa.

Although taxon- β quantifies relative differences in the rate of bleaching response increase, taxon- α further contextualizes the response of the target taxon by indicating its species-specific sensitivity to weak stress in the absence of assemblage response (Table 1). Considered together, the 16 Caribbean species fall under two main categories of response with a trade-off between taxon- α and taxon- β : (1) corals that are overly-sensitive to weak stress in the absence of assemblage bleaching (taxon- $\alpha > 0$) but under-responsive to increasing thermal stress compared to assemblage bleaching response (taxon- $\beta < 1$, Fig. 3a quadrant II; Fig. 3b); or (2) corals that are insensitive to weak stress in the absence of assemblage bleaching (taxon- $\alpha < 0$) but over-responsive to increasing thermal stress compared to assemblage bleaching response (taxon- $\beta > 1$; Fig. 3a, quadrant IV). Additionally, a few species were either overly-sensitive and over-responsive relative to their assemblages (taxon- $\alpha > 0$ and taxon- $\beta > 1$; Fig. 3a quadrant I) or insensitive and under-responsive relative to their assemblages (taxon- $\alpha < 0$ and taxon- $\beta < 1$; Fig. 3a quadrant III).

Bleaching responses of corals with a trade-off between taxon- α and taxon- β proceed on opposing trajectories (Fig. 3a quadrants II and IV). Corals within the high taxon- α and low taxon- β category (Fig. 3a quadrant II, Fig. 3b) demonstrate a saturation bleaching response where corals over-respond compared to the baseline assemblage response, but under-respond as the assemblage response increases. Corals within the low taxon- α and high taxon- β category (Fig. 3a quadrant IV) demonstrate a threshold bleaching response where corals under-respond compared to the baseline assemblage response, but over-respond as the assemblage response increases. Survival of a mild or short thermal-stress event would be of greater concern for corals with a saturation bleaching response, while survival of a severe or long thermal-stress event would be of greater concern for corals with a threshold bleaching response. Corals within the high taxon- α and high taxon- β category (Fig. 3a quadrant I) would be considered as taxa of highest concern (due to consistent over-response), while those within the low taxon- α and taxon- β category (Fig. 3a quadrant III) would be considered as taxa of least concern (due to consistent under-response)..

Limitations and general considerations

Accuracy of taxon- α and - β (standard error, p -value of regression, and y-intercept; Table 1) depends on the number of sites where a taxon is surveyed and on accuracy with which assemblage bleaching response is determined. The latter, in turn, depends on (1) the number of taxa surveyed at each site (which was the primary factor determining accuracy in our dataset), (2) how representative those taxon responses are of assemblage response, and (3) other factors including differences in survey methods and bleaching criteria which have been accounted for by the standardization of individual B_{jk} records (Swain et al. 2016a). A low p -value of the linear regression corresponds to a smaller standard error of the estimation of taxon- β (Table 1). Although some of the regressions are significant ($p < 0.05$), many are non-significant due, in part, to small site sample sizes. The accuracy of taxon- α and - β should increase as more surveys of bleaching response become available, particularly with inclusion of sites with a large number of taxa presenting a wide range of bleaching responses.

By relating the response of a coral to its assemblage, extrinsic factors in the bleaching response are removed and the effect of individual intrinsic factors can be assessed through analysis of variance of taxon- α and - β . Individual intrinsic factors could be identified experimentally by their effect on the bleaching response, and by ranking their importance as bleaching determinants by the portion of taxon- α and - β variance that they could explain. If the number and total effect of intrinsic factors are known, the approximate upper bound on the effect of the remaining intrinsic factor could be inferred. However, individual intrinsic factors may not act independently (e.g., the effect of *Symbiodinium* thermotolerance may be influenced by skeletal light scattering; Swain et al. 2016b) and extrinsic factors such as thermal history may lead to acclimation or adaptation of corals (Guest et al. 2012; Pratchett et al. 2013).

The intrinsic capacity of the holobiont to resist stress (taxon- β) and its species-specific stress sensitivity in the absence of assemblage response (taxon- α) provide tools for comparative assessments of the connection between species traits and bleaching responses to inform conservation and management efforts. Estimates of variance in bleaching response among corals are critical for assessing the resilience of individual reefs and coral species to climate change (Maynard et al. 2015). These new metrics can be expanded and updated as additional bleaching records become available and can target locations in time or space. Changes in bleaching response over time could be evidence of adaptation to climate change (Guest et al. 2012; Pratchett et al. 2013) and taxon- α and - β could be used to identify suitable candidate species for interventive conservation efforts, such as selective breeding or assisted migration (van Oppen et al. 2015).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

This research was supported by National Science Foundation (EFRI-1240416, EFRI-0937987 and CBET-1249311) and National Institutes of Health (CA-128641, EB-003682).

References

- Ban SS, Graham NAJ, Connolly SR. Evidence for multiple stressor interactions and effects on coral reefs. *Glob Chang Biol*. 2014; 20:681–697. [PubMed: 24166756]
- Barshis DJ, Ladner JT, Oliver TA, Seneca FO, Traylor-Knowles N, Palumbi SR. Genomic basis for coral resilience to climate change. *Proc Natl Acad Sci USA*. 2013; 110:1387–1392. [PubMed: 23297204]
- Fitt WK, Mcfarland FK, Warner ME, Chilcoat GC. Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. *Limnol Oceanogr*. 2000; 45:677–685.
- Guest JR, Baird AH, Maynard JA, Muttaqin E, Edwards AJ, Campbell SJ, Yewdall K, Affendi YA, Chou LM. Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. *PLoS One*. 2012; 7:e33353. [PubMed: 22428027]
- Howells EJ, Berkelmans R, van Oppen MJH, Willis BL, Bay LK. Historical thermal regimes define limits to coral acclimatization. *Ecology*. 2013; 94:1078–1088. [PubMed: 23858648]

- Marcelino LA, Westneat MW, Stoyneva V, Henss J, Rogers JD, Radosevich A, Turzhitsky V, Siple M, Fang A, Swain TD, Fung J, Backman V. Modulation of light-enhancement to symbiotic algae by light-scattering in corals and evolutionary trends in bleaching. *PLoS One*. 2013; 8:e61492. [PubMed: 23630594]
- Maynard JA, McKagan S, Raymundo L, Johnson S, Ahmadi GN, Johnston L, Houk P, Williams GJ, Kendall M, Heron SF, van Hooidonk R, McLeod E, Tracey D, Planes S. Assessing relative resilience potential of coral reefs to inform management. *Biol Conserv*. 2015; 192:109–119.
- McClanahan TR, Maina J, Ateweberhan M. Regional coral responses to climate disturbances and warming is predicted by multivariate stress model and not temperature threshold metrics. *Clim Change*. 2015; 131:607–620.
- McClanahan TR, Maina J, Moothien-Pillay R, Baker AC. Effects of geography, taxa, water flow, and temperature variation on coral bleaching intensity in Mauritius. *Mar Ecol Prog Ser*. 2005; 298:131–142.
- Muscantine, L. The role of symbiotic algae in carbon and energy flux in reef corals. In: Dubinsky, Z., editor. *Coral reefs*. Elsevier; Amsterdam: 1990. p. 75-87.
- Pratchett MS, McCowan D, Maynard JA, Heron SF. Changes in bleaching susceptibility among corals subject to ocean warming and recurrent bleaching in Moorea, French Polynesia. *PLoS One*. 2013; 8:e70443. [PubMed: 23922992]
- Swain TD, Vega-Perkins JB, Oestreich WK, Triebold C, DuBois E, Henss J, Baird A, Siple M, Backman V, Marcelino L. Coral bleaching response index: a new tool to standardize and compare susceptibility to thermal bleaching. *Glob Chang Biol*. 2016a; 22:2475–2488. [PubMed: 27074334]
- Swain TD, DuBois E, Gomes A, Stoyneva VP, Radosevich AJ, Henss J, Wagner ME, Derbas J, Grooms HW, Velazquez EM, Traub J, Kennedy BJ, Grigorescu AA, Westneat MW, Sanborn K, Levine S, Schick M, Parsons G, Biggs BC, Rogers JD, Backman V, Marcelino LA. Skeletal light-scattering accelerates bleaching response in reef-building corals. *BMC Ecol*. 2016b; 16:10. [PubMed: 26996922]
- van Oppen MJH, Oliver JK, Putnam HM, Gates RD. Building coral reef resilience through assisted evolution. *Proc Natl Acad Sci U S A*. 2015; 112:2307–2313. [PubMed: 25646461]
- Wilkinson, C. Status of the coral reefs of the world: 2008. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre; Townsville, Australia: 2008.
- Wooldridge SA. Differential thermal bleaching susceptibilities amongst coral taxa: reposing the role of the host. *Coral Reefs*. 2014; 33:15–27.
- Yee SH, Santavy DL, Barron MG. Comparing environmental influences on coral bleaching across and within species using clustered binomial regression. *Ecol Modell*. 2008; 218:162–174.

Fig. 1.

Response of coral assemblages (SBRI_k) at 36 Caribbean sites (numerals correspond to site numbers in Electronic supplementary material Table S1) to thermal anomalies (6 months max degree heating weeks: DHW). Site bleaching response increases with thermal anomalies ($r^2 = 0.22$, $p < 0.01$; **a**), across the Caribbean at DHW of >8 (**b**), $4-8$ (**c**) and < 4 (**d**). Shading of site markers corresponds to the gradient of SBRI_k values, with lightest markers representing highest bleaching response values. Maps constructed using Mapbox and OpenStreetMap

Fig. 2.

Taxon- β for Caribbean corals. Responses of corals (B_{jk}) relative to their assemblages (sB_{jk}) for 16 coral species (a) and exemplars of species with taxon- $\beta > 1$ indicating over-response (b), taxon- $\beta < 1$ indicating under-response (c), and taxon- $\beta \sim 1$ indicating similar response (d)

Fig. 3. Relationship between taxon- α and taxon- β for Caribbean corals ($r^2 = 0.56$, $p < 0.001$; **a**), with an exemplar species (**b**) demonstrating a relatively high α (9.94) but low β (0.48) values typical of quadrant II (**a**)

Table 1
Taxon- β and taxon- α values and associated errors, sample sizes, and significance for 16 coral species

Taxon	Taxon β	Taxon α	Std error	Correlation coefficient (r^2)	No of sites	Mean taxa/site	p-value
<i>Montastraea cavernosa</i>	0.15	10.25	0.38	0.02	9	12.7	0.708
<i>Porites porites</i>	0.15	23.85	0.39	0.02	9	13.2	0.709
<i>Madracis myriaster</i>	0.22	-1.25	0.33	0.13	5	15.4	0.56
<i>Porites astreoides</i>	0.29	14.76	0.43	0.04	13	10.8	0.509
<i>Madracis decactis</i>	0.37	-5.75	0.12	0.72	6	15.5	0.033
<i>Meandrina meandrites</i>	0.48	9.94	0.50	0.15	7	14.7	0.386
<i>Agaricia agaricites</i>	0.70	33.54	1.41	0.04	8	12.4	0.635
<i>Diploria labyrinthiformis</i>	0.79	-6.37	0.24	0.58	10	11.9	0.011
<i>Orbicella faveolata</i>	1.06	7.56	1.31	0.12	7	13.3	0.455
<i>Colpophyllia natans</i>	1.12	-10.24	0.34	0.61	9	12.6	0.013
<i>Orbicella annularis</i>	1.16	-6.42	0.60	0.25	13	10.0	0.08
<i>Siderastrea sideraea</i>	1.18	-10.00	0.21	0.82	9	12.9	0.0007
<i>Diploria strigosa</i>	1.28	-13.62	0.47	0.51	9	12.6	0.031
<i>Favia fragum</i>	1.46	10.15	0.58	0.76	4	9.0	0.127
<i>Diploria clivosa</i>	2.38	-37.04	0.55	0.95	3	17.3	0.145
<i>Acropora pulvinata</i>	2.53	-30.29	0.98	0.77	4	6.0	0.124