ECOLOGY

Trophic strategy and bleaching resistance in reef-building corals

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Ocean warming increases the incidence of coral bleaching, which reduces or eliminates the nutrition corals receive from their algal symbionts, often resulting in widespread mortality. In contrast to extensive knowledge on the thermal tolerance of coral-associated symbionts, the role of the coral host in bleaching patterns across species is poorly understood. Here, we applied a Bayesian analysis of carbon and nitrogen stable isotope data to determine the trophic niche overlap between corals and their symbionts and propose benchmark values that define autotrophy, heterotrophy, and mixotrophy. The amount of overlap between coral and symbiont niche was negatively correlated with polyp size and bleaching resistance. Our results indicated that as oceans warm, autotrophic corals lose their competitive advantage and thus are the first to disappear from coral reefs.

INTRODUCTION

The delineation of trophic niche is vital for understanding the ecology and evolution of a species, as energy and nutrients derived from the diet are essential for growth and reproduction (*1*, *2*). Speciation can be driven by niche partitioning to avoid direct competition for limiting resources. Niche partitioning has been evidenced by foraging studies (behavior) and functional traits (morphology) that underpin nutrient acquisition across many taxa, including plants, crustaceans, lizards, birds, and mammals (*3*–*6*). However, for reef-building corals, defining a trophic niche across the wide diversity of species has been elusive for several reasons; corals can exploit a variety of nutritional resources, exhibit a high degree of morphological variation at the colony and polyp level, and maintain nutritional symbioses with photosynthetic dinoflagellates (also known as symbiodinian algae). For these reasons, a coral's "diet" can be highly variable, and hypotheses pertaining to diet and morphology [e.g., corals with large polyps and lower surface area–to–volume (SA:V) ratio must capture more food, and of larger size; (*7*, *8*)] are generally untested. Here, we estimated coral trophic niches by applying a Bayesian analysis to stable isotope carbon and nitrogen values from paired coral hosts and symbionts, and investigated morphological features underpinning niche separation.

The most confounding aspect of coral nutrition is symbiosis. Most reef-building corals maintain an endosymbiotic association with algae of the family Symbiodiniaceae [formerly *Symbiodinium*; (*9*)], which provide energy (carbon) and building blocks for growth (nitrogen). Of these, carbohydrates are often produced in excess of metabolic needs (*10*, *11*), while nitrogen is a growth-limiting nutrient (*12*–*15*). Symbiosis, therefore, provides pathways for resource sharing and recycling within the coral-algal holobiont: from host to symbiont through heterotrophic feeding and translocation of carbon compounds and nitrogenous wastes and from symbiont to host via direct assimilation of dissolved inorganic nitrogen and carbon (DIN and DIC) and translocation of amino acids and sugars (*16*). For this reason, corals have enjoyed a competitive advantage over other organisms in oligotrophic oceans (*13*–*15*). Limited studies of few species have determined that the extent to which corals rely on each of these resources can vary across species (*17*, *18*) and conditions (*19*–*22*).

Yet, this inherent nutritional flexibility poses a practical challenge for determining the trophic niche of the holobiont, requiring an exhaustive examination of putative resources across a continuum of nutrient pools: those accessible by the symbiont (DIC and DIN) and those by the host [dissolved and particulate organic matter (POM), including plankton; reviewed in (*13*)]. Conventional observational methods (i.e., feeding assays or gut content analyses) are therefore insufficient for estimating a coral's trophic niche without the concomitant determination of photosynthetic performance (i.e., photosynthesis to respiration ratio) and symbiotic nutritional exchanges (i.e., isotope tracer experiments). The exhaustive and time-consuming requirements of these approaches have limited research to commonly studied species [i.e., *Acropora* spp. (*15*) and *Porites* spp. (*19*, *23*)]; thus, research has yet to reveal the functional significance of morphological and physiological variation among the nearly 800 known reef-building species of coral and diverse lineages of their symbionts. This issue is compounded when considering the thousands of possible host-symbiont pairings, each of which could have a distinctive trophic niche.

Despite these challenges, determining the trophic niche of corals remains a critically important task, as evidence suggests that nutritional flexibility underpins resilience to stressors, including climate change (*21*, *24*). Observations of bleaching (whitening of corals caused by the expulsion of symbionts) have revealed consistent patterns in susceptibility across coral species that are unexplained by differences in the thermal tolerance of their symbionts. For instance, branching corals with thinner tissues bleach earlier and more extensively compared to massive or encrusting coral species with thicker tissues (*24*–*29*). These traits are the same as those postulated to be associated with nutrient acquisition [attributes that increase or decrease SA:V ratio; (*24*)]. While heterotrophy and lipid reserves improve the survivorship and recovery of bleached corals (*21*, *30*, *31*), their link to bleaching resistance is speculative (*24*), in part due to the difficulty of defining corals' trophic niche. Our inability to determine the trophic niche of corals may therefore undermine accurate predictions of the coral species that will be "winners" and "losers" under climate change

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(*27*). Here, we investigated whether our novel estimates of coral trophic niches predict relative bleaching susceptibility across species.

RESULTS AND DISCUSSION

Defining coral trophic niches with stable isotope analysis

We measured the trophic niches of seven coral genera within five scleractinian (hard or stony corals) families (Acroporidae, Agariciidae, Dendrophyllidae, Merulinidae, and Poritidae) from 23 sites across Hong Kong (table S1), by applying a Bayesian statistical model [Stable Isotope Bayesian Ellipses in R (SIBER) (*32*)] to stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values of paired coral hosts and their symbionts (table S2). The overlap between host and symbiont standard ellipse area corrected for sample size (SEA_c, a proxy for trophic niche) ranged from 94% (high degree of resource sharing) to 0% (low degree of resource sharing), indicating a gradient ranging from autotrophy to heterotrophy (Fig. 1 and table S3). There was near-complete overlap of host and symbiont isotopic niche areas in *Acropora* and *Goniopora* (94 and 82%, respectively), and the hosts and symbionts did not occupy distinct isotopic spaces (Fig. 1, A and B, and table S4), suggesting a tight link between host and symbiont nutrient sources. Conversely, three genera (*Favites*, *Platygyra*, and *Turbinaria*) had no or only a slight overlap (0 to 1%) between the host and symbiont isotopic niches and occupied distinct isotopic spaces (Fig. 1, E to G, and table S4), indicating a decoupling of host and symbiont nutrition driven by host heterotrophy. Last, *Pavona* and *Porites* displayed partial niche overlap (31 and 62%, respectively), occupying distinct isotopic spaces (Figs. 1, C and D, and table S4), indicating that these genera are mixotrophic and blend autotrophic and heterotrophic nutrition. We therefore propose the following amounts of host and symbiont isotopic niche overlap as cutoffs indicating each trophic strategy: ≥70% overlap indicates autotrophy, ≤10% indicates heterotrophy, and overlap >10 and <70% indicates mixotrophy.

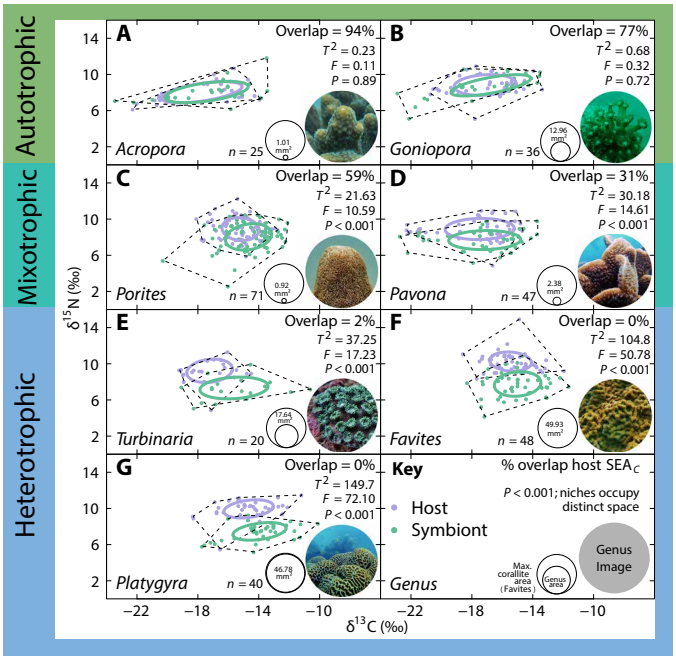

Fig. 1. SIBER analysis of paired coral host and algal symbiont stable isotope data. Across species, there is variation in the overlap of the isotopic niches of the coral (purple) and algal (green) partners indicating trophic strategies that fall on a continuum ranging from autotrophic [(**A**) *Acropora* and (**B**) *Goniopora*] to mixotrophic [(**C**) *Porites* and (**D**) *Pavona*] to heterotrophic [(**E**) *Turbinaria*, (**F**) *Favites*, and (**G**) *Platygyra*). See bottom right for a key to (A) to (G). Dotted lines represent convex hulls, solid lines represent Standard Ellipse Areas corrected for sample size (SEA_c). Significant *P* values generated from a Residual Permutation Procedure and Hotelling's T^2 test indicate genera where coral and symbiont niches occupy distinct isotopic spaces. The corallite area of each species is displayed relative to the largest corallite area included in this study (*F. abdita*; 49.9 mm^2). Photo credit: Philip D. Thompson, The University of Hong Kong.

We observed that the strongest discriminator of trophic niche overlap was the difference between host and symbiont $\delta^{15}N$, not $\delta^{13}C$, highlighting the important role of nitrogen in the coral symbiosis. In the genera with the greatest difference in host-symbiont trophic niche placement (*Favites*, *Pavona*, *Platygyra*, *Porites*, and *Turbinaria*), the host had consistently higher $\delta^{15}N$ values than the symbiont (table S5). Lower $\delta^{15}N$ values in some hosts resulted in overlap with symbiont isotopic niches, suggesting that they shared the same nitrogen source that may include nitrogen recycling within the holobiont (*13*, *15*). This reflects the limiting nature of nitrogen on reefs (*14*) and demonstrates how corals evolved symbiosis as an adaptation to oligotrophic conditions. Conversely, $\delta^{13}C$ was not consistently diagnostic of trophic strategy; significant differences between host and symbiont $\delta^{13}C$ were present in only three of the five genera (*Platygyra*, *Porites*, and *Turbinaria*) that had distinct host and symbiont isotopic niche areas (table S5). Our data support $\delta^{15}N$ as a better indicator of dietary contributions via heterotrophy than $\delta^{13}C$, although this conclusion may vary with different environmental conditions encountered within other study sites. Ultimately, SIBER includes both carbon and nitrogen isotope values, allowing for the trophic dynamics of both nutrients within the symbiosis to be investigated.

In the absence of nitrogen recycling within the coral-algal holobiont, trophic fractionation from heterotrophic feeding increases host $\delta^{15}N$ values relative to their symbionts. Specifically, if a coral were to obtain all of their nitrogen from feeding on POM, then we would expect their $\delta^{15}N$ value to be higher than that of the POM by 2.5 to 3.5‰, the amount by which $\delta^{15}N$ is typically enriched each step up the food chain (*33*, *34*). Host genera with isotopic niches distinct from those of their symbionts (i.e., *Favites*, *Platygyra*, and *Turbinaria*; table S4) fit this expectation: Host $\delta^{15}N$ values (9.2 ± 1.3‰ to 10.4 ± 1.0‰) were offset from POM (7.7 ± 1.6‰) collected from nine of the same collection sites (table S2), by approximately one trophic level (2.5 to 3.5‰). These observations do not preclude resource sharing between heterotrophic coral host and symbiont. Trophic fractionation is a result of preferential excretion of ^{14}N over ^{15}N (*33*, *34*); thus, assimilation of host nitrogenous waste would result in depleted $\delta^{15}N$ values in associated Symbiodiniaceae. However, the lack of overlap in the isotopic niches of the symbiotic partners suggests that the translocation of nitrogen from symbiont to host does not occur in these species, regardless of whether the depleted nitrogen in the symbiont originates from DIN or host waste. Conversely, genera that had a high degree of niche overlap with their symbionts had mean $\delta^{15}N$ values that were only 0.5 to 1.3‰ greater than the mean POM value, suggesting that they are on the same trophic level as their symbionts. These species are likely obtaining all of their nitrogen from either their symbionts, or there is a high amount of nitrogen recycling within the holobiont that reduces or eliminates nitrogen trophic fractionation (*35*). In either scenario, these coral hosts are more dependent on their symbionts to either obtain or conserve nitrogen, resulting in a more tightly coupled symbiosis. Alternative to overlap, the distance

between host and symbiont SEA_C centroids (means) can therefore also be used as an indicator of trophic strategy: species with <1, >2, and 1 to 2‰ centroids can be classified as autotrophic, heterotrophic, and mixotrophic respectively.

Identifying trophic morphological characteristics

Next, we used a mesocosm experiment to evaluate stable isotope variations within a captive population of corals exposed to identical ambient conditions (table S5). We observed the same pattern of variation in $\delta^{15}N$ difference between coral hosts and symbionts ($\delta^{15}N_{Host} - \delta^{15}N_{Sym}$) grown in the mesocosms (table S6) as was observed across field sites (table S2), supporting $\delta^{15}N_{Host} - \delta^{15}N_{Sym}$ as an indicator of trophic strategy. Further, we identified corallite area (table S6) as a key functional trait linked to trophic strategy (Fig. 2). Corallites are cup-like skeletal structures containing individual coral polyps, and thus, corallite area is a good proxy for polyp size (*36*). $\delta^{15}N_{Host} - \delta^{15}N_{Sym}$ values measured in eight coral species (*Acropora samoensis*, *Acropora pruinosa*, *Favites abdita*, *Goniopora lobata*, *Pavona decussata*, *Platygyra carnosus*, *Porites lobata*, and *Turbinaria peltata*) representing the seven genera collected in the field were significantly correlated with corallite area (Fig. 2B) but not with coral surface tissue thickness ($r^2 = 0.23$, $F = 1.75$, $P = 0.23$; table S7). When we merged the field and common garden observations, we found that corallite area of mesocosm corals was a significant predictor of the distance between the centroids of the $\delta^{13}C$ and $\delta^{15}N$ SEA_Cs of the host and symbiont field samples (Fig. 2A). Both smaller polyps (*7*, *18*, *37*) and thinner tissues (*27*) have previously been proposed as traits that increase the SA:V ratio of a coral, which enhances the capture of light and dissolved nutrients required for autotrophy. Further, some studies have linked larger polyps and lower SA:V with increased dependence on heterotrophy (*8*, *37*). Our results support polyp size (inferred from corallite area), but not tissue thickness, as an important trait for nutrient acquisition.

We posit that variation in polyp size is an evolutionary consequence of the trade-offs inherent to optimizing autotrophy or heterotrophy

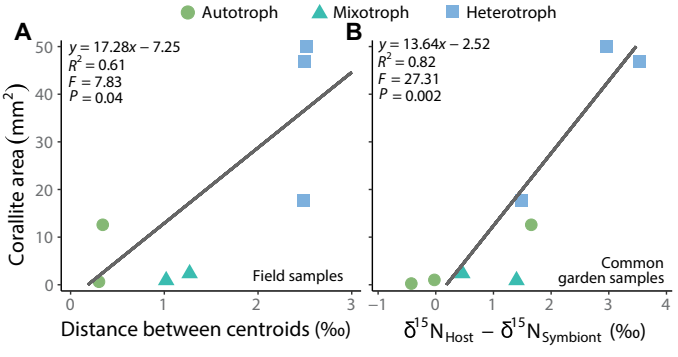

Fig. 2. Correlation between corallite area and trophic strategy. Corallite area, a proxy for polyp area, was significantly correlated with two estimates of trophic strategy: (**A**) the distance between the centroid (mean) of host and symbiont SEA_c ellipses generated with SIBER analysis and (**B**) the difference of host and symbiont $\delta^{15}N$. SEA_cs were fitted to $\delta^{15}N$ and $\delta^{13}C$ values measured in *Acropora*, *Favites*, *Goniopora*, *Pavona*, *Porites*, *Platygyra*, and *Turbinaria* collected in the field, while $\delta^{15}N_{Host} - \delta^{15}N_{Symbiont}$ values were calculated from $\delta^{15}N$ values of eight species grown in a common garden: *A. samoensis*, *A. pruinosa*, *F. abdita*, *G. lobata*, *P. decussata*, *P. lobata*, *P. carnosus*, and *T. peltata*. The colors and shapes of the points indicate trophic strategy, as determined from the isotopic niche separation of hosts and symbionts in field samples (i.e., distance between host and symbiont ellipse centroids).

(*7*). Our data support the contentious hypothesis (*19*, *37*, *38*) that small-polyped corals (i.e., *Acropora*) with high SA:V ratios are adapted to autotrophy and nutrient recycling within the holobiont, resulting in little to no difference between host and symbiont $\delta^{15}N$ and high (≥70%) overlap of host and symbiont niches (Figs. 1 and 2). Conversely, corals with larger polyps and lower SA:V ratios (*Favites* and *Platygyra*) had higher $\delta^{15}N$ values than their symbionts and, therefore, separation of the host and symbiont niches (≤10% overlap; Figs. 1 and 2), resulting from less efficient light capture and the capacity to entrain larger POM and planktonic prey. Furthermore, the only corals included in this study with branching colony morphologies (*Acropora* spp.) had the highest overlap between the host and symbiont niches (94%) and the lowest $\delta^{15}N_{Host} - \delta^{15}N_{Sym}$ (*A. pruinosa*, −0.38‰; *A. samoensis*, 0.02‰) of all the species examined. Branching is thought to further increase the SA:V ratio of the coral colony and is likely also an adaptation to optimize autotrophy (*7*, *19*). These highly productive, fast-growing branching corals are strong competitors for space in high-light environments, often outgrowing and shading massive species (*24*). However, corals that can supplement their nutrition through heterotrophy are more competitive in lower-light environments, where photosynthesis alone is not always able to meet the energetic requirements of the holobiont (*11*). Further, corals that exhibit morphological plasticity (*39*), particularly from shallow to mesophotic depths, may be altering or expanding their trophic niche to maintain a competitive advantage under different conditions. The advantage gained by heterotrophic corals, however, is contingent upon the availability and quality of particulate food, as well as suitable currents to deliver it (*40*). Despite this, when symbiosis is disrupted, so too is the advantage gained by autotrophic corals, and thus, heterotrophic corals with alternative sources of nutrition have been shown to be more likely to persist under bleaching conditions compared with those corals that rely heavily on autotrophy (*18*, *21*, *24*).

The role of trophic strategy in bleaching resistance

While bleaching recovery and resilience have been linked to heterotrophy in some coral species, the consistent patterns of bleaching resistance remain unexplained (*24*–*29*). We tested heterotrophy, as determined by stable isotope analysis (SIA), as a predictor of bleaching resistance in seven species (*A. samoensis*, *A. pruinosa*, *F. abdita*, *G. lobata*, *P. carnosus*, *P. lobata*, and *T. peltata*) by monitoring their bleaching state with standardized color cards (*41*) during a prolonged warming experiment. All seven corals host the same species of Symbiodiniaceae [*Cladocopium* sp.; previously subclade C1 (*42*)], with the exception of *P. lobata*, which hosts another congeneric species (*42*) with similar thermotolerance (*43*). This comparison isolated host identity as the only variable by limiting variation in symbiont thermotolerance. Over the course of 70 days (fig. S1), autotrophic corals bleached earlier than heterotrophic corals (Fig. 3). For example, >50% of *A. samoensis* and *A. pruinosa*, the two branching species included in the experiment, bleached [i.e., four of seven replicates dropped by ≥2 saturation/brightness categories on the color cards; (*41*)] when the accumulated heat stress reached above 4°C-weeks [degree heating weeks (DHW); Fig. 3], which is a known threshold for susceptible coral species (*44*). All but one species (*F. abdita*) bleached by 8°C-weeks, the threshold known to cause widespread bleaching and mortality in most of the corals (*44*). Bleaching susceptibility (the amount of heat stress necessary to cause bleaching in >50% of individuals) was significantly correlated with three indicators of trophic strategy: distance between host and symbiont SEA_C

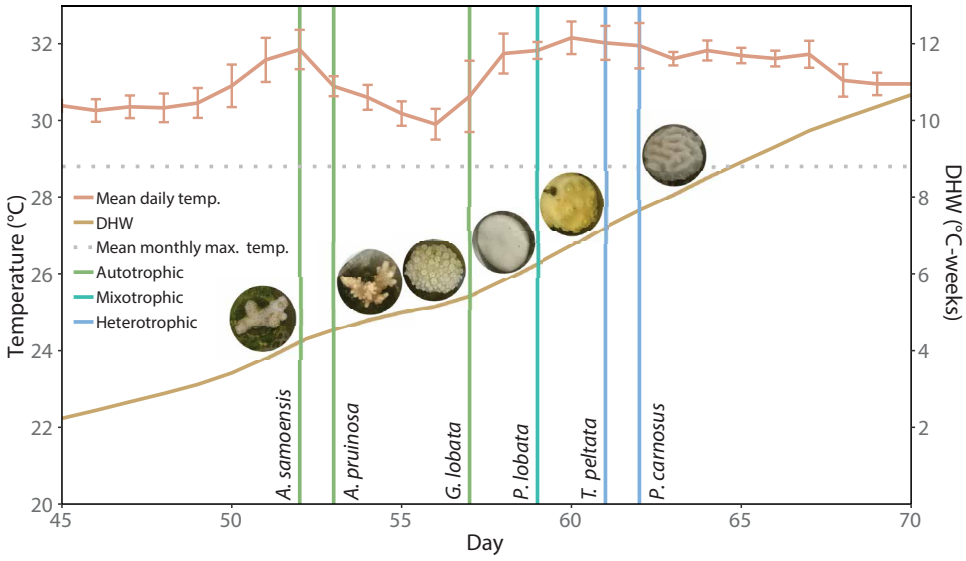

Fig. 3. Mean daily water temperature and number of DHW (degree heating weeks) from days 45 to 70 of the warming experiment. Mean daily water temperature (orange line; error bars represent SD) and number of DHW [goldenrod line; a measurement of accumulated thermal stress that incorporates both magnitude and duration; see (*44*)] from days 45 to 70 of the warming experiment. The gray dashed line indicates the maximum monthly mean [the temperature above which corals experience thermal stress (*44*)] water temperature of a Hong Kong coral community over the past 10 years. The vertical lines indicate the day when >50% of the individuals within a species bleached as determined with color cards (*41*). The vertical line color indicates the trophic strategy of each species, as determined from the isotopic niche separation of hosts and symbionts in field samples (i.e., amount of overlap between host and symbiont isotopic niches). Photo credit: Nara L. Oliveira, Universidade Estadual de Santa Cruz.

centroids measured from the field samples (Fig. 4A), proportion of host niche overlapping symbiont niche measured from the field samples (Fig. 4B), and $\delta^{15}N_{Host} - \delta^{15}N_{Sym}$ measured from the mesocosm samples (Fig. 4C).

We investigated the pertinence of our results from the mesocosm experiment to field conditions by exploring bleaching data previously reported from the field (*28*). Since SIA data were not available for these species or locations, we used corallite area (*40*–*43*) as a proxy for trophic niche, as demonstrated with our mesocosm corals (Fig. 2). We found a significant relationship between corallite area and the percentage of colonies bleached off the eastern coast of Africa during the 1997/1998 El Niño (Fig. 5), demonstrating the susceptibility of autotrophic corals and the robustness of heterotrophic corals in situ during elevated temperatures. Similarly, our data support the hypothesis that the trophic strategy of coral species explains the variation in bleaching susceptibility during an isolated warming event both in the lab and in the field, even without accounting for thermotolerance of the associated Symbiodiniaceae.

CONCLUSIONS

Decades of research on scleractinian coral nutrition and metabolism have struggled to delineate trophic niches across a diversity of species, despite this having been done for a wide range of other taxa using trait-based approaches (*3*–*6*). We demonstrated that SIA of paired coral hosts and symbionts can be used to rapidly assess the trophic niche of a coral, revealing a spectrum of trophic strategies across seven coral genera within five scleractinian families. Future studies should aim to confirm whether the patterns identified in this study hold across other coral taxa and geographic regions, where intraspecific morphology and behavior can vary. In addition, we demonstrated a trade-off of these strategies: Predominantly, autotrophic corals had an

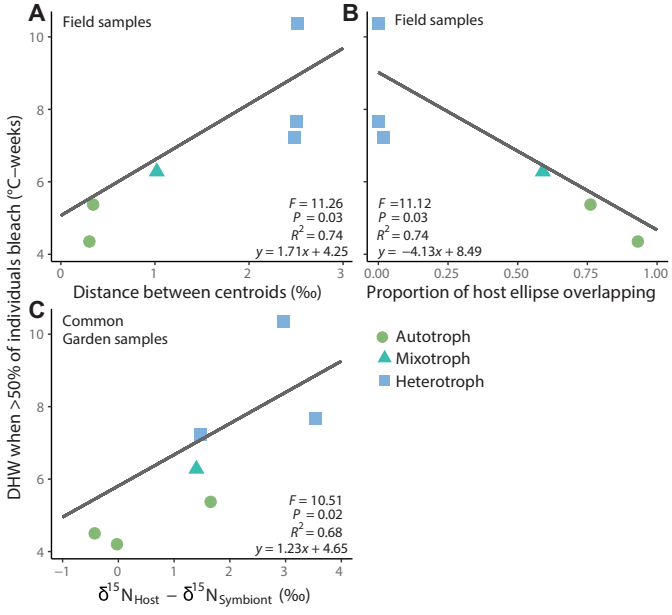

Fig. 4. Correlation between bleaching resistance and trophic strategy. Bleaching resistance of seven coral species was significantly correlated with three different estimates of trophic strategy (**A**) the distance between the centroid (mean) of host and symbiont standard ellipse areas corrected for sample size (SEA_c) generated by SIBER analysis, (**B**) the proportion of host SEA_c overlapping the symbiont SEA_c, and (**C**) the difference of host and symbiont $\delta^{15}N$. SEA_cs were fitted to $\delta^{15}N$ and $\delta^{13}C$ values measured in *Acropora*, *Favites*, *Goniopora*, *Porites*, *Platygyra*, and *Turbinaria* collected in the field while $\delta^{15}N_{Host} - \delta^{15}N_{Symbiont}$ values were calculated from $\delta^{15}N$ values of seven species grown in a common garden: *A. samoensis*, *A. pruinosa*, *F. abdita*, *G. lobata*, *P. lobata*, *P. carnosus*, and *T. peltata*. The colors and shapes of the points indicate the trophic strategy as determined from isotopic niche separation of hosts and symbionts in field samples.

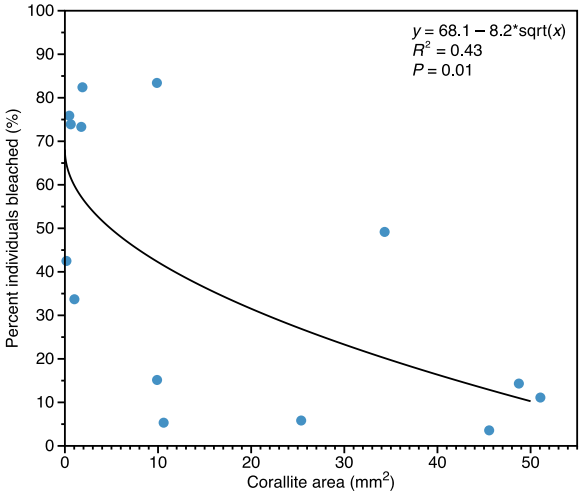

Fig. 5. Correlation between bleaching resistance and corallite area under field conditions. Despite uncontrolled field conditions, corallite area (a proxy for trophic strategy) explains 43% of the variation in bleaching susceptibility among corals off the east coast of Africa during the 1997 bleaching event (*28*). Black line represents a power function fit to the data using a square root transformation of corallite area. A power function was chosen in consideration of the upper and lower bound constraints on percentage of minimum and maximum corallite diameters used in the calculation of corallite area. Corallite diameter values were extracted from the Coral Trait Database (*51*–*54*).

advantage under ambient conditions in high-light environments, whereas heterotrophic corals were more tolerant of increasing temperatures and, therefore, are likely to be winners in the face of climate change. However, as thermal anomalies become more frequent, corals may not recover fully from one bleaching event before another begins (*45*). Future studies should aim to determine the role of heterotrophy on bleaching resistance and resilience under repeat bleaching scenarios.

The trophic strategy of corals can either be assessed relatively rapidly using SIA or estimated with corallite area and coupled with our understanding of the thermotolerance of the dominant Symbiodiniaceae to provide a complete picture of bleaching susceptibility. As humans continue to alter the ecological conditions of the planet, ecological niche theory provides a framework for understanding how ecosystems, communities, and species will respond. The tools we present for estimating the trophic niches of corals can be applied to coral communities to predict which species occupy niches that will be most affected by climate change, and broadly, we demonstrate that corals more reliant on autotrophy (i.e., *Acropora* and *Goniopora*) will lose their competitive advantage in high-light environments and are likely to be the first to disappear from reef communities. This highlights the importance of water quality in reef management and a critical trade-off; interventions focused exclusively on autotrophic coral restoration are misguided in the face of ocean warming, while heterotrophic coral communities will provide limited reef rugosity and ecosystem functioning.

MATERIALS AND METHODS

Sample collection

Between 26 September and 22 November 2013, 40 marine sites within the Hong Kong Special Administrative Region of the People's Republic of China were visited to collect coral samples for SIA. These sites were selected because they were known to support coral communities (*46*, *47*), and they were as widely distributed across Hong Kong waters as possible. At each site, between one and three fragments of 6 cm length were collected from corals of each genus present at depths of ≥5 m [in Hong Kong, corals associated with Symbiodiniaceae are typically found between 1.3- and 2.3-m depths; (*48*)]. Fragments were collected with a hammer and chisel using SCUBA, placed into individual Whirl-Paks (Nasco, USA), rinsed with deionized water, transported to the laboratory on ice, and stored at −20°C. Of the genera sampled, seven (*Acropora*, *Favites*, *Goniopora*, *Pavona*, *Platygyra*, *Porites*, and *Turbinaria*) from 23 sites (table S1) had enough total replication (≥20) for isotopic niche determination (*49*). POM was sampled from the surface of each site by filtering 1.5 liters of seawater through precombusted 47-mm glass fiber filters (pore size, 0.7 μm; Advantec GF-75, Japan). The filters with POM captured on them were folded and wrapped individually with aluminum foil, transported on ice, and stored at −20°C.

To compare species from similar environments, three to five fragments of eight coral species (*A. samoensis*, *A. pruinosa*, *F. abdita*, *G. lobata*, *P. decussata*, *P. carnosus*, *P. lobata*, and *T. peltata*) from the Swire Institute of Marine Sciences (SWIMS) mesocosm system [described in (*50*)] were used for baseline isotope and morphological measurements. The fragments had been living in common garden mesocosms for 2 to 5 years and were harvested for the current study in July 2013. The mesocosms constantly received minimally filtered seawater from the Cape d'Aguilar Marine Reserve, thus closely mimicking in situ conditions.

Corals for inclusion in an experiment to determine relative bleaching susceptibility were harvested from Bluff Island (22.325063 N, 114.354311 E) on 5 May 2017. Seven fragments of the seven species (*A. samoensis*, *A. pruinosa*, *T. peltata*, *G. lobata*, *F. abdita*, *P. lobata*, and *P. carnosus*; 56 fragments total) were collected and acclimated to mesocosm conditions for 6 days.

Laboratory analysis

Tissues of the coral samples used for isotope measurements were removed from each coral skeleton with an airbrush (Single Action Internal Mix Airbrush, Paasche, USA) loaded with deionized water. The resulting mixture of host and symbiont tissues was homogenized with a Tissue-Tearor homogenizer (model 985370, Biospec Products Inc., USA) and separated using one of two protocols. Homogenate from the SWIMS mesocosms corals was centrifuged at 700*g* for 5 min, and the supernatant was poured off and centrifuged again at 3000*g* for 5 min, after which the host fraction (supernatant) was saved, and the pellet was discarded. The symbiont pellet from the first centrifugation was resuspended in deionized water and spun twice at 10,000*g*. Homogenate from the field corals was separated using an updated protocol that improved the yield of the host fraction: The mixture was centrifuged at 1700*g* for 5 min; the host fraction (supernatant) was poured off, and the symbiont pellet was resuspended in deionized water and centrifuged again at 600*g* for 5 min. The final pellet was saved as the symbiont fraction and was freeze-dried overnight, as were the host supernatant fractions and POM filters. Each tissue sample was weighed (1.0 ± 0.2 mg), and POM was scrapped off of filters into a 4 mm × 6 mm silver capsule and acidified with direct application of 10 μl of high-performance liquid chromatography–grade 6N HCl to remove residual carbonate.

All samples were dried overnight at 60°C and combusted and analyzed on an environmental analyzer (Eurovector EA3028, Italy)

coupled with a stable isotope ratio mass spectrometer (Nu Instruments Perspective, UK) at the University of Hong Kong. The precision was better than 0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$. Of the 23 sites included in this study, only 8 had a high enough mass of filtered POM to yield isotope data (table S1).

Morphological measurements were taken from colonies of the same eight species in the SWIMS common garden mesocosms. Calipers were used to measure the maximum and minimum diameters of five corallites of each species, with the exception of *P. decussata*, for which additional corallites were measured ($n = 27$) because corallite size was more variable in this species. The corallite area was estimated from these measurements by calculating the area of an ellipse with the mean minimum and maximum corallite diameters used as the length and breadth, respectively. Tissue thickness was determined by fragmenting four to five corals of each species and using calipers to measure the depth to which tissue extended into the skeleton from the center of the corallite. Additional measurements of *F. abdita* ($n = 9$), *P. carnosus* ($n = 7$), and *P. lobata* ($n = 16$) were taken because these species had more variable tissue thicknesses.

Warming experiment

The relative bleaching susceptibility of seven of the same eight coral species detailed above (excluding *P. decussata*) was determined by incubating fragments ($n = 7$) in individual 0.5-liter flow-through microcosms (i.e., each fragment in its own microcosm; $n = 49$) placed in an outdoor water bath in ambient sunlight beneath an opaque, 3-m-high fiberglass cover that protected the mesocosms from rain and reduced light intensity to mimic the high turbidity of Hong Kong waters (*50*). The temperature of the water bath was set and maintained using three STC-1000 temperature controllers coupled to 600 W titanium heaters (Schego, Germany). Seawater was pumped from one of the SWIMS mesocosms through an array of polyvinyl chloride pipes that delivered water to the bottom of each microcosm, which were allowed to overflow into the water bath. The microcosm flow was slow enough so that an elevated temperature could be sustained but quick enough to maintain coral health (>1 ml s^{-1}, with complete water turnover at least every 9 min). The fragments were allowed to acclimate under microcosm conditions at ambient temperature (26.0° ± 0.1°C) for 2 weeks (days 1 to 14). From the start of the third week (day 15) onward, the temperature of the water bath was increased by 1°C/week until a maximum of 32°C was reached (fig. S1). Control fragments ($n = 3$) were maintained in microcosms in an ambient temperature water bath to ensure that any effects on coral health (including bleaching) were a result of the experimental treatment alone (i.e., increased temperature). To provide representative temperature measurements, we distributed HOBO pendant temperature loggers (Onset UA-002-64, USA) randomly among four microcosms in both the experimental and control setups. The density of Symbiodiniaceae was estimated every other day starting on day 8 (after 1 week of acclimation) using bleaching color cards (*41*). Bleaching was defined as a drop in two saturation/brightness categories, and a species was considered bleached when >50% (at least four of seven) of individuals were bleached. While ambient temperatures in the control treatment did increase from day 21 (27.2° ± 0.7°C) to 32 (30.3° ± 0.5°C) due to unusually warm summer temperatures, the control temperature was 28.6° ± 0.8°C for the remainder of the experiment, and only *A. pruinosa* bleached in the control treatment, as compared to bleaching observed in all but one species in the experimental treatment.

In situ bleaching resistance

To investigate the validity of the correlation between trophic strategy and bleaching resistance under field conditions, we used the bleaching responses (percentage of colonies that bleached) of 14 species (*Acropora eurystoma*, *Echinopora gemmacea*, *Favites pentagona*, *Favia favus*, *Galaxea astreata*, *Galaxea fascicularis*, *Hydnophora exesa*, *Montipora tuberculosa*, *Pavona varians*, *Platygyra daedalea*, *Pocillopora damicornis*, *Pocillopora verrucosa*, *Porites lutea*, *Porites nigrescens*) from 32 sites reported by Obura (*28*) from the eastern coast of Africa (Kenya and Madagascar) during a bleaching event that resulted from the 1997/1998 El Niño. Obura's dataset was selected because the percentages of bleached colonies were reported for each species rather than the coral community overall, corals were identified to species rather than genus allowing for more accurate morphometric estimates, and the data were reported at a time point during the bleaching event when varying susceptibility could be detected (i.e., not too early in the event when very few species had bleached and not late in the event when most or all species had bleached). The "typical" (*51*) minimum and maximum corallite diameters of each of the 14 species were extracted from the Coral Trait Database (*51*–*54*) and used to estimate corallite area by calculating the area of an ellipse with the mean minimum and maximum corallite diameters used as the length and breadth, respectively . Corallite area was used as a proxy for trophic strategy.

Statistical analysis

The isotopic niches of the host and symbiont fractions of each genus were determined by fitting an ellipse to their $\delta^{13}C$ and $\delta^{15}N$ values plotted on an isotope biplot and estimating the standard ellipse area corrected for sample size (SEA_C) of their distribution (*32*). The SEA_C contains 40% of the variation of a group and has been demonstrated to be a robust metric for comparing groups with different sample sizes above a threshold of 20 (*49*). To determine whether the relative placements of the host and symbiont niche differed, the Euclidean distance between the centroids (means) of the two was calculated, and a residual permutation procedure and Hotelling T^2 test were used to evaluate significance, with $P < 0.05$ indicating that niches occupy significantly different isotopic space (*55*).

The trophic strategy of each coral species was quantified with three parameters: (i) the amount of overlap between host and symbiont SEA_C, (ii) the distance between the centroids of the host and symbiont SEA_Cs, and (iii) the difference between host and symbiont $\delta^{15}N$ values ($\delta^{15}N_{Host} - \delta^{15}N_{Symbiont}$) of the mesocosm corals. We classified corals as autotrophic, mixotrophic, and heterotrophic based on the distance between centroids: Autotrophic species were defined as those with ≤1‰ between the centroids of host and symbiont SEA_Cs, mixotrophic species were those with >1 and <2‰ between the centroids of host and symbiont SEA_Cs, and heterotrophic species were defined as those with ≥2‰ between the centroids of host and symbiont SEA_Cs. The relationships between trophic strategy and morphological parameters (i.e., corallite area and tissue thickness), as well as bleaching susceptibility, were investigated using linear regressions (generalized linear model). The relationship between corallite area and bleaching susceptibility in the field data was investigated using a power function with a square root transformation of corallite area. A power function was chosen in consideration of the upper and lower bound constraints on percentage of minimum and maximum corallite diameters used in the calculation of corallite area. All statistical analyses were conducted using the software R version

3.5.1 (*56*), with the exception of the power function that was fit using the software JMP (Version 13, SAS Institute Inc., Cary NC, USA).

Thermal stress in the warming experiment was estimated by calculating DHW (°C-weeks), a summation of the magnitude and duration of heat stress over a rolling 6-week period (*57*). One °C-week is equivalent to 1 week spent at a temperature 1°C above the mean temperature of the warmest month [mean monthly maximum (MMM)]. Two °C-weeks is equivalent to either 1 week spent 2°C above the MMM or 2 weeks spent 1°C above the MMM. The MMM used in this experiment was determined with data collected by the Hong Kong Environmental Protection Department (*58*) from the site closest to Bluff Island (site PM11; 22.325063 N, 114.354311 E; >2 km from coral collection site), where the corals were collected. Since corals in Hong Kong typically occur between 1.3 and 2.3 m in depth (*48*), the surface temperature measurement taken at 1 m was used. Temperature data at PM11 measured monthly over the past 10 years were averaged together to determine the mean temperature of August, the warmest month of the year. For each day of the experiment, the °C-weeks of stress over the previous 6 weeks were summed to obtain the total DHW, the coral experienced at that point in time.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/6/15/eaaz5443/DC1

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