Similar impacts of fishing and environmental stress on calcifying organisms in Indian Ocean coral reefs

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ABSTRACT: Calcification and reef growth processes dominated by corals and calcifying algae are threatened by climate and fishing disturbances. Twenty-seven environmental, habitat, and species interaction variables were tested for their influence on coral and calcifier cover in 201 western Indian Ocean coral reefs distributed across ~20° of latitude and longitude and up to 20 m deep. These variables predicted more of the total between-site variance of calcifying organism cover (~50%) than coral cover (~20%). Satellite-derived environmental variables of temperature, light, and water quality predicted more of the coral and calcifier cover than feeding interactions when groups of related variables were analyzed separately. Nevertheless, when simultaneously evaluating all variables, the environmental variables better predicted coral cover, but proxies of feeding interactions better predicted calcifier cover. Coral and calcifier cover were most consistently negatively influenced by sea surface temperature distributions (right skewness), but the orange-lined triggerfish *Balistapus undulatus* consistently had a strong positive association with coral and calcifier cover. Herbivorous fish and Diadematidae sea urchins were not positively associated with coral and calcifier cover. A primary prey of *B. undulatus,* the rock-boring sea urchin *Echinometra mathaei*, had a strong negative association with coral cover and particularly calcifier cover. Island reefs had higher calcifier abundance than fringing reefs, which probably results from high *Acropora* and *B. undulatus* but low *E. mathaei* abundance. When comparing all variables and models, these taxonomic associations had more influence than environmental stress variables on calcifiers. Given the important predatory role of *B. undulatus* in controlling *E. mathaei* populations, fishing restrictions on this species could help attenuate calcification losses predicted by climate change.

KEY WORDS: Benthic cover · Calcium carbonate · Ecosystem-based management · Climate change · Predation · Resilience

INTRODUCTION

Calcifying organisms, calcification processes, and reef growth are under threat by multiple forces, including the direct impacts of poor water quality, climate and thermal anomalies, and ocean acidification, as well as the indirect forces of trophic cascades — often catalyzed by fishing (Carreiro-Silva & McClanahan 2012, Johnson & Carpenter 2012, Andersson & Gledhill 2013, Kroeker et al. 2013). These forces are likely to combine and undermine the process of calci-

fication and reef growth with the potential to influence reef fisheries and the capacity of reefs to grow and respond to rising sea levels (Wild et al. 2011). Geographic factors are expected to influence the exposures to these forces and interact with fisheries intensity and management to influence local responses (Ateweberhan et al. 2011, Selig et al. 2012). Given the contemporary and projected threats to these organisms and ecological processes, it behooves coral reef investigators to more fully understand the factors associated with and potentially influencing calcifiers.

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Benthic organisms in coral reefs are primarily composed of taxa that have made evolutionary, energetic, and functional tradeoffs between organic and inorganic carbon production (Vermeij 1987). The main functional groups contributing to organic production are primarily small turf and larger erect non-calcifying algae and seagrass (McClanahan et al. 2002). Calcifying organisms are primarily composed of hard corals and red coralline and green calcareous algae. All these organisms contribute to primary production, but calcifiers also contribute to reef growth and use the net energy from organic production to support calcification (Albright et al. 2013, Koweek et al. 2015, Shaw et al. 2015). While calcification is expected to increase an organism's survival and fitness in coral reefs (Vermeij 1987), life histories and dominance are expected to change with shifting water temperatures, quality and consumer environments (Bell et al. 2013, Sunday et al. 2014). Thus, niches and taxonomic configurations can shift as reef environments change, with consequences for the organic/inorganic carbon production.

Reef type, geographic locations, oceanographic and physical features, depth, and exposure to physical energy influence species, community composition, and the distribution of calcifiers in coral reefs (McClanahan & Karnauskas 2011, Gove et al. 2015). Reef consumers, in turn, influence reef growth directly by eroding calcium carbonate skeletons, but also indirectly by influencing competition between calcifying and non-calcifying organisms (Smith et al. 2010, Kennedy et al. 2013, Bronstein & Loya 2014). For example, some herbivorous consumers, such as surgeonfish, primarily crop algae or clean calcium carbonate surfaces whereas other consumers, including excavating parrotfish and some sea urchin species, consume calcium carbonate skeletons and increase reef bioerosion (Bellwood et al. 2012, Marshell & Mumby 2012, Qiu et al. 2014). The various controlling roles of herbivore groups — surgeonfish, parrotfish, rabbitfish, and sea urchin species — in reef interactions and processes is of considerable practical interest to reef condition (Burkepile & Hay 2010, Thibaut & Connolly 2013, Humphries et al. 2014, Nash et al. 2015, Russ et al. 2015). For example, the proportion of common bioeroding sea urchins (i.e. the Diadematidae versus Echinometridae) may influence reef growth depending on the abundance of their respective populations in different reef environments (McClanahan et al. 1999, Bronstein & Loya 2014, McClanahan & Muthiga 2016).

Investigations into the maintenance of calcification and reef structure have often ignored or underestimated the role of reef carnivores and subsequent effects on reef ecology and ecosystem services. Yet, there is good evidence that trophic cascades initiated above the herbivore level influence reef structure and processes (O'Leary & McClanahan 2010, McClanahan & Muthiga 2016). Macro-invertebrate feeders consume a mixture of calcifying primary producers, such as hard corals, but also preferentially prey on various mobile invertebrate herbivores and bioeroders, including sea urchins (McClanahan 1999, 2000). Consequently, the diversity and complexity of ecological interactions on coral reefs creates the opportunity for evaluating the important and novel roles of carnivores on reef growth. Carnivores are amenable to local fisheries restrictions and appropriate management could potentially moderate climate impacts that are threatening corals and calcifier populations.

The physical environment interacting with the coral holobiont has been shown to influence coral responses to thermal anomalies (McClanahan & Maina 2003, Golbuu et al. 2007, Howell et al. 2011). Similarly, there are notable variations in the acclimation/adaptation and refuge potential of corals globally, including the Indian Ocean region (Maina et al. 2011, McClanahan et al. 2011a, Chollett & Mumby 2013). Studies in the Indian Ocean have uncovered the influences of a number of environmental variables and how they interact to create stressful conditions and vice versa (Maina et al. 2008, McClanahan et al. 2015a). For example, background variation in light and temperature influences the acclimation rates and survival of corals disturbed by climate anomalies (McClanahan et al. 2005, Ateweberhan & McClanahan 2010). Consequently, the persistence of corals and calcifying organisms is expected to reflect the recent history of environmental conditions.

Given the above findings, the roles of environmental thermal stress and competition mediated by consumers are the most likely factors influencing reef calcifiers and calcification processes. This study evaluates the potential roles and influences of the physical environment and trophic cascade ecology on corals and calcium carbonate-forming organisms. We used data from a broad survey of tropical western Indian Ocean coral reefs collected over ~20° of longitude and latitude and a depth range of 20 m. Factors examined included reef type, coral growth-form dominance, distance from shore, exposure to the open sea, depth, complexity of the bottom, thermal and light intensity and variation, a multivariate stress model (Maina et al. 2011), the abundance of various herbivore and sea urchin predators, and dominant
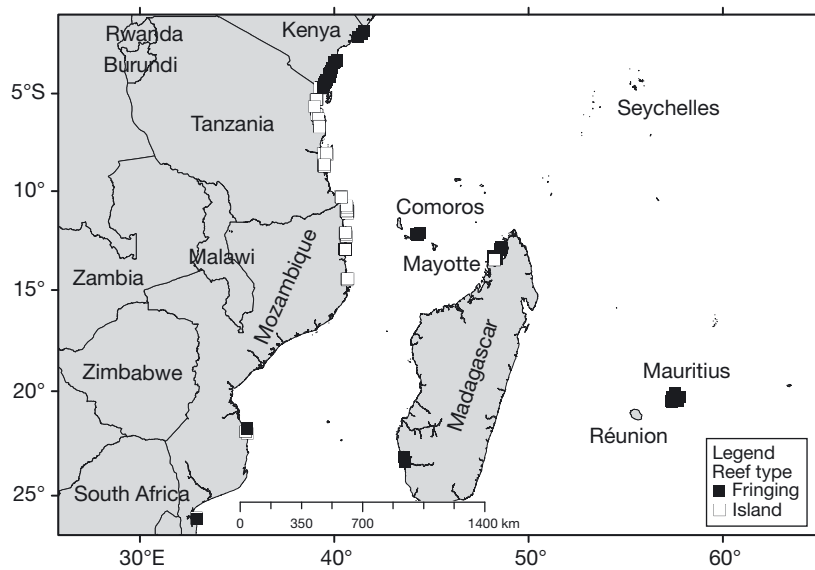
Fig. 1. Location of study sites in the western Indian Ocean region and the distribution of fringing (filled squares) and island (open squares) reef sites

coral taxa. Using step-wise regression modeling and inclusive (Akaike information criteria, AIC) and exclusive (Bayesian information criteria, BIC) stopping rules, we compared the strength of these factors in predicting coral and calcifying organism cover. This work was undertaken to further test and refine existing hypotheses about environmental versus ecological control of the reef calcification process.

MATERIALS AND METHODS

Study sites

Fringing reefs and offshore island reefs are the common reef types and *Acropora* and massive *Porites* the dominant coral growth forms in the western Indian Ocean (Fig. 1, Perry et al. 2015, Ateweberhan & McClanahan 2016). Large fringing reefs are found in southern Kenya, southwest and northeast Madagascar, and surrounding the island of Mauritius. Offshore island reefs are common in the Mozambique Channel from southern Kenya to northern Mozambique and northwest Madagascar. Offshore island reefs are living coral growing on the edges of Pleistocene carbonate islands and submerged banks. Both reef types have an exposed reef edge and sheltered back reef or lagoon where the physical forces of waves are reduced. The reef types, nearest distance to shore (Google maps), as well as the depth and exposure to open sea were recorded for each site.

Field methods

We undertook ecosystem-level studies of coral reefs in the western Indian Ocean reefs (see Supplement at www.int-res.com/articles/suppl/m560 p087_supp.pdf). These ecological field study data were combined with satellite-derived environmental data for a total of 27 variables to be tested for their influences on coral and calcifying cover. These variables included 6 physical factors, 7 herbivore metrics, 5 macro-invertebrate predator metrics, and 9 environmental variables. Measurements at the site level included sampling the benthos, sea urchins, and fish numbers and their biomass (see Supplement). The benthic substrate was sampled using 2 methods, one was the standard 10 m line-intercept transect methodology (McClanahan & Shafir 1990) and the other was a visual estimate method, which was most frequently used in deeper water where the time required to do the field work was limited (McClanahan et al. 2007a).

Using the line-intercept method, organisms under a loosely draped line were measured and classified into functional groups of hard and soft coral, algae (fleshy, red coralline, i.e. *Amphiroa, Jania, Hydrolithon* and green calcareous, i.e. *Halimeda*), seagrass (i.e. *Thalassia* and *Thallasodendron*), sponge and sand. Six to 9 replicate transects were done per site and the total lengths of each group were summed and the percent cover was calculated for each substrate category per site. The topographic complexity of the bottom was estimated by the ratio of the bottom contour to straight-line distance using the same 10 m transect line (McClanahan 1994). The coral structure of the reefs was estimated by calculating the ratio of the dominant branching *Acropora* to dominant massive *Porites.* These are the 2 most common branching and massive taxa on these reefs and their cover has influences on the structure and calcification rates on these reefs (Perry et al. 2015).

The visual estimate method classifies cover of hard and soft coral and erect algae into 5% cover increments in ~20 replicate and haphazardly placed 2 m² quadrats per site. This method does not estimate calcifying algae cover and so data collected by this method is only used in tests where coral cover is the response variable. This led to 2 separate analyses, one based on 97 reef site × time replicates where all

variables were available, and another based on 168 site × time replicates with only hard coral. The first analysis had a greater proportion of shallow reefs represented than the second analysis.

Sea urchins were sampled in 9 haphazardly placed 10 m^2 circular quadrats where all individuals were counted and recorded to species level. Haphazard samples of >20 individuals of each species were collected and their wet weights measured for converting population densities to wet weight biomass. Sea urchin diversity was calculated as a modification of the Simpson's index ($D = 1 - (\sum_{s=1}^{n} ni/N_t)^2$), such that 0 represents the lowest and 1 the highest proportional diversity based on individuals (*i*) per species (*s*) and the total number of individuals (N_t) in the sample. The predation rates on sea urchins were estimated in selected reefs by tethering 30 sea urchins and counting the numbers remaining after 24 h (McClanahan & Muthiga 1989).

Fish biomass and numbers were estimated in 500 m^2 belt transects (McClanahan 1994). Fish biomass was based on counts of their numbers, and estimates of body sizes in 10 cm intervals, with no individuals <3 cm counted for 20 families (McClanahan et al. 2015b). Fish were counted in a number of passes of the belt transect where, during the first pass, the individual's family and size were recorded while in subsequent passes, the species were recorded. The wet weight of the fish in each family group was estimated from length–weight relationships for these families combining FishBase reports (www.FishBase. org) and measurements in Kenyan fish landing sites (McClanahan & Kaunda-Arara 1996).

Environmental exposure data are from the CoR-TAD environmental satellite database (www.nodc. noaa.gov/sog/cortad/) and can grossly be categorized into temperature, light, and water quality metrics (chlorophyll and suspended solids). The data used were the satellite time series data collected from 1983 up to the time when the ecological data were collected. We calculated various sea surface temperature (SST) metrics including median, SD, skewness, kurtosis, mean, maximum, and frequency of thermal stress anomalies. Light variables included the median and maximum photosynthetic radiation (PAR) and water quality included the median chl *a* and suspended solids. We also evaluated a climate exposure and stress model that combined and weighted exposure variables based on their influence on coral bleaching (Maina et al. 2008, 2011). These data were tested for autocorrelation and we selected only one variable when related variables had high correlation (i.e. mean vs maximum temperature and light).

Data analyses

Line-transect benthic cover data were pooled into calcium carbonate and non-carbonate producer taxonomic groups. The calcium carbonate producer group was the sum of hard coral, red coralline, and green calcareous algae cover. The non-carbonate producer group was the sum of the turf, fleshy algae, sponge, and soft coral cover. Two response variables were used in the analysis, one based on line transects, which measured all calcifying organisms. The second was hard coral cover, which was based on both the line and visual estimate methods. Benthic cover data were logit transformed before analyses (Warton & Hui 2011). Fish groups were summed to produce a herbivorous fish group and a macro-invertebrate feeder group. Herbivorous fish were calculated as the sum of the acanthurids, scarids, and siganids. Macro-invertebrate feeders were estimated as the sum of triggerfish (after eliminating the plankti-vorous triggerfish *Odonus niger*) and wrasses with body lengths <20 cm (McClanahan et al. 2015b).

Step-wise regressions were undertaken where groups of related variables were tested for possible significance and then a final comprehensive model included all of the significant factors. To reduce autocorrelation and over-fitting of models, the variables were first tested for autocorrelation and variance inflation factor (VIF) before deciding on the final set of variables to be used in the regression analyses (Mansfield & Helms 1982). Separate forward step-wise regression analyses were done for coral and calcifying organisms. We also used adequate/liberal AIC and restrictive/conservative BIC stopping rules to identify the key variables acceptable for inclusion in the final comprehensive model. The use of both stopping rules allows for both inclusive and exclusive decisions when deciding on a variable's possible influence. Because the BIC method penalizes the addition of variables, BIC stopping rules provide the simplest explanation but can under-fit model variables; while AIC stopping rules are more inclusive, can over-fit models, but also have higher predictive ability (Burnham & Anderson 2002). In some cases, the 2 stopping rules produced the same results, in which case we present only the restrictive BIC results.

Tests for associations were done for physical associations, which include reef type, coral growth form, depth, exposure, distance from shore, and topographic complexity, for herbivore associations, which include various fish and sea urchin abundance variables hypothesized to influence coral–algal relationships, for the macro-invertebrate predator associa-

tions, and for thermal and environmental stress associations. Finally, the significant variables identified in these specific association analyses were combined and tested in the final comprehensive model. We undertook this modular approach in order to assess possible influences resulting from evaluating related sets of variables that are often hypothesized and tested together without measuring or considering other non-related but potentially influential variables. This type of restricted-variable hypothesis testing is common in ecology and can lack the holism required to evaluate complex systems. This modular and 2-stopping rule approach better distinguishes weak and strong factors and possible statistical acceptance/rejection errors (Type I and II) in the final models. Models were run in JMP version 11.0 (Sall et al. 2001).

RESULTS

Comparison of reef types

Island reefs were further from shore than fringing reefs and there were a number of differences in the benthic cover of these reef types (Table 1). Island reefs had more hard coral and sponge cover, a greater ratio of *Acropora* to massive *Porites* and more calcifying organism cover than fringing reefs. Fringing reefs had a greater cover of turf algae, seagrass, soft coral, and sand and non-calcifying algae overall. Calcifying organism cover was 31% higher on island than fringing reefs but there were no differences in topographic complexity and fleshy and coralline algal cover.

There was high variability in total sea urchin biomass with no significant differences between fringing and island reefs for the total biomass and associated diversity (Table 1). There were, however, differences at the species level with higher biomass of *Echinometra mathaei*, *Tripneustes gratilla*, *Stomopnuestes variolaris*, and *Toxopneustes pileolus* on fringing compared to island reefs. *E. mathaei* was the most abundant sea urchin species, had high between-reef variability, and its biomass (mean ± SD, 746 ± 1595 kg ha^{-1}) was 16 times higher on fringing than on patch reefs. *Diadema setosum* was more abundant on island than on fringing reefs but none of the other species-level Diadematidae comparisons (*Diadema savignyi*, *Echinothrix diadema*, and *E. calamaris*) were statistically different for reef type. The weighted ratio of Echinometridae to Diadematidae was, therefore, high in fringing reefs.

The mean biomass of all herbivorous fish was ~190 kg ha^{-1} and ~20% higher on island than on fringing reefs, attributable to more surgeonfish and parrotfish on island reefs. The main difference in the macro-invertebrate feeding community between reef types was the abundance of orange-striped triggerfish *Balistapus undulatus*, being twice as abundant on island than on fringing reefs, which led to more macro-invertebrate predator biomass overall. There was, however, only a marginally higher predation index (p < 0.06) on island than fringing reefs where this tethering experiment was undertaken (Table 1).

Coral cover relationships

All significant variables combined predicted a better fit to calcifier (BIC r^2 = 0.47, n = 97) than hard coral cover alone (best BIC r^2 = 0.21, best AIC r^2 = 0.27, n = 168) (Tables 2 & 3). Further, for both hard coral cover and calcifier cover, the satellite-derived environmental stress variables predicted more variance than the ecological variables when the variable associations were analyzed separately. Coral cover was better predicted by environmental variables than calcium carbonate cover, which was better predicted by taxonomic associations. The full or comprehensive models often found possible ecological feeding interactions were significant and more predictive, especially in the final calcium carbonate model.

The step-wise regression analyses with coral cover as the response variable found that AIC and BIC stopping rules were different for physical, herbivore and environmental variables (Table 2). Including all of the physical variables of reef type, depth, distance to shore, exposure, *Acropora*/massive *Porites* ratio, and topographic complexity found that *Acropora*/massive *Porites* was the strongest factor, followed by reef type, and distance to shore was only included as significant in the AIC stopping rules. The combined variables predicted 17 and 20% of the coral cover variance by BIC and AIC stopping rules, respectively (Table 2, Fig. 2). Among the herbivores, coral cover declined with the biomass of *E. mathaei* by both stopping rules. *E. mathaei* and the Acanthuridae explained 8 to 11% of the BIC and AIC variance, respectively. Among the carnivores, coral cover was significantly positively associated with the triggerfish *B. undulatus*, and negatively with the *Coris* wrasses, and 10% of the variance was explained.

The coral cover environmental associations model included 3 significant variables in the restrictive BIC and 5 variables in the AIC criteria. BIC criteria pre-

Table 1. Summary (mean ± SD) and comparison tests of significance (Kruskal-Wallis) of ecological metrics on fringing and island reefs in the western Indian Ocean showing (a) physical reef structure, (b) benthic cover, (c) sea urchin biomass and diversity, (d) herbivorous fish biomass, and (e) fish predators and predation index. χ^2 is the chi-squared value and $p > \chi^2$ is the probability the comparison test is greater than random

Variable	Fringing reef (N = 108)	Island reef (N = 73)	χ^2	$p > \chi^2$
(a) Physical reef structure				
Distance to shore (km)	1.08 ± 1.46	2.59 ± 2.99	12.86	0.0003
Topographic complexity, straight line/bottom contour distance (m m^{-1})	1.22 ± 0.08	1.23 ± 0.06	0.52	0.50
Acropora/massive *Porites* ratio	3.47 ± 8.88	6.88 ± 9.60	23.5	0.0001
(b) Benthic cover (%)				
Hard coral	27.87 ± 15.88	37.38 ± 13.35	17.04	0.0001
Algal turf	35.53 ± 12.15	31.23 ± 7.91	4.47	0.03
Calcareous algae	1.15 ± 2.62	0.45 ± 0.78	0.83	0.36
Fleshy algae	14.93 ± 14.58	11.91 ± 11	1.31	0.25
Coralline algae	9.52 ± 6.94	12.33 ± 10.19	1.46	0.23
Seagrass	3.24 ± 4.31	0.51 ± 1.02	13.12	0.0003
Soft coral	11.08 ± 17.11	9.62 ± 8.86	4.59	0.03
Sponge	0.69 ± 1.32	0.8 ± 1.39	3.93	0.05
Sand	7.1 ± 6.7	3.19 ± 2.66	8.11	0.004
Calcifying organisms	38.15 ± 15.32	51.17 ± 14.12	16.03	0.0001
Non-calcifying organisms	54.49 ± 16.66	45.64 ± 13.97	7.52	0.006
(c) Sea urchin biomass (kg ha^{-1})				
Diadema savignyi	156.15 ± 492.95	328.15 ± 680.43	0.96	0.33
Diadema setosum	279.46 ± 847.9	465.23 ± 1119.3	5.66	0.02
Echinometra mathaei	667.8 ± 1551.81	35.76 ± 124.96	8.41	0.004
Echinostrephus molaris	29.18 ± 128.98	16.89 ± 36.95	0.00	0.99
Echinothrix calamaris	50.46 ± 314.22	14.01 ± 36.28	0.89	0.35
Echinothrix diadema	616.45 ± 1189.24	559.97 ± 950.05	0.42	0.52
Toxopneustes pileolus	4.39 ± 14.6	0.28 ± 2.18	11.83	0.001
Tripneustes gratilla	126.38 ± 289.83	9.47 ± 47.19	17.21	0.0001
Stomopneustes variolaris	1.21 ± 4.71	0	12.57	0.0004
Others	0.06 ± 0.58	0	2.05	0.15
Diadematidae	1052.06 ± 1520.05	1353.35 ± 1692.59	0.24	0.62
Total sea urchin biomass	1931.54 ± 2253.32	1429.76 ± 1730.97	2.74	0.10
Sea urchin diversity, *D*	0.25 ± 0.25	0.26 ± 0.24	0.12	0.73
(d) Herbivorous fish biomass (kg ha^{-1})				
Acanthuridae	109.28 ± 119.85	131.32 ± 112.62	4.75	0.03
Scaridae	57.65 ± 145.13	69.49 ± 73.8	20.14	0.0001
Siganidae	8.56 ± 24.4	10.39 ± 33.23	0.13	0.72
Total herbivorous fish biomass	175.38 ± 245.85	211.2 ± 165.8	9.93	0.002
(e) Macro-invertebrate predators				
Triggers and wrasses >20 cm (kg ha^{-1})	29.17 ± 39.15	55.21 ± 51.86	18.93	0.0001
Balistapus undulatus (ind. 500 m^{-2})	0.71 ± 1.08	1.43 ± 1.82	10.78	0.001
Cheilinus trilobatus (ind. 500 m^{-2})	1.01 ± 1.03	1.25 ± 1.76	0.08	0.78
Coris spp. (ind. 500 m^{-2})	0.52 ± 0.97	0.47 ± 0.77	0.06	0.81
Lethrinus spp. (ind. 500 m^{-2})	0.58 ± 1.2	0.52 ± 1.29	0.98	0.32
Predation index (0 to 1)	0.22 ± 0.25	0.26 ± 0.19	3.54	0.06

dicted a negative relationship with temperature skewness and weaker relationships with light and the global stress model and 11% of the variance was predicted. The AIC criteria explained 21% of the variance and the mean thermal stress anomaly and chlorophyll were positively associated, and suspended solids and global stress model were negatively associated, with coral cover. The mean thermal stress anomaly analyzed alone indicates a weak negative association with coral cover ($t = -2.06$, $p < 0.04$, $r^2 = 0.02$) but the relationship becomes positive after removing temperature skewness from the total variance. Consequently, thermal anomalies were not negatively influencing coral cover after accounting for temperature distribution properties. Therefore, temperature skewness was the strongest environmental factor by both criteria and in the final full model. The final full models also included *Acropora*/massive *Porites* ratio, *Coris*

Table 2. Coral cover model results based on forward stepwise regression results for BIC and AIC stopping rules. Logit-transformed coral cover responses to sets of analyses, including (a) physical factors, (b) herbivores, (c) predators of macro-invertebrates, (d) satellite-derived environmental factors, and (e) all significant variables combined. The BIC stopping rules are presented only if not different from AIC results. Sections (f), (g), (h), and (i) present AIC results that were different from BIC results. Results are based on analysis of 168 study site replicates. Echino/Diade = Echinometridae/Diadematidae; VIF = variance inflation factor; p > F is the probability the comparison test is greater than random; SST = sea surface temperature; NS = not significant. VIF only reported when more than one factor is significant. When no values are given, they are not significant

Parameter	Estimate (mean ± SE)	t-ratio	F-ratio	p > $|t|$	VIF	R^2	p > F
BIC STOPPING RULES							
(a) Physical factors							
Intercept	−0.10 ± 0.07	−13.37	0.0	0.0001		0.17	<0.0001
Acropora/massive *Porites* ratio	0.03 ± 0.01	4.03	14.03	0.0001	1.03		
Reef type (fringing)	−0.23 ± 0.07	−3.43	6.35	0.0008	1.03		
Distance to shore (km)			3.39	NS			
Exposed vs. sheltered			2.29	NS			
Depth (m)			1.68	NS			
Rugosity (m m^{-1})			0.10	NS			
(b) Herbivore metrics (kg ha^{-1})							
Intercept	−0.81 ± 0.07	−11.85	0.0	0.0001		0.08	0.002
Echinometra mathaei	−0.0003 ± 0.0001	−3.76	13.05	0.0002			
Acanthuridae			4.08	NS			
Herbivorous fish			3.49	NS			
Diadematidae			2.05	NS			
Scaridae			1.66	NS			
Echino/Diade weighted ratio			0.17	NS			
Siganidae			0.07	NS			
(c) Predators of macro-invertebrates (ind. 500 m^{-2} or kg ha^{-1})							
Intercept	−0.91 ± 0.09	−9.83	0.0	0.0001		0.10	0.0003
Coris spp.	−0.25 ± 0.07	−3.33	9.21	0.001	1.0		
Balistapus undulatus	0.13 ± 0.06	2.37	8.33	0.02	1.0		
Cheilinus trilobatus			1.10	NS			
Lethrinus spp.			0.42	NS			
Triggers and wrasses			0.02	NS			
(d) Environmental variables							
Intercept	−0.72 ± 0.08	−9.12	0.0	0.0001		0.11	0.0001
SST skewness	−1.37 ± 0.3	−4.62	21.34	0.0001			
PAR median (E m^{-2} d^{-1})			4.45	0.04			
Global stress model			3.64	0.06			
Suspended solids median (g m^{-3})			2.88	0.1			
Mean thermal stress anomaly (°C)			2.76	0.1			
SST median (°C)			0.92	NS			
Chlorophyll median (mg m^{-3})			0.68	NS			
Climate exposure			0.27	NS			
SST kurtosis			0.01	NS			
(e) Full model							
Intercept	−0.79 ± 0.10	−8.25	0.0	0.0001		0.21	0.0001
SST skewness	−1.09 ± 0.31	−3.54	12.51	0.0005	1.09		
Acropora/massive *Porites* ratio	0.02 ± 0.01	3.28	10.74	0.001	1.09		
Coris spp.	−0.17 ± 0.07	−2.31	5.35	0.02	1.05		
Reef type (fringing)			4.16	0.04			
Balistapus undulatus			3.62	0.06			
Echinometra mathaei			0.52	NS			
AIC STOPPING RULES							
(f) Physical factors							
Intercept	−0.86 ± 0.07	−9.24	0.0	0.0001		0.20	0.0001
Acropora/massive *Porites* ratio	0.03 ± 0.01	3.88	12.95	0.0001	1.04		
Reef type (fringing)	−0.29 ± 0.07	−4.13	9.07	0.0008	1.20		
Distance to shore (km)	−0.07 ± 0.03	−2.43	3.39	0.02	1.16		
Depth (m)			1.49	NS			
Exposure			1.26	NS			
Rugosity (m m^{-1})			0.10	NS			

Table 2. Continued

Parameter	Estimate (mean ± SE)	t-ratio	F-ratio	$p > |t|$	VIF	R^2	$p > F$
(g) Herbivore metrics (kg ha^{-1})							
Intercept	−0.69 ± 0.10	−6.87	0.0	0.0001		0.11	0.0003
Echinometra mathaei	−0.0004 ± 0.0001	−4.02	16.15	0.0001	1.06		
Acanthuridae	−0.001 ± 0.001	−2.02	4.08	0.04	1.06		
Diadematidae			1.00	NS			
Echino/Diade weighted ratio			0.27	NS			
Scaridae			0.22	NS			
Herbivorous fish			0.17	NS			
Siganidae			0.00	NS			
(h) Environmental variables							
Intercept	2.62 ± 1.52	1.72	0.0	0.09		0.21	0.0001
SST skewness	−1.97 ± 0.43	−4.62	21.31	0.0001	2.29		
Mean thermal stress anomaly	0.09 ± 0.03	2.51	6.29	0.01	2.50		
Chlorophyll median (mg m^{-3})	1.83 ± 0.73	2.50	6.23	0.01	7.68		
Suspended solids median (g m^{-3})	−2.00 ± 0.91	−2.20	4.85	0.03	6.74		
Global stress model	−1.31 ± 0.74	−1.78	3.16	0.08	2.42		
PAR median (E m^{-2} d^{-1})	−0.05 ± 0.04	−1.49	2.23	NS	1.69		
SST median (°C)			0.15	NS			
Climate exposure			0.02	NS			
SST kurtosis			0.003	NS			
(i) Full model							
Intercept	−1.15 ± 0.22	−5.14	0.0	0.0001		0.27	0.0001
SST skewness	−1.72 ± 0.42	−4.11	16.91	0.0001	2.15		
Acropora/massive *Porites* ratio	0.03 ± 0.01	3.78	14.32	0.0002	1.18		
Acanthuridae	−0.001 ± 0.001	−2.07	4.30	0.04	1.17		
Mean thermal stress anomaly	0.06 ± 0.03	2.00	4.00	0.05	2.23		
Balistapus undulatus	0.10 ± 0.05	1.96	3.85	0.05	1.13		
Coris spp.	−0.12 ± 0.07	−1.74	3.04	0.08	1.08		
Distance to shore (km)			1.10	NS			
Reef type (fringing)			0.99	NS			
Chlorophyll median			0.57	NS			
Echinometra mathaei			0.19	NS			
Suspended solids median (g m^{-3})			0.02	NS			

spp., and *B. undulatus* for both criteria. The AIC also included Acanthuridae and the thermal stress anomaly but excluded reef type, which was included in the final BIC model.

Calcifier cover relationships

There were no differences in BIC and AIC criteria results for calcifier cover–predictor variable relationships. The *Acropora*/massive *Porites* cover ratio and reef type were the 2 significant physical factors and predicated 29% of the variance (Table 3, Fig. 3). Among the herbivores, only the abundance of *E. mathaei* biomass was significant, negatively associated with calcifier cover, and predicted 29% of the variance. Among the carnivores, the number of *B. undulatus* was positively associated with calcifier cover and, combined with a negative association with *Coris* wrasses, predicted 20% of the variance. Among the environmental variables, SST kurtosis was most negatively associ-

ated with calcifier cover and, together with skewness, explained 37% of the variance. The final full model found *B. undulatus* abundance was the strongest variable, followed by SST skewness, *Coris* spp., and SST kurtosis.

DISCUSSION

This large-scale study indicates the relative importance of a number of factors predicted to influence hard coral and all calcifiers. While regression analysis has limits to developing truly causative and predictive models, uncovering association and inclusion criteria is valuable for comparing existing information and planning future experimental research. For example, failure to find associations in regression analyses can indicate that hypotheses that predict causation are probably not well founded. Consequently, insignificant findings provide a basis for modifying hypotheses and developing experiments needed to better understand causation. The existing

Table 3. Calcifier cover model results based on forward stepwise regression analyses for BIC stopping rules. Logit-transformed coral cover responses to sets of analyses, including (a) physical factors, (b) herbivores, (c) predators of macro-invertebrates, (d) satellite-derived environmental factors, and (e) all significant variables combined. Results are based on analysis of 97 study site replicates. Echino/Diade = Echinometridae/Diadematidae; VIF = variance inflation factor; p > F is the probability the comparison test is greater than random; SST = sea surface temperature; NS = not significant. VIF only reported when more than one factor is significant. When no values are given, they are not significant

Parameter	Estimate (mean ± SE)	t-ratio	F-ratio	p > |t|	VIF	R^2	p > F
(a) Physical factors							
Intercept	−0.40 ± 0.08	−5.33	0.0	0.0001		0.29	0.0001
Acropora/massive *Porites* ratio	0.02 ± 0.01	4.27	17.45	0.0001	1.02		
Reef type (fringing)	−0.25 ± 0.07	−3.68	14.74	0.0004	1.02		
Exposed vs. sheltered			1.80	NS			
Depth (m)			1.39	NS			
Distance to shore (km)			0.39	NS			
Rugosity (m m^{-1})			0.13	NS			
(b) Herbivore metrics (kg ha^{-1})							
Intercept	−0.20 ± 0.07	−1.71	0.0	0.09		0.29	0.0001
Echinometra mathaei	−0.0004 ± 0.0001	−5.86	30.49	0.0001			
Siganidae			1.04	NS			
Acanthuridae			0.14	NS			
Echino/Diade weighted ratio			0.08	NS			
Diadematidae			0.001	NS			
Scaridae			0.0	NS			
Herbivorous fish			0.0	NS			
(c) Predators of macro-invertebrates (ind. 500 m^{-2})							
Intercept	−0.32 ± 0.09	−3.58	0.0	0.001		0.20	0.0001
Balistapus undulatus	0.32 ± 0.08	3.81	23.25	0.0003	1.01		
Coris spp.	−0.24 ± 0.08	−3.13	7.63	0.002	1.01		
Lethrinus spp.			1.01	NS			
Cheilinus trilobatus			0.60	NS			
Triggers and wrasses			0.47	NS			
(d) Environmental variables							
Intercept	−0.35 ± 0.16	−2.12	0.0	0.04		0.37	0.0001
SST kurtosis	−0.58 ± 0.21	−2.76	8.28	0.007	2.12		
SST skewness	−1.08 ± 0.4	−2.69	6.71	0.007	2.12		
Global stress model			0.92	NS			
Suspended solids median (g m^{-3})			0.69	NS			
Mean thermal stress anomaly (°C)			0.57	NS			
PAR median (E m^{-2} day^{-1})			0.36	NS			
Chlorophyll median (mg m^{-3})			0.12	NS			
SST median (°C)			0.11	NS			
Climate exposure			0.03	NS			
(e) Full model							
Intercept	−0.35 ± 0.17	−2.04	0.0	0.04		0.47	0.0001
Balistapus undulatus	0.27 ± 0.07	3.85	14.82	0.0002	1.02		
SST skewness	−1.04 ± 0.40	−2.62	6.85	0.01	2.16		
Coris spp.	−0.15 ± 0.07	−2.32	5.39	0.02	1.07		
SST kurtosis	−0.48 ± 0.21	−2.31	5.35	0.02	2.22		
Reef type			1.21	NS			
Acropora/massive *Porites* ratio			0.88	NS			
Echinometra mathaei			0.53	NS			

experimental and correlational literature also form a basis for interpreting findings from regression analyses, which can help distinguish potentially competing hypotheses. Finally, evaluating many factors expands the practical limits of experimental studies. Here, we found that there are many likely influences on corals and calcifiers and yet even the best multivariate models explained no more than half of the between-site variance for calcifiers and one quarter for corals. This indicates the complexity of the coral reef environment and the possible role of factors not measured here.
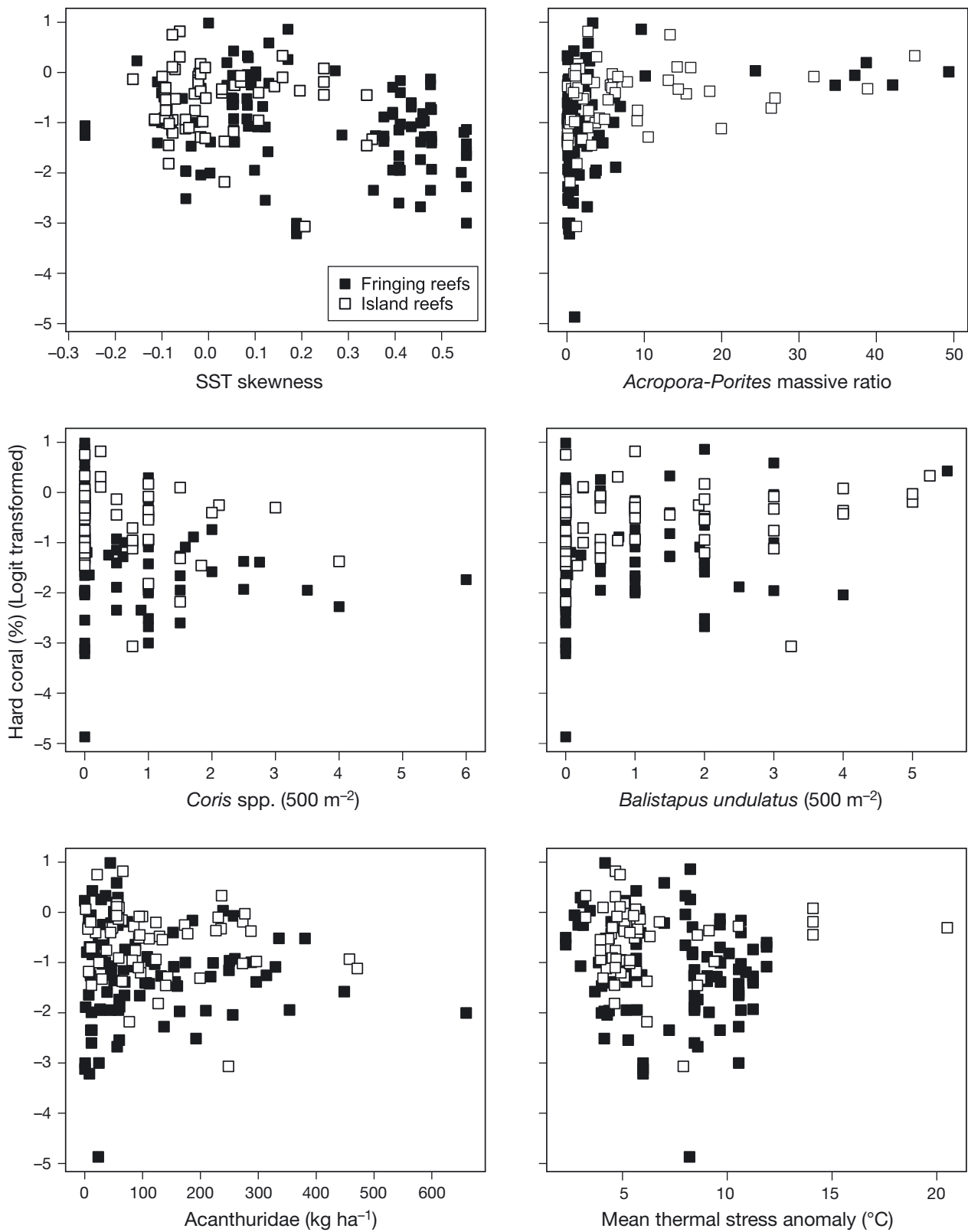
Fig. 2. Scatterplots of significant environmental and ecological relationships for coral cover, distinguishing fringing and island reefs
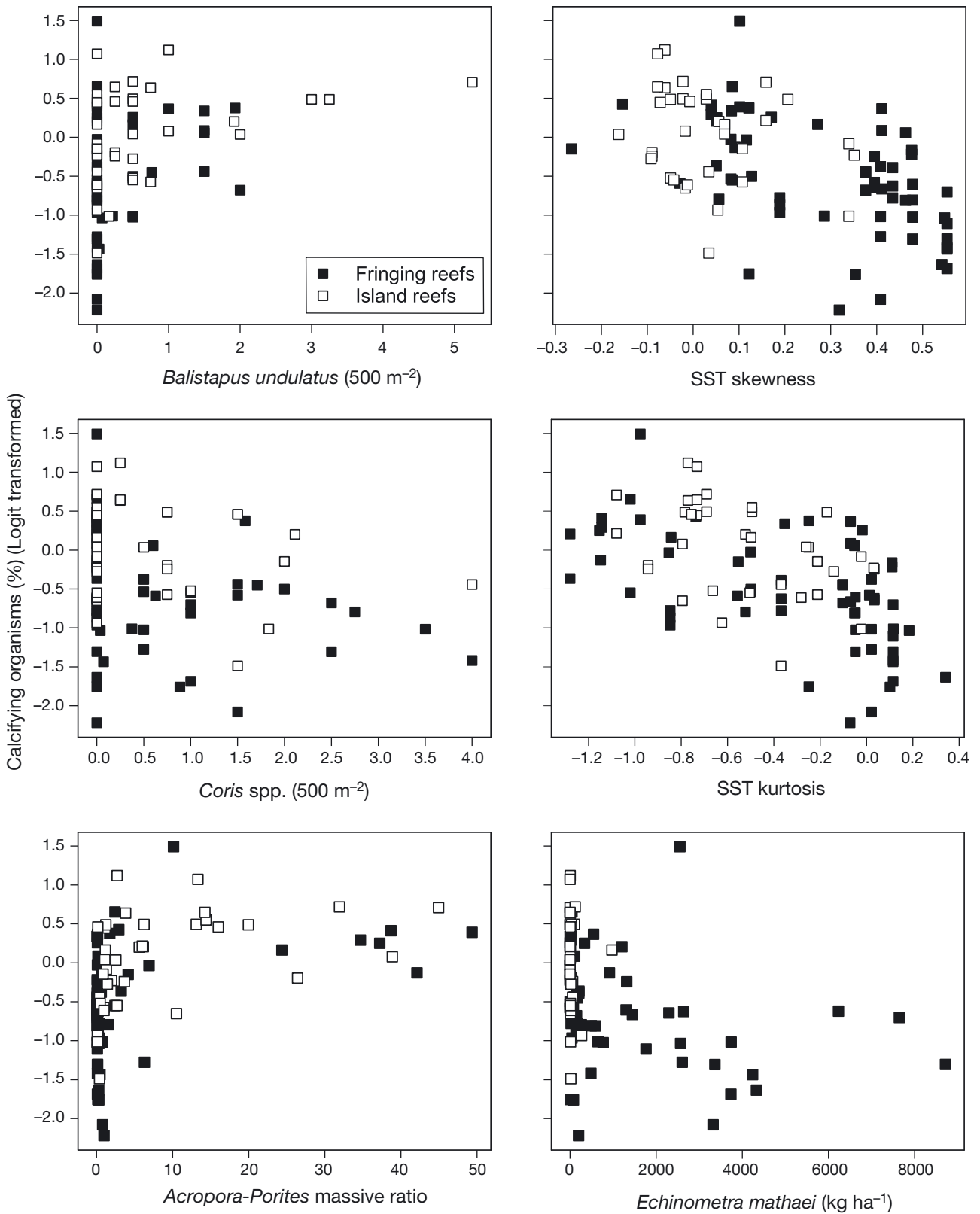
Fig. 3. Scatterplots of significant environmental and ecological relationships for calcifier cover, distinguishing fringing and island reefs

Satellite-derived environmental variables associated with thermal variation were among the dominant influences associated with both coral and calcifiers. This is likely to reflect a history of environmental stress and the associated change and adaptation (Ateweberhan & McClanahan 2010). For example, the right skew in temperature distribution was most strongly negatively associated with coral cover and also for all calcifiers. Skewness and kurtosis were positively correlated (r = 0.80) and both were positively associated with the various thermal stress anomalies (skewness vs. mean thermal stress = 0.71, kurtosis vs. mean thermal stress = 0.82). Consequently, anomalies can be seen as key factors that reflect SST disturbances but there were, for example, opposite influences with right skewness having a negative and the mean thermal stress anomaly having a positive association with coral cover once the skewness variance was removed. This suggests that anomalies are less important than background temperatures for determining whether or not an anomaly is detrimental to corals (McClanahan et al. 2007b). Flat temperature distributions or negative kurtosis was positively associated with coral cover and this is expected based on proposed anomaly/acclimation mechanisms (Ateweberhan & McClanahan 2010).

The *Acropora*/massive *Porites* ratio and reef type were the physical features that were significantly related to coral and calcifier cover, with higher coral and calcifying cover on island than fringing reefs. Island reefs had about twice the *Acropora*/massive *Porites* ratios than fringing reefs and this is likely to explain the higher estimated calcification rates on islands (Perry et al. 2015). While direct comparisons indicate that coral cover was ~40% and calcifying cover ~30% higher on island than fringing reefs, the step-wise regression indicates that these 2 variables explained <30% of the total variance. The distance to shore was expected to influence corals and calcifiers due to reduced anthropogenic impacts of fishing, dive tourism, and water quality offshore (Fabricius 2005, Smith et al. 2008, Brewer et al. 2013). Nevertheless, we failed to find any strong onshore–offshore influences, which may be due to the limited range of distances (~0.02 to 10.6 km) and the sites' mean closeness to shore. Nevertheless, other studies have failed to find strong patterns of coral degradation with distance from shore (Lirman & Fong 2007, Bruno & Valdivia 2016) while others have found higher calcifier but not coral cover in remote Pacific reefs (Smith et al. 2016). Climate and warm water impacts, which have been widespread, may have played a role in these patterns where reefs lacked the

capacity to tolerate stress (McClanahan et al. 2015a). Yet, the thermal anomalies were positively rather than negatively related to coral cover after accounting for temperature skewness in our study. Because coral cover generally recovers within 10 yr, the impacts of thermal disturbances to corals maybe short-lived (Ateweberhan et al. 2011, Gilmour et al. 2013). Consequently, high variation in the time since thermal disturbance is a likely reason the global stress model had a weak relationship with coral cover. Our data were collected over many years during a period of thermal stress but without knowledge of when each site was disturbed by the stresses (McClanahan et al. 2015a).

The grazer community and their biomass were hypothesized to influence coral and calcifier patterns. Given the hypothesized grazer role in promoting coral by controlling algal–coral relationships and subsequent fishing restriction recommendations, this result is unexpected (Lewis 1986, Hughes et al. 2003, Mumby et al. 2006, Game et al. 2009, Bellwood et al. 2012, Rasher et al. 2012, Edwards et al. 2014). Here, we found no evidence that any herbivorous fish were positively associated with calcifiers. The one weak association was a negative association between acanthurids and coral cover that would indicate their preference for feeding on dead coral surfaces (Marshell & Mumby 2012). While this does not support some ecosystem management recommendations, it does correspond with a number of large-scale studies that have failed to find significant coral–parrotfish associations, identified other factors, or found that herbivorous fish passively associate with, rather than actively control, algae–coral relationships (McClanahan et al. 2011b, Wilson et al. 2012, Carassou et al. 2013, Graham et al. 2015, Russ et al. 2015, Suchley et al. 2016).

The lack of biomass differences in surgeonfish and parrotfish between reef types suggests that their influence was weak and also not habitat specific. Parrotfish impacts are suggested to differ between hard and soft coral dominated ecosystems (Mumby 2016) but Indian Ocean reefs have few reefs dominated by soft corals. Overall, parrotfish biomass was low in most of the studied reefs and previous studies suggest they recover slowly (>10 yr) from fishing in this region's no-take closures (McClanahan et al. 2007c, McClanahan & Humphries 2012). Consequently, while herbivorous fish may contribute to grazing and the promotion of calcifiers, the *B. undulatus–E. mathaei* cascade could override any positive effects herbivorous fish may have on calcifier cover. A number of regional studies indicate that grazing is

influenced by a high diversity of grazing functional groups, not just fish (Humphries et al. 2014, McClanahan 2014). If so, it may be that diversity and redundancy provide some of the capacity to maintain grazing and calcifier cover but each grazer species or functional group provides only a small and difficult to detect impact (Thibaut & Connolly 2013).

It is likely that a combination of factors influenced the ecological outcomes including the well-studied fishing–macro-invertebrate predator–sea urchin herbivore–calcifier trophic cascade (McClanahan & Shafir 1990, O'Leary & McClanahan 2010). The triggerfish *B. undulatus* was included in most significant regression models, including the restrictive BIC models. Further, difference between reef types may be due to higher abundance of *B. undulatus* and *Acropora* on island than fringing reefs. Predation rates on tethered *E. mathaei* were not, however, very different between island and fringing reefs. Yet, *E. mathaei* was considerably more abundant on fringing than island reefs. Consequently, *E. mathaei* may benefit from other habitat characteristics of fringing reefs and taxa-specific nuances in the abundance and ratio of Echinometridae/Diadematidae and *Acropora*/massive *Porites* that could be important in explaining the higher calcifier cover on island reefs. Given the role of reef type in mediating these key coral and sea urchin taxa and the trophic cascade, it is also expected that calcification rates will differ between reef types (Koweek et al. 2015).

Why reef type creates these differences in the dominant corals, fish taxa and reef process is unlikely to be clarified without further study; but the combination of substrate consolidation, isolation, waves, and water flow are likely to be key explanatory factors. For example, distribution studies of *Diadema* and *Echinometra* often emphasize the greater abundance of *Echinometra* in high water flow environments receiving algal drift common to fringing reefs and *Diadema* in environments with more limited water flow (Russo 1977, Tuya et al. 2007, Bronstein & Loya 2014). Perry et al. (2015) also reported that *Porites* community cover is higher in high water flow environments than *Acropora* dominated reefs in the central Indian Ocean. Consequently, high water flow is likely to be promoting *Porites* and *E. mathaei* and low water flow *Acropora* and *Diadema* dominance. While reef exposure was not important relative to reef type, high numbers of *E. mathaei* were observed in the shallow and wave-protected leeward sides of fringing reefs (McClanahan & Kurtis 1991). This suggests breaking waves versus water flow have some unmeasured influences in the observed patterns. It was common to observe high numbers of the 2 *Echinothrix* species at depth or in high water flow environments without waves. Therefore, these habitat, wave, water flow, and depth variables are likely to be influencing the niches of these sea urchins with possible consequences for calcifiers (McClanahan & Muthiga 2016).

Some combination of unmeasured environmental factors and higher Diadematidae grazing relative to Echinometridae on island reefs may influence coral and calcifier cover. Numerous studies of grazing by sea urchins on coral and algae indicate that, at moderate abundance, sea urchins reduce algae and this promotes coral recruitment (Edmunds & Carpenter 2001), but other studies indicate negative effects of sea urchin grazing on corals and their recruits at moderate to high sea urchin grazing (Sammarco 1980, O'Leary et al. 2012, 2014, Qiu et al. 2014). Lower coral recruitment could be due to lower coralline algae cover in urchin-dominated reefs but we found no difference in coralline algal cover between island and fringing reefs. No published studies have successfully separated the grazing and density-dependent effects of *Echinometra* and *Diadema* on coral recruitment or coralline and coral cover. Consequently, our findings identify these experiments as an important area for future study. A companion study found differences in coral cover associated with the 2 dominant species of *Diadema*, with higher coral cover associated with the less common *D. setosum* compared to *D. savignyi* (McClanahan & Muthiga 2016). Consequently, evaluating species-level differences may be important for understanding ecological outcomes for calcifers.

Many of the dominant environmental and ecological factors expected to influence calcifier cover were studied but potentially important factors such as water flow, nutrient concentrations, fishing or destructive gear use, and the common problem of attributing correlation to causation remain potential weaknesses of this study. One likely example of a false correlation–causation problem is the consistent association between *Coris* wrasses and low coral cover. The *Coris* recorded here were largely juveniles, and we suggest the association occurs because juvenile *Coris* are commonly observed feeding on small invertebrates or foraging on dead invertebrate carcasses in low coral cover, sand, and rubble environments. Direct negative or indirect effects of *Coris* on corals have not been observed or expected and it is more likely that *Coris* are scavengers on dead *E. mathaei* in low coral cover reefs. Juvenile *Coris* wrasses are competitively subordinate to *B. undula-*

tus in sea urchin feeding experiments, *Coris* mostly scavenge on sea urchin carcasses, but in the absence of *B. undulatus* due to fishing, *Coris* are relatively more common predators (McClanahan 2000).

The same habitat-association patterns could explain the positive association between *B. undulatus* and coral cover. While *B. undulatus* hides in coral and other crevices, there is direct observational evidence that they control sea urchin populations (McClanahan 2000, 2014). Additionally, studies where fishing has been stopped have shown that when *B. undulatus* numbers increase, sea urchin numbers and their feeding impacts on coralline algal cover decline (O'Leary & McClanahan 2010, O'Leary et al. 2012, 2014, McClanahan 2014). Consequently, while the high spatial and temporal replication of this study and the restrictive BIC criteria is likely to reduce the chances of spurious statistical associations, consistent fish-habitat associations can mistakenly imply causation. Consequently, observation and experimental results are needed to support regression analysis studies. Future tests of the proposed cascade impact will require experimental or applied management research where *B. undulatus* populations are manipulated and the long-term ecological consequences evaluated.

The implication of this and related studies is that the interaction between reef type, sea urchin associations, and the feeding behavior of *B. undulatus* produces differences in grazing sea urchins with consequences for benthic calcifiers. Calcification and reef growth is a threatened ecological service that requires management to prevent its further loss from current and projected climate disturbances (Cooper et al. 2008, De'ath et al. 2009, Tanzil et al. 2009, 2013, Kennedy et al. 2013, Silverman et al. 2014) but can vary and be less threatened depending on other factors, such as habitat and latitude (McClanahan et al. 2005, 2007a, Golbuu et al. 2007, Cantin et al. 2010, Cooper et al. 2012). The western Indian Ocean region has been influenced by temperature anomalies that have reduced coral cover in many places, but some mortality has been followed by recovery and shifts in the dominant coral taxa (McClanahan et al. 2014). In some cases, losses of coral cover are followed by increases in coralline algal cover, which may help to stabilize the calcifying community (O'Leary & McClanahan 2010).

The patterns described here indicate a food web–habitat mechanism potentially influential in the maintenance of reef calcifiers and amenable to management with some capacity to compensate for the negative effects of climate disturbances on calcification. The maintenance or protection of *B. undulatus*

populations is a species-specific management recommendation arising from this research. The study also suggests that island reefs have greater potential to promote calcification because of the interactions between reef type, *B. undulatus*, and sea urchin grazer dominance. This knowledge may be useful for planning and prioritizing reef management restrictions that favor the persistence of reef calcification. Regardless, policy and management priorities will need to consider interactions between climate and reef ecology.

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