Vol. 586: 1–10, 2018
https://doi.org/10.3354/meps12445

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published January 11

FEATURE ARTICLE

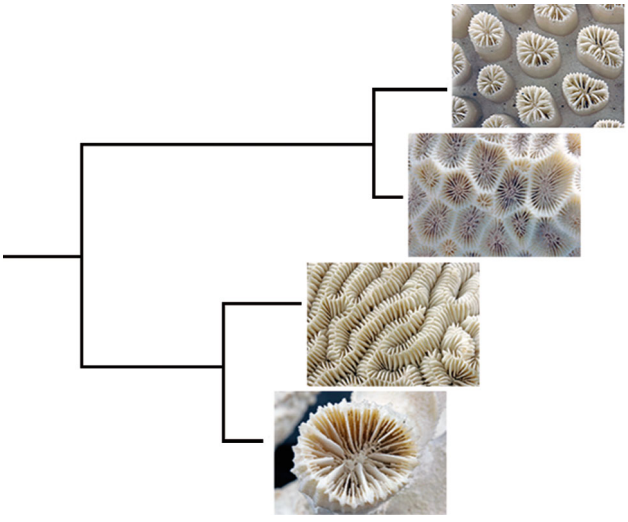
Physiological integration of coral colonies is correlated with bleaching resistance

Timothy D. Swain[1,2], Emily C. Bold[1], Phillip C. Osborn[1], Andrew H. Baird[3], Mark W. Westneat[4], Vadim Backman[5], Luisa A. Marcelino[1,2,*]

[1]Department of Civil and Environmental Engineering, Northwestern University, Evanston, IL 60208, USA
[2]Integrative Research Center, Field Museum of Natural History, Chicago, IL 60605, USA
[3]ARC Center of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, 4811, Australia
[4]Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL 60637, USA
[5]Department of Biomedical Engineering, Northwestern University, Evanston, IL 60208, USA

ABSTRACT: Inter-module physiological integration of colonial organisms can facilitate colony-wide coordinated responses to stimuli that strengthen colony fitness and stress resistance. In scleractinian corals, whose colonial integration ranges from isolated polyps to a seamless continuum of polyp structures and functions, this coordination improves responses to injury, predation, disease, and stress and may be one of the indications of an evolutionary origin of *Symbiodinium* symbiosis. However, observations of species-specific coral bleaching patterns suggest that highly integrated coral colonies may be more susceptible to thermal stress, and support the hypothesis that communication pathways between highly integrated polyps facilitate the dissemination of toxic byproducts created during the bleaching response. Here we reassess this hypothesis by parameterizing an integration index using 7 skeletal features that have been historically employed to infer physiological integration. We examine the relationship between this index and bleaching response across a phylogeny of 88 diverse coral species. Correcting for phylogenetic relationships among species in the analyses reveals significant patterns among species characters that could otherwise be obscured in simple cross-species comparisons using standard statistics, whose assumptions of independence are violated by the shared evolutionary history among species. Similar to the observed benefits of increased coloniality for other types of stressors, the results indicate a significantly reduced bleaching response among coral species with highly integrated colonies.

KEY WORDS: Colony integration · Colony form · Coral bleaching · Phylogenetically corrected analysis



Stylized representation of the phylogeny and morphologies that allowed detection of decreased thermal bleaching with greater polyp integration (coloniality).

Photos: Gary Parr

INTRODUCTION

Colonial organisms are composed of repeated modules that are genetic clones of an original founding unit. One of the most important advantages of coloniality is that inter-module physiological integration can allow for resource translocation among modules and colony-wide coordinated responses to stimuli (Mackie 1986, Oren et al. 2001, Fine et al. 2002). Physiological integration can homogenize the distribution of resources acquired through prey capture and symbiont photosynthesis and allow for a more

*Corresponding author: l-marcelino@northwestern.edu

Publisher: Inter-Research · www.int-res.com

effective colony-wide response to injury, predation, disease, and stress (Pearse & Muscatine 1971, Rinkevich & Loya 1983, Fang et al. 1989, Gladfelter et al. 1989, Oren et al. 1997, Fine et al. 2002, Roff et al. 2006).

In scleractinian corals there is a wide diversity of integration among modules, ranging from species whose colonial modules (polyps) are connected only by non-living skeleton to species whose polyps are an almost indistinguishable continuum of structures and functions (Coates & Oliver 1973, Coates & Jackson 1987). In extant coral taxa, this diversity occurs as a continuum of physiological integration (rather than discrete extremes) that is challenging to directly quantify. Evidence of physiological integration in corals has historically been inferred from skeletal features that reflect pathways of (or barriers to) communication between polyps and indicate a degree of reliance upon, or coordination between, other polyps within the colony for basic life functions (Coates & Oliver 1973, Coates & Jackson 1987, Soong & Lang 1992). Communication pathways include skeletal features that allow the gastrovascular cavities of neighboring polyps to be continuous, such as skeletal voids (perforate skeleton, commonly found in genera such as *Acropora*, *Montipora*, and *Porites*; van Woesik et al. 2013) that allow tissue to transverse through the skeleton (Yost et al. 2013), or inter-polyp alignment of septa (continuity of costosepta, such as the confluent costosepta of *Favites abdita* or *Favites halicora*; Huang et al. 2014) that demonstrate alignment of mesenteries and may allow tissue connections to continue above the surface of the skeleton (Coates & Oliver 1973, Coates & Jackson 1987). Inferences of reliance and coordination among polyps include polymorphic calices that reflect differential functions of polyps and division of labor among colonial modules (polymorphic polyps, such as the apical polyps of *Acropora* at the growing tips of branches that are larger, have fewer tentacles, lower *Symbiodinium* density, and no gonads compared to the axial polyps; Oliver 1984, Hemond et al. 2014) and complex colony morphologies that require coordinated skeletal construction to maintain colony dimensions, symmetry, and balance (growth form, such as branching *Acropora palmata* or *Seriatopora caliendrum*; Madin et al. 2016) (Coates & Oliver 1973, Coates & Jackson 1987). These characters constitute morphological evidence of physiological integration (inferred), rather than direct measurements of interpolypoidal movements of materials or chemical signals (experimentally determined; e.g. Gladfelter et al. 1989, Oren et al. 2001, Roff et al. 2006). However, these inferences also represent the extent of currently available data for cross-species comparative analysis, as experimental evidence is confined to a few exemplar species.

The evolution of highly integrated coral colonies is also hypothesized to be an indicator of the origin of the symbiosis with the photosynthetic endosymbiotic dinoflagellates representing the genus *Symbiodinium.* Coates & Jackson (1987) identified a pattern in corals where multiserial colonial forms with small, highly integrated corallites are almost exclusively symbiotic, whereas species that have solitary or uniserial colonial forms with large, poorly integrated corallites are almost exclusively asymbiotic, suggesting that increased colony integration is one of the indications of an evolutionary origin of *Symbiodinium* symbiosis. Although the pattern is imperfect (Frankowiak et al. 2016) and is not the product of a linear evolutionary progression toward increased colonial integration and symbiosis, but is due to a more complex history of repeated acquisition and loss of coloniality and symbiosis that were not always concurrent (Barbeitos et al. 2010), it remains a conspicuous motif among extant species. *Symbiodinium* photosynthesis is the primary source of fixed carbon for reef-building corals (Muscatine 1990), and disassociation of *Symbiodinium* and coral hosts through thermal stress (bleaching) can result in decreased growth, regeneration, reproduction, and competitive abilities, and increased incidence of disease, predation, and mortality (Brown 1997, Jokiel 2004, Jones 2008, McClanahan et al. 2009). Although increased physiological integration may indicate an evolutionary origin of *Symbiodinium* symbiosis, highly integrated colonies are also hypothesized to be among those most susceptible to bleaching. Baird & Marshall (2002) identified a pattern of heightened bleaching and mortality among coral species whose colonies display high physiological integration (inferred from morphology). They hypothesized that highly integrated polyps were incapable of isolating damage, or the products of damage (e.g. reactive oxygen species), to areas of the colony that were directly affected by stress, effectively homogenizing the colony-wide response and increasing its susceptibility to bleaching. In contrast, colonies where polyps function as independent units were thought to have greater resistance to bleaching by localizing damage and polyp death (Baird & Marshall 2002).

As global temperatures continue to increase under climate change, the disruption of coral–*Symbiodinium* symbioses has become an urgent focus of intense research (Hoegh-Guldberg et al. 2007, Baker et al. 2008, Frieler et al. 2013, Hughes et al. 2017). The identification of factors that increase colony susceptibility to thermal stress and its associated bleaching

response has become critical to predicting and mitigating future bleaching events. Here we assess the physiological integration bleaching hypothesis of Baird & Marshall (2002) using 88 coral species whose coloniality ranges from solitary to highly integrated. We identified 7 skeletal features that have been historically employed to infer physiological integration and used them to parameterize a species-specific integration index and examine its relationship to bleaching response within a phylogenetic framework.

MATERIALS AND METHODS

We collected coral colony integration characters from museum specimens, literature, or trait databases (values and their sources are reported in Supplement 1 at www.int-res.com/articles/suppl/m586p001_supp.xls) and assessed their relationship to bleaching response using phylogenetically corrected linear and logistic regression analyses. This analysis targeted 88 coral species previously characterized for light scattering properties of their skeletons (Marcelino et al. 2013) and bleaching response (Swain et al. 2016c).

We used the coral Bleaching Response Index (BRI) values of Swain et al. (2016c) as our metric for bleaching response. The BRI is based on taxon-specific bleaching and mortality records collected during mass coral bleaching events from 1982–2006 and was calculated as the mean percent tissue area affected by bleaching across all sites and years where a taxon was observed during these events (Swain et al. 2016c). Bleaching response values for species with fewer than 3 reports of bleaching and mortality in Swain et al. (2016c) were used here as the mean of responses across the genus (Supplement 1).

Adapting characters discussed by Coates & Oliver (1973) and Soong & Lang (1992), we identified 7 characters and their directionality for the inference of increasing colony integration (Supplement 2 at www.int-res.com/articles/suppl/m586p001_supp.pdf). Detailed explanations of how these characters are thought to reflect the degree of potential physiological integration among polyps within a colony can be found in e.g. Coates & Oliver (1973), Soong & Lang (1992), Baird & Marshall (2002), and we provide only a brief outline here (see also Table 1, Supplement 1). (1) *Colony growth form* refers to the overall colony morphology and is an indicator of the inter-polyp communication that would be necessary to coordinate colony growth and polyp budding patterns to create complex 3 dimensional shapes (Soong & Lang 1992). (2) *Polyp budding* can occur either within the corallite wall (intracalicular) and may result in partially incomplete polystomal polyps (i.e. indicates a higher level of integration), or outside the corallite wall (extracalicular) and result in complete polyps (i.e. individuality; indicates a lower level of integration) (Budd & Stolarski 2011). (3) *Colony formation* is the arrangement and proximity of polyps — e.g. cerioid colonies where corallites are juxtaposed (indicates lower integration) or meandroid colonies where corallites are arranged in series (indicates greater integration) — and (4) *coenosteum amount* within a colony is an indicator of the separation between polyps within a colony — e.g. cerioid colonies with fused corallite walls and no coenosteum (indicates high integration) or plocoid colonies where corallites are separated by coenosteum (indicates low integration) (Coates & Oliver 1973, Budd & Stolarski 2011). (5) A *perforate skeleton* permits an additional level of interconnection and communication between

Table 1. Colony integration characters, character states, homoplasy (retention index, range: 0–1, 0 = homoplastic), and references. Coding: scale of 0–1, with values of 1 indicating greatest integration

Character	Character states and coding	Retention index (RI)	Justification reference
Colony growth form	Massive, encrusting, or columnar = 0, laminar = 0.5, branching or digitate = 1	0.66	Soong & Lang (1992)
Polyp budding	Extracalicular = 0, mixed = 0.5, intracalicular = 1	0.81	Coates & Oliver (1973)
Colony formation	Phaceloid or solitary = 0, plocoid = 0.25, cerioid = 0.5, meandroid = 0.75, hydnophoroid = 1	0.54	Coates & Oliver (1973)
Coenosteum amount	Phaceloid or solitary = 0, extensive = 0.25, moderate = 0.5, limited = 0.75, fused walls = 1	0.65	Coates & Oliver (1973)
Perforate skeleton	Imperforate = 0, perforate = 1	0.91	Coates & Oliver (1973)
Inter-corallite continuity of costosepta	Mostly not confluent = 0, mostly confluent = 1	0.65	Coates & Oliver (1973)
Polymorphic polyps	Not polymorphic = 0, polymorphic = 1	0.88	Soong & Lang (1992)

polyps beneath the surface of the skeleton by allowing gastrovascular canals to transverse the skeleton (indicating high integration), which is not possible if the skeleton is imperforate (indicating low integration) (Coates & Oliver 1973). (6) *Inter-corallite continuity of costosepta* is an indicator of the potential interconnection and communication between polyps. Septa (which support individual mesenteries in the gastrovascular cavity of the polyp) that trace through the costae across the surface of the coenosteum and align with septa in adjacent corallites provide for the continuity of mesenteries and gastrovascular canals and alignment of polyp orientation (indicating high integration) (Coates & Oliver 1973, Budd & Stolarski 2011). Colonies that exhibit (7) *polyp polymorphism* have polyps that are of different sizes or serve different functions, and demonstrates division of labor among polyps (high integration) (Soong & Lang 1992).

While some characters are discrete and can be categorized by presence or absence (e.g. perforate or imperforate skeleton), others have 2 or more character states (e.g. growth form: massive or encrusting, laminar and branching corals). We reasoned that we could derive a quantitative integration index by averaging these 7 characters and weighting them by the number of states of each character, such that each character was scored on a scale of 0–1, with 1 representing the highest colony integration state (Table 1, Supplement 1). The weighted average of multiple character-states avoided over-representation of characters with more than 2 states and resulted in a species-level integration index score that potentially ranged from 0–7 and weighted each character equally. This integration index is therefore reflective of the progression of character states that are hypothesized to indicate the degree to which individual polyps within a colony are physiologically integrated. For example, massive or encrusting growth forms (considered the least integrated) were given a score of 0, branching or digitate growth forms (considered the most integrated) were given a score of 1, and laminar growth forms were given an intermediate score of 0.5. To assess the effect of differential character selection, we also calculated 7 additional integration index scores that systematically excluded one character from each.

Coral colony integration characters were mapped onto a molecular phylogeny for assessment of individual character homoplasy and for phylogenetically corrected linear and logistic regression analyses. Species data are related through evolution, violating an assumption of standard statistical analyses that individual data points are independent; therefore, it was necessary to correct for this phylogenic effect (Felsenstein 1985, Revell 2010). Correcting for phylogeny can reveal significant associations among species characters that could be obscured or misleading in simple cross-species comparisons that apply standard statistics (Harvey 1996, Freckleton et al. 2002). However, inappropriately correcting data that lack a phylogenetic signal can result in poor statistical performance compared to uncorrected regression (Revell 2010). We trimmed the coral phylogeny of Huang (2012) to include only the targeted 88 species, using the Phylotools R package (Revell 2012) to preserve proper branch lengths. This trimmed phylogeny was used to define the evolutionary relationships and distances between species for the phylogenetic correction of the raw data. Characters were mapped onto the trimmed Huang (2012) phylogeny using Mesquite 2.75 (Maddison & Maddison 2011) and visualized with Evolview (Zhang et al. 2012). Homoplasy in the categorical character-state and bleaching data was assessed using the Retention Index (RI, ranges from 0–1, where 0 is homoplastic) in Mesquite. The RI is the fraction of apparent synapomorphy (characters shared exclusively among an ancestor and all of its descendants) retained after mapping onto the phylogeny (Farris 1989). Homoplasious characters provide a better opportunity (by enabling the detection of correlations between characters that may otherwise closely reflect evolutionary history) to reveal the underlying relationships between character states after correction for phylogenetic non-independence among species. Phylogenetic signal within the continuous integration and bleaching ordinary least squares (OLS) regression residuals was assessed by mapping their values to the phylogeny and fitting phylogenetic and non-phylogentic models. This was performed using maximum likelihood (ML) model fitting (Oakley et al. 2005) using the Continuous-character Model Evaluation and Testing (CoMET) module (Lee et al. 2006) in Mesquite. The relationships among continuous variables whose OLS regression residuals fit a phylogenetic model (indicating phylogenetic signal) were assessed using the Phylogenetic Independent Contrasts (PIC) tool within the Phenotypic Diversity Analysis Programs (PDAP) of Mesquite, which corrects an ordinary least squares linear regression for non-independence due to evolutionary relationships among species (Midford et al. 2010). This rendition of PIC (Felsenstein 1985) returns a correlation coefficient and a significance value that are mathematically and statistically equivalent to those of a least-squares regression (Midford et al. 2010). Rela-

tionships between continuous and binary variables were assessed with phylogenetically corrected logistic (phylo log) regressions performed using the Phylogenetic Generalized Linear Mixed Model (PGLMM; Ives & Helmus 2011, Ives & Garland 2014) in APE v.4.1 in R. This rendition of the phylo log regression simultaneously performs a test for phylogenetic signal in the residuals using an approximate likelihood ratio test. The binary variables that we targeted included colony growth form (using just those coral species that could be classified as massive, coded as 0, n = 44, or branching, coded as 1, n = 27) and presence of a perforate skeleton (imperforate coded as 0, n = 55, perforate as 1, n = 33) and were assessed against continuous bleaching response, as these 2 characters may influence bleaching irrespective of their role in physiological integration (Santos et al. 2009, McCowan et al. 2012, Yost et al. 2013).

RESULTS

Colony integration index scores ranged from 0 for the solitary corals *Cycloseris curvata* and *Fungia fungites* to 4.25 for the meandroid coral *Merulina scabricula* and perforate *Porites porites*, out of a possible range of 0–7 (Fig. 1). Mapping the 7 colony integration characters onto the phylogeny demonstrates moderate to low homoplasy values (RI = 0.54–0.91, Table 1) for each of the characters (Fig. 1), indicating that variation in these characters generally mirrors the phylogeny and that closely related coral species are likely to have similar character states.

Values for coral species-specific bleaching responses (BRI) ranged from 2.75 (for phaceloid *Euphyllia glabrescens*) to 72.85 (for plocoid *Montipora informis*) out of a possible range of 0–100 (Fig. 1). Mapping the BRI values onto the phylogeny demonstrated high homoplasy in bleaching response (RI = 0.33; Fig. 1), indicating that variation in bleaching response does not generally mirror the phylogeny and that closely related coral species are unlikely to have similar bleaching responses. High homoplasy of bleaching responses facilitates the detection of significant correlations with the skeletal characters. For example, the relationship between corals with polyp polymorphism (RI = 0.88) and those with perforate skeletons (RI = 0.91) may be entirely explainable through the evolutionary relationships among species because the characters so closely reflect evolutionary history.

Phylogenetically corrected regression (PIC) revealed a significant inverse relationship between BRI and colony integration (Pearson product-moment Correlation Coefficient, PCC = −0.22, p = 0.04, n = 88, best-fit ML model = pure phylogenetic/equal). This relationship and its significance are not detectable through ordinary least squares linear regression (r^2 = 0.02, p = 0.17, n = 88), nor are they highly sensitive to individual character exclusion. Exclusion of a single character in a step-wise reanalysis of integration resulted in the same trends with similar fits (PCC ranged from −0.13 to −0.29) and significance values at or below the 5% threshold for all but 2 excluded characters (colony formation and coenosteum amount; Table 2). Additionally, phylogenetically corrected logistic regression analyses of the presence of a perforate skeleton (Z = 0.75, p = 0.45, n = 88, phylogenetic signal p < 0.001) or branching colony growth form (Z = −0.58, p = 0.56, n = 71, phylogenetic signal p < 0.001) are not significantly related to bleaching response when considered independently of other colony integration characters.

Table 2. Sensitivity analysis results for Phylogenetic Independent Contrasts (PIC) analysis of integration against bleaching response. PCC: Pearson Product-moment Correlation Coefficient. Bold values indicate change in significance from the full analysis

Character excluded	PCC	p
Colony growth form	−0.29	0.01
Polyp budding	−0.24	0.03
Colony formation	−0.17	**0.11**
Coenosteum amount	−0.14	**0.21**
Perforate skeleton	−0.23	0.03
Inter-corallite continuity of costosepta	−0.22	0.04
Polymorphic polyps	−0.21	0.05

DISCUSSION

Coral colonies exhibit a continuum of physiological integration among modules, ranging from phaceloid species with no tissue connections between polyps, to hydnophoroid species with little separation between polyps embedded in a continuous coenosarc that maintain adjoining gastrovascular cavities (Coates & Oliver 1973). Baird & Marshall (2002) observed heightened bleaching responses among some anthozoan taxa with high levels of physiological integration, in particular *Acropora* spp., soft coral *Sinularia* spp., and hydrocoral *Millepora* spp. They hypothesized that highly integrated coral colonies were more susceptible to bleaching because communicating polyps were incapable of isolating damage, or the products of damage, to stress-affected areas of the colony. Our re-examination of the relationship be-

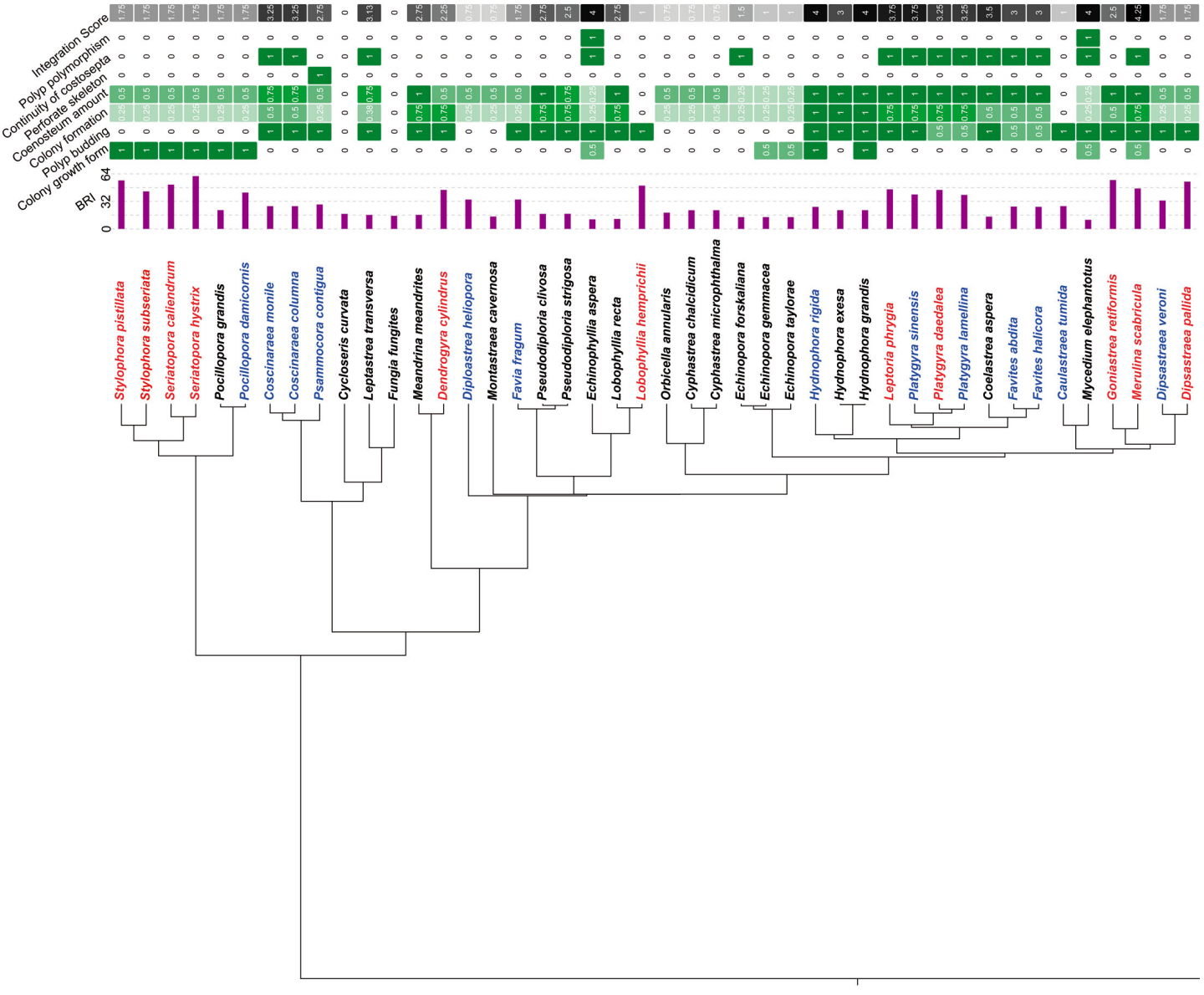


Fig. 1. Coral phylogeny of 88 species, modified from Huang (2012), with colony integration characters thought to indicate the physiological integration among coral polyps within a colony. Coral species are color coded for species-specific historical bleaching response (Bleaching Response Index [BRI; Swain et al. 2016c]; black = low, blue = medium, red = high bleaching response). Heat maps in green are the per-character scores (0–1) for the 7 characters indicating increasing colony integration (darker colors); heat map in greyscale is the integration score (sum of the character scores) indicating increasing colony integration (darker colors). Lower colony integration values are associated with increased bleaching response (Pearson Product-moment Correlation Coefficient [PCC] = −0.224, p = 0.036)

(Fig. 1 continued next page)

tween inferred colony integration and bleaching response indicates that, contrary to the observations of Baird & Marshall (2002), lower physiological integration (as inferred by the 7 characters in our analysis) is significantly associated with increased bleaching response among the targeted 88 coral species (Fig. 1).

There are multiple, non-mutually exclusive, potential explanations for the detection of opposing patterns between the work of Baird & Marshall (2002) and this study. Much of the basic data collection (bleaching, mortality, growth, and reproduction after a single event vs. parameterized indices of historical bleaching and mortality response), taxon selection

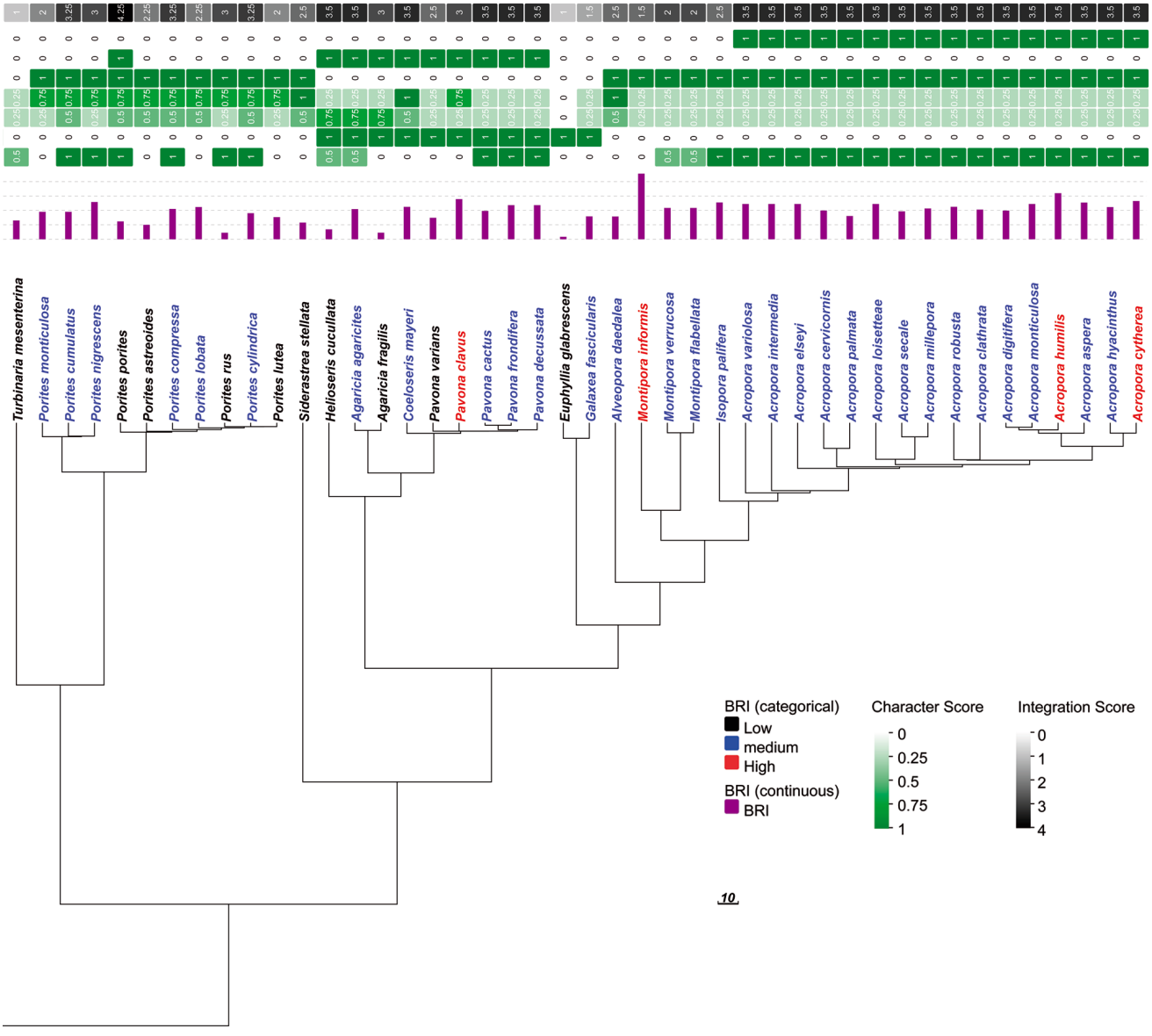


Fig. 1. (continued)

(4 coral species and Alcyonacea and Milleporidae vs. 88 coral species), geographic and temporal constraints (1998 bleaching event in the Indo-Pacific vs. the mean of events collected pan-tropically between 1982 and 2006), and data analysis (observation vs. phylogenetically corrected statistical analyses) differ dramatically between the 2 studies. The work presented here is both an expansion and refocusing of the original concept to critically assess the resulting hypothesis on the potential mechanisms of stress management across differential colonial integration. Along with the expansion in scope, this study also highlights the importance of phylogenetically correcting cross-species analyses. The characters of species do not represent independently sampled replicates, as species and their character states are related through evolution and may be more similar among close relatives regardless of the relationship between characters (Felsenstein 1985, Revell 2010). Similar bleaching responses among coral species could be caused by similar mechanisms or by similar evolutionary history. By not adequately accounting for the pattern of evolution, significant associations among species characters could be obscured or misinterpreted (Harvey 1996, Freckleton et al. 2002). In the present study, ordinary least squares linear regression was unable to detect a significant relationship between BRI and integration. Only a phylogeneti-

cally corrected analysis was able to tease apart similarity due to relationships among species (evolution) from similarity due to relationships among character states (potential mechanisms).

A recent assessment of a similar set of field observations and hypotheses (using broad data and correction for evolutionary relationships) led to a similar conclusion. McCowan et al. (2012) reassessed the long-standing hypothesis that coral species with branching colony forms are more susceptible to bleaching and bleaching-related mortality than species with massive forms. Their field data—compiled from all targeted species—supported the conclusion that branching and tabular corals bleached significantly more than massive corals, but when those corals were grouped into higher taxa (families), the pattern became obscured. For example, among the Faviidae, branching species bleached less than massive species, but the opposite trend was observed among the Acroporidae and Poritidae. McCowan et al. (2012) suggest that the disparity between the field observations and the results of their analyses is due to the heightened susceptibility of certain taxonomic groups of coral species and that those taxa also happen to be predominantly branching species (i.e. the observation of increased bleaching response among branching corals was the result of phylogeny). Our phylogenetically corrected assessment of diverse branching and massive species reported here is similarly unable to identify a significant relationship between colony growth form and bleaching response.

The inverse relationship between colony integration and bleaching suggests that the response to moderate thermal stress may be akin to moderate predation, injury, or disease, where integration among modules may contribute to the effectiveness of the colony-wide response by permitting unaffected polyps to aid those in distress or to selectively isolate damage and reallocate resources from non-vital life history functions (Pearse & Muscatine 1971, Rinkevich & Loya 1983, Fang et al. 1989, Gladfelter et al. 1989, Oren et al. 1997, Fine et al. 2002, Roff et al. 2006). Lesion induction has been shown to activate directional transport of photosynthates toward the injured tissue from modules up to 10 cm away, and to reduce reproductive investment up to 15 cm away from the lesion (Oren et al. 1997, 2001, Roff et al. 2006). Disease has been shown to activate directional transport of photosynthates away from the affected area, as if to reduce nutrient availability to the infecting pathogen and restrict resource loss to polyps that cannot be saved (Roff et al. 2006). Bleaching that reduces *Symbiodinium* densities by as little as 40% is capable of halting inter-module translocation of photosynthates altogether, effectively isolating each polyp to fend for itself during stress events (Fine et al. 2002). Our results are consistent with the observed responses to other stressors where physiological integration aids in the stress response.

The integration characters applied here are an indirect indication of physiological integration, and direct measurements or selection of different characters or differential weighting of characters may alter the results. Our sensitivity assessment of the analysis reported here resulted in the same trends at similar fits, although the exclusion of either colony formation or coenosteum amount resulted in the loss of statistical significance, and the exclusion of colony growth form strengthened the observed relationship (Table 2). This strengthened relationship is likely due to the lack of correlation between colony growth form and bleaching response that we observed through the phylo log regression. Additionally, direct measurements have demonstrated, through directional intracolony translocation of photosynthetic assimilates to adjacent injured polyps, energy integration in the absence of structural characters that would indicate integration (Brickner et al. 2006). Pairing direct measurements of chemical translocation with physical indications of communicating pathways may improve precision of assessments of the effects of physiological integration on stress resistance and on the mechanism by which integration may contribute to an improved stress response.

We have focused here on the relationship between coloniality and bleaching response, linked through the potential intermodule communication and coordination, but other possible mechanisms stem from skeletal architecture and could affect bleaching resistance. For example, skeletal light scattering can increase light availability to *in hospite Symbiodinium* (Enríquez et al. 2005, Stambler & Dubinsky 2005, Terán et al. 2010) and is modulated by calcium carbonate microstructure (Marcelino et al. 2013, Swain et al. 2016b) in concert with optical properties of coral tissues (Kühl et al. 1995, Wangpraseurt et al. 2012, 2014, 2017). Coloniality may be intertwined with the relationship between internal light enhancement and bleaching response as a contributing factor to observed species-specific differential bleaching resistance, or it may directly influence the internal light environment itself (Enríquez et al. 2017) and thereby contribute to differential bleaching. Clearly, there is a need for a comprehensive approach, where the major hypothesized contributing factors to species-specific differential bleaching response (including

symbiont characters such as phylotype-specific thermotolerance; Berkelmans & van Oppen 2006, Swain et al. 2016a) are properly weighed against the observed bleaching patterns.

Acknowledgements. We thank R. Bieler and J. Gerber of the Field Museum of Natural History for expertise and access to the FMNH museum collections and S. Cairns and T. Coffer of the National Museum of Natural History for expertise and access to the NMNH museum collections. Special thanks to D. Huang for providing us with the tree files for his comprehensive phylogeny of corals. This research was supported by the U.S. National Science Foundation (EFRI-1240416 and CBET-1249311) and U.S. National Institutes of Health (EB 003682). Additional funding came from 108 contributors to a crowdfunding campaign, and the Coral Reefs Challenge Grant, via Experiment.com.

LITERATURE CITED

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

Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. Estuar Coast Shelf Sci 80:435–471

Barbeitos MS, Romano SL, Lasker HR (2010) Repeated loss of coloniality and symbiosis in scleractinian corals. Proc Natl Acad Sci USA 107:11877–11882

Berkelmans R, van Oppen MJH (2006) The role of zooxanthellae in the thermal tolerance of corals: a 'nugget of hope' for coral reefs in an era of climate change. Proc R Soc B 273:2305–2312

Brickner I, Oren U, Frank U, Loya Y (2006) Energy integration between the solitary polyps of the clonal coral *Lobophyllia corymbosa*. J Exp Biol 209:1690–1695

Brown BE (1997) Coral bleaching: causes and consequences. Coral Reefs 16:S129–S138

Budd AF, Stolarski J (2011) Corallite wall and septal microstructure in scleractinian reef corals: comparison of molecular clades within the family Faviidae. J Morphol 272: 66–88

Coates AG, Jackson JBC (1987) Clonal growth, algal symbiosis, and reef formation by corals. Paleobiology 13: 363–378

Coates AG, Oliver WAJ (1973) Coloniality in zoantharian corals. In: Boardman RS, Cheetham AH, Oliver WAJ (eds) Animal colonies: development and function through time. Dowden, Hutchinson and Ross, Stroudsburg, PA, p 3–28

Enríquez S, Méndez ER, Iglesias-Prieto R (2005) Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. Limnol Oceanogr 50:1025–1032

Enríquez S, Méndez ER, Hoegh-Guldberg O, Iglesias-Prieto R (2017) Key functional role of the optical properties of coral skeletons in coral ecology and evolution. Proc R Soc B 284:20161667

Fang LS, Chen YWJ, Chen CS (1989) Why does the white tip of stony coral grow so fast without zooxanthellae? Mar Biol 103:359–363

Farris JS (1989) The retention index and the rescaled consistency index. Cladistics 5:417–419

Felsenstein J (1985) Phylogenies and the comparative method. Am Nat 125:1–15

Fine M, Oren U, Loya Y (2002) Bleaching effect on regeneration and resource translocation in the coral *Oculina patagonica*. Mar Ecol Prog Ser 234:119–125

Frankowiak K, Kret S, Mazur M, Meibom A, Kitahara MV, Stolarski J (2016) Fine-scale skeletal banding can distinguish symbiotic from asymbiotic species among modern and fossil scleractinian corals. PLOS ONE 11:e0147066

Freckleton RP, Harvey PH, Pagel M (2002) Phylogenetic analysis and comparative data: a test and review of evidence. Am Nat 160:712–726

Frieler K, Meinshausen M, Golly A, Mengel M, Lebek K, Donner SD, Hoegh-Guldberg O (2013) Limiting global warming to 2 degrees C is unlikely to save most coral reefs. Nat Clim Chang 3:165–170

Gladfelter EH, Michel G, Sanfelici A (1989) Metabolic gradients along a branch of the reef coral *Acropora palmata*. Bull Mar Sci 44:1166–1173

Harvey PH (1996) Phylogenies for ecologists. J Anim Ecol 65:255–263

Hemond EM, Kaluziak ST, Vollmer SV (2014) The genetics of colony form and function in Caribbean *Acropora* corals. BMC Genomics 15:1133

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS and others (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742

Huang DW (2012) Threatened reef corals of the world. PLOS ONE 7:e34459

Huang DW, Benzoni F, Fukami H, Knowlton N, Smith ND, Budd AF (2014) Taxonomic classification of the reef coral families Merulinidae, Montastraeidae, and Diploastraeidae (Cnidaria: Anthozoa: Scleractinia). Zool J Linn Soc 171:277–355

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG and others (2017) Global warming and recurrent mass bleaching of corals. Nature 543:373–377

Ives AR, Garland T (2014) Phylogenetic regression for binary dependent variables. In: Garamszegi LZ (ed) Modern phylogenetic comparative methods and their application in evolutionary biology. Springer-Verlag, Berlin, p 231–261

Ives AR, Helmus MR (2011) Generalized linear mixed models for phylogenetic analyses of community structure. Ecol Monogr 81:511–525

Jokiel PL (2004) Temperature stress and coral bleaching. In: Rosenberg E, Loya Y (eds) Coral health and disease. Springer-Verlag, Berlin, p 401–425

Jones RJ (2008) Coral bleaching, bleaching-induced mortality, and the adaptive significance of the bleaching response. Mar Biol 154:65–80

Kühl M, Cohen Y, Dalsgaard T, Jorgensen BB, Revsbech NP (1995) Microenvironment and photosynthesis of zooxanthellae in scleractinian corals studied with microsensors for O_2, pH and light. Mar Ecol Prog Ser 117:159–172

Lee CH, Blay S, Mooers AO, Singh A, Oakley TH (2006) CoMET: A Mesquite package for comparing models of continuous character evolution on phylogenies. Evol Bioinformatics 2:183–186

Mackie GO (1986) From aggregates to integrates: physiological aspects of modularity in colonial animals. Philos Trans R Soc Lond, B 313:175–196

Maddison WP, Maddison DR (2011) Mesquite: a modular system for evolutionary analysis. http://mesquiteproject.org

Madin JS, Anderson KD, Andreasen MH, Bridge TCL and others (2016) The Coral Trait Database, a curated database of trait information for coral species from the global oceans. Sci Data 3:160017

Marcelino LA, Westneat MW, Stoyneva V, Henss J and others (2013) Modulation of light-enhancement to symbiotic algae by light-scattering in corals and evolutionary trends in bleaching. PLOS ONE 8:e61492

McClanahan TR, Weil EJ, Cortes J, Baird AH, Ateweberhan M (2009) Consequences of coral bleaching for sessile reef organisms. In: van Oppen MJH, Lough JM (eds) Coral bleaching: patterns, processes, causes and consequences. Ecol Stud 205:121–138

McCowan DM, Pratchett MS, Baird AH (2012) Bleaching susceptibility and mortality among corals with differing growth forms. Proc 12th Int Coral Reef Symp 9A:1–6

Midford PE, Garland T Jr, Maddison WP (2010) PDAP package. http://mesquiteproject.org

Muscatine L (1990) The role of symbiotic algae in carbon and energy flux in reef corals. In: Dubinsky Z (ed) Coral reefs, 25. Elsevier, Amsterdam, p 75–87

Oakley TH, Gu ZL, Abouheif E, Patel NH, Li WH (2005) Comparative methods for the analysis of gene-expression evolution: an example using yeast functional genomic data. Mol Biol Evol 22:40–50

Oliver JK (1984) Intra-colony variation in the growth of *Acropora formosa*: extension rates and skeletal structure of white (zooxanthellae-free) and brown-tipped branches. Coral Reefs 3:139–147

Oren U, Rinkevich B, Loya Y (1997) Oriented intra-colonial transport of ^{14}C labeled materials during coral regeneration. Mar Ecol Prog Ser 161:117–122

Oren U, Benayahu Y, Lubinevsky H, Loya Y (2001) Colony integration during regeneration in the stony coral *Favia favus*. Ecology 82:802–813

Pearse VB, Muscatine L (1971) Role of symbiotic algae (zooxanthellae) in coral calcification. Biol Bull 141: 350–363

Revell LJ (2010) Phylogenetic signal and linear regression on species data. Methods Ecol Evol 1:319–329

Revell LJ (2012) Phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol Evol 3:217–223

Rinkevich B, Loya Y (1983) Oriented translocation of energy in grafted reef corals. Coral Reefs 1:243–247

Roff G, Hoegh-Guldberg O, Fine M (2006) Intra-colonial response to acroporid 'White syndrome' lesions in tabular *Acropora* spp. (Scleractinia). Coral Reefs 25:255–264

Santos SR, Toyoshima J, Kinzie RA III (2009) Spatial and temporal dynamics of symbiotic dinoflagellates (*Symbiodinium*: Dinophyta) in the perforate coral *Montipora capitata*. Galaxea 11:139–147

Soong K, Lang JC (1992) Reproductive integration in reef corals. Biol Bull 183:418–431

Stambler N, Dubinsky Z (2005) Corals as light collectors: an integrating sphere approach. Coral Reefs 24:1–9

Swain TD, Chandler J, Backman V, Marcelino L (2016a) Consensus thermotolerance ranking for 110 *Symbiodinium* phylotypes: an exemplar utilization of a novel iterative partial-rank aggregation tool with broad application potential. Funct Ecol 31:172–183

Swain TD, DuBois E, Gomes A, Stoyneva VP and others (2016b) Skeletal light-scattering accelerates bleaching response in reef-building corals. BMC Ecol 16:10

Swain TD, Vega-Perkins JB, Oestreich WK, Triebold C and others (2016c) Coral bleaching response index: a new tool to standardize and compare susceptibility to thermal bleaching. Glob Change Biol 22:2475–2488

Terán E, Méndez ER, Enríquez S, Iglesias-Prieto R (2010) Multiple light scattering and absorption in reef-building corals. Appl Opt 49:5032–5042

van Woesik R, van Woesik K, van Woesik L, van Woesik S (2013) Effects of ocean acidification on the dissolution rates of reef-coral skeletons. PeerJ 1:e208

Wangpraseurt D, Larkum AWD, Ralph PJ, Kühl M (2012) Light gradients and optical microniches in coral tissues. Front Microbiol 3:316

Wangpraseurt D, Larkum AWD, Franklin J, Szabo M, Ralph PJ, Kühl M (2014) Lateral light transfer ensures efficient resource distribution in symbiont-bearing corals. J Exp Biol 217:489–498

Wangpraseurt D, Holm JB, Larkum AWD, Pernice M, Ralph PJ, Suggett DJ, Kühl M (2017) *In vivo* microscale measurements of light and photosynthesis during coral bleaching: Evidence for the optical feedback loop? Front Microbiol 8:59

Yost DM, Wang LH, Fan TY, Chen CS, Lee RW, Sogin E, Gates RD (2013) Diversity in skeletal architecture influences biological heterogeneity and *Symbiodinium* habitat in corals. Zoology 116:262–269

Zhang HK, Gao SH, Lercher MJ, Hu SN, Chen WH (2012) EvolView, an online tool for visualizing, annotating and managing phylogenetic trees. Nucleic Acids Res 40: W569–W572

Editorial responsibility: Peter Edmunds, Northridge, California, USA

Submitted: July 7, 2017; Accepted: December 4, 2017
Proofs received from author(s): January 10, 2018