Microbial invasion of the Caribbean by an Indo-Pacific coral zooxanthella

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Human-induced environmental changes have ushered in the rapid decline of coral reef ecosystems, particularly by disrupting the symbioses between reef-building corals and their photosymbionts. However, escalating stressful conditions enable some symbionts to thrive as opportunists. We present evidence that a stress-tolerant "zooxanthella" from the Indo-Pacific Ocean, *Symbiodinium trenchii*, has rapidly spread to coral communities across the Greater Caribbean. In marked contrast to populations from the Indo-Pacific, Atlantic populations of *S. trenchii* contained exceptionally low genetic diversity, including several widespread and genetically similar clones. Colonies with this symbiont tolerate temperatures 1–2 °C higher than other host–symbiont combinations; however, calcification by hosts harboring *S. trenchii* is reduced by nearly half, compared with those harboring natives, and suggests that these new symbioses are maladapted. Unforeseen opportunism and geographical expansion by invasive mutualistic microbes could profoundly influence the response of reef coral symbioses to major environmental perturbations but may ultimately compromise ecosystem stability and function.

invasive species | climate change | reef corals | calcification | symbiosis

Biological invasions and global climate change are drastically altering the diversity, distribution, and ecology of all biota on the planet (1–4), which negatively affects human well-being (5). Although the body of literature on invasive plants and animals is voluminous, invasions by nonpathogenic microbes and their impacts on ecosystem functions are poorly documented (6). Microbial invasions are difficult to detect, especially among free-living or mutualistic species, and their introduction and proliferation into new regions proceed without recognition. These invasions may alter the composition of a host community and affect the functional capacity of ecosystems (6, 7). Additional climate warming and ecosystem degradation will likely facilitate increasing numbers of successful invasions, which may further exacerbate negative ecological impacts (8).

Global change, especially ocean warming, continues to diminish the functional importance of reef corals by reducing their productivity, biodiversity, and capacity to precipitate calcium carbonate (9). The symbiotic dinoflagellates found in reef-building corals (*Symbiodinium*) are crucial to the maintenance and photosynthetic productivity of coral reef ecosystems, thus underscoring the importance of microbes and symbioses to ecosystem viability. Anomalous episodes of warm ocean temperatures destabilize these mutualistic partnerships, resulting in mass coral "bleaching" (i.e., symbiont expulsion) and mortality over broad geographic expanses (10). Predicting the response of present day host–symbiont combinations to increasing anthropogenic warming and environmental degradation is a matter of considerable debate and involves broad speculation on whether stress-tolerant symbionts might emerge to facilitate a rapid eco-physiological response to changing conditions (11–14). However, it is unclear how symbiont replacement, or displacement (referred to as "switching" or "shuffling"), will progress in diverse

coral communities distributed across broad geographic areas over the decadal ecological timescales that are necessary to keep pace with the current rate of warming.

Research on the diversity and ecology of coral symbionts suggests that episodes of stressful warming may facilitate the spread of ecologically rare or opportunistic species (13). The severe mass bleaching and mortality of eastern Caribbean corals in 2005 corresponded with an increased prevalence and abundance of *Symbiodinium trenchii* (formerly *D1a*, or *D1-4*) (15), a species in Clade D. This group is distantly related to other lineages of *Symbiodinium* and is primarily known for occurring in animals at the margins of their environmental tolerance (15). Before, during, and after this bleaching event, *S. trenchii* spread to many coral species, especially among those ultimately showing the greatest signs of physiological trauma (i.e., bleaching). Colonies with high densities of this symbiont seemed to tolerate significant thermal stress. Indeed, photosynthetic rates of *S. trenchii* (in hospite) remain unaffected at temperatures that are typically stressful to other *Symbiodinium* spp. (16–18). When environmental conditions stabilized, however, *S. trenchii* was inexorably displaced (requiring months or years) by host-typical symbionts (13, 19). Therefore, the persistence of *S. trenchii* within a coral colony may depend on chronic, or acute, stressors.

We suspected, for several reasons, that *S. trenchii* populations in the northwestern tropical Atlantic (i.e., Greater Caribbean)

Significance

This research documents the spread of an opportunistic coral endosymbiont, *Symbiodinium trenchii*, from the Indo-Pacific into the Greater Caribbean, a region afflicted by human-related impacts including climate warming and environmental degradation. As a symbiont, it increases the resilience of photosynthetic corals to environmental perturbation but may diminish the animal's capacity to calcify and build reefs. This work exposes a critical need to better understand the consequences of microbial introductions (even mutualistic species) on ecosystem stability and function and raises questions about the long-term impact of new, but maladapted, symbioses on the productivity of reef coral communities in the Atlantic Ocean.

ECOLOGY

were not native, motivating our population genetic investigation. Indeed, detailed phylogenetic analyses are unable to distinguish *S. trenchii* in the Greater Caribbean from those in the Indo-Pacific (15). Moreover, several other host-specialized Clade D *Symbiodinium* spp. often occur with *S. trenchii* in equatorial coral communities of the Indo-Pacific (20), but *S. trenchii* is the only species of Clade D found in the Atlantic. Finally, as mentioned above, *S. trenchii* behaves opportunistically and can successfully invade the colonies of many coral species experiencing physiological stress (analogous in some ways to "disturbed habitats") (16, 21). Therefore, we tested the hypothesis that populations of Atlantic *S. trenchii* represent a recent invasion by examining interindividual genotypic diversity and divergence across the Indo-Pacific and Greater Caribbean using high-resolution microsatellite loci (22, 23).

Results

Population Genetic Diversity of *S. trenchii* in the Indo-West Pacific. Most samples of reef corals with *S. trenchii* from the eastern Indian and western Pacific Oceans contained a single multilocus genotype (MLG), or strain, and different samples usually contained a distinct MLG (Fig. 1 *A–C* and Dataset S1). About 10–20% of samples contained mixtures of genotypes and, therefore, were not included in subsequent genetic analyses. Interindividual variation among genotypes was high, and allele sizes often differed at multiple (>4–6) loci (Fig. 2 and Tables S1 and S2). Although most MLGs were discovered only once (Figs. 1 *B* and *C*), those that were found on several occasions were obtained from host animals living in the same vicinity (1–50 m apart on the same reef). Host communities on reef systems separated by as

little as 10 km contained distinct MLG assemblages of *S. trenchii* (Table 1 and Fig. 1 *B* and *C*). Moreover, populations from Indo-Pacific locations contained a high diversity of alleles, including many that were unique either to the eastern Indian or western Pacific Oceans (Table 1).

Population Genetic Diversity of *S. trenchii* in the Greater Caribbean. Atlantic populations of *S. trenchii* were highly clonal and consisted of only a few MLGs (= clonal lineages) relative to the number of samples analyzed (Table 1). Many clones were widely distributed throughout the Greater Caribbean basin, found in multiple locations separated by hundreds of kilometers (Figs. 1 *D* and *E*). The most notable of these common clones was the one genotype comprising 42% of all samples (Figs. 1*E* and 2*A*). The distribution of this single clone (genotype α) (Fig. 1*E*) spanned thousands of kilometers and was found in every Greater Caribbean location, except the Gulf of Mexico (Fig. 1 *D* and *E*). There were several other common and widely distributed clones (Fig. 1*E*), but all were genetically similar to genotype α (Fig. 2*A*) and differed from each other by just 1 or 2 loci, out of 24 (Fig. 2 *A* and *B*). The principal coordinate analysis plot (with axis 1 and axis 2 explaining 34% and 17% of variation, respectively) relates the low diversity in the Greater Caribbean, where all but a few individuals clustered tightly together, to the more genetically divergent genotypes from the Indo-West Pacific scattered across the plot (Fig. 2*A*). The low diversity in the Greater Caribbean, accompanied by noticeably fewer rare alleles (Table 1, *Supporting Information*, and Fig. S1), indicates a reduced effective population size either from a recent population bottleneck or from a founding event (24, 25). Finally, of additional significance, no alleles were restricted to the Greater Caribbean,
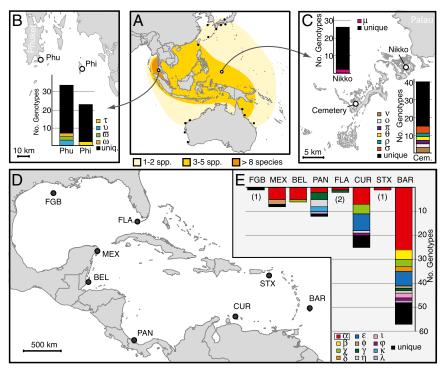

Fig. 1. The diversity and prevalence of individual multilocus genotypes from populations of the endosymbiotic dinoflagellate, *S. trenchii*, obtained from reef corals in the Indian, Pacific, and Atlantic Oceans. (*A*) Available biogeographic data indicate that the "species" diversity among stress-tolerant *Symbiodinium* clade D is centered around Southeast Asia and probably Indonesia. (*B*) Most multilocus genotypes (MLGs = strains or clones) characterized from coral colonies in the Andaman Sea were unique (black shading) and seemed restricted in their distribution to a single reef (MLGs that were found more than once are designated by a color and Greek letter). (*C*) Similarly, populations characterized from coral communities dwelling in the rock island habits of Palau were genotypically diverse with no overlap in the distribution of MLGs between sites. (*D*) Samples of *S. trenchii* were collected from locations across the Greater Caribbean, where (*E*) genotypic diversity was low and populations were composed of several geographically widespread and genetically similar clones. The most prevalent of these genotypes, "α" (red), was found at seven of eight locations separated in some cases by thousands of kilometers.
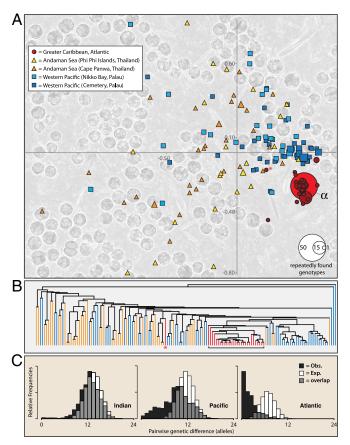
Fig. 2. Low genetic diversity and high clonality of *S. trenchii* in the Greater Caribbean relative to the Indo-Pacific. Although many genotypes occurred, analyses of allelic differences across 12 loci show that most strains differed at only one or two loci in collections from the Atlantic. (*A*) Principal coordinate analysis of MLGs shows the extent of genetic differentiation found among genotypes (the two axes describe 34% and 17% of the total variation). Symbol shape corresponds to ocean basin whereas symbol size relates to the number of times that a particular MLG was recovered. The most represented and widely distributed clone was genotype α from the Greater Caribbean. Cells of *S. trenchii* found in each host colony often comprised a distinct clonal population, or MLG (background image). (*B*) UPGMA tree showing the distance-based relationship between unique MLGs of *S. trenchii* obtained from the Indian (orange), Pacific (blue), and Atlantic (red) Oceans. The red asterisk in *A* and *B* signifies an unusual Atlantic genotype found in the Gulf of Mexico (FGB). (*C*) Pairwise comparisons of genotypes found in each of three oceans further indicate that the frequency of related individuals in the Greater Caribbean (Atlantic) is significantly higher than expected in a pan-mictic population.

meaning that all alleles found in this region were also found in populations from the Indo-Pacific (Table 1).

The unweighted pair group method with arithmetic mean (UPGMA) tree clustered all MLGs from the Greater Caribbean using short branch lengths (with the exception of one MLG from the Flower Garden Banks in the Gulf of Mexico) (Fig. 2*B*). The Atlantic cluster was embedded within the range of genetic differentiation found in the Indo-Pacific MLGs and not a distinct lineage outside of the Indo-Pacific grouping (Fig. 2*B*). The occurrence of a divergent genotype in the Flower Garden Banks southwest to the entrance of the Mississippi River suggests that independent introductions of *S. trenchii* might have occurred (signified by asterisks in Fig. 2 *A* and *B*). In contrast, most of the individuals from the Indo-Pacific fall at the end of long branches, reflecting large differences in allelic composition among MLGs from this region.

Disparity in Clonal Structure Among Populations of *S. trenchii*. For each population, we generated an expected distribution of pairwise differences under an assumed model of sexual recombination based on the number and frequency of observed alleles found (code available in *Supporting Information*). Although clonality was evident in each, populations in the Andaman Sea, Indian Ocean exhibited the broadest diversity of genotypes and minimal clonality, which was consistent with our expected distribution (Fig. 2*C*). Such patterns of genotypic diversity and disparity (number of pairwise differences between MLGs) are typical for populations of other *Symbiodinium* species ([Fig. S2](#)). The bimodal distribution in pairwise differences found for populations of *S. trenchii* from the Pacific Ocean (Palau) shows that some proportion of the population comprises similar genotypes and repeated clones (Fig. 2*C*). This distribution pattern was influenced most by samples from the southern location in Palau (Cemetery), which contained a higher proportion of clones that were found more than once (Figs. 1*C* and 2*A*). The population examined from the Greater Caribbean exhibited the highest degree of clonality and the lowest mean in pairwise differences. The distribution of pairwise differences for this population had the greatest departure from the expected (Fig. 2*C*).

Photosynthesis and Instantaneous Calcification Rates in Corals with Different *Symbiodinium* spp. The identity of the resident *Symbiodinium* spp. in colonies of the dominant reef builder, *Orbicella faveolata,* did not seem to significantly affect rates of photosynthesis over a broad range of irradiances (Fig. 3 *A* and *B*, [Fig. S3](#), and [Table S3](#)). Maximum photosynthesis (P_{max}) values, inferred from rates of oxygen evolution, for *S. trenchii* (2.8 ± 0.29 SE μmol O_2 cm^{-2}·h^{-1}) fall well within the range and is not significantly different in a pairwise *t* test from values measured for the three other *Symbiodinium* spp. associated with *O. faveolata* (Fig. 3*B*; *P* values listed on [Table S3](#)). This similarity suggests that photosynthetic rates for *S. trenchii* in hospite are similar to the *Symbiodinium* spp. normally found with *O. faveolata* and that, therefore, it can generate similar amounts of fixed carbon.

However, significant differences in instantaneous calcification rates (up to 50%), measured at temperatures ranging between 24 °C and 32 °C, were observed in colonies dominated by *S. trenchii* (Fig. 3*C* and [Table S4](#)). The dichotomy between photosynthesis and calcification by *S. trenchii* symbioses suggests that, whereas *S. trenchii* may assimilate carbon at rates similar to other symbionts, it probably does not contribute the same benefits (e.g., translocated organic carbon) to its host. A wide variance was observed in calcification rates measured from colony to colony, which may be attributed to genotypic differences between host individuals and symbiont clones. In pairwise comparisons, instantaneous calcification rates in hosts with *Symbiodinium A3* and *B17* were significantly higher than colonies with *S. trenchii* (*Supporting Information* and [Table S4](#)). However, no significance difference was observed between colonies with *C7* and *S. trenchii* across the range of temperatures investigated (Fig. 3*C* and [Table S4](#)). Calcification rates in corals with *C7* were also not significantly different from those with *A3* and *B17*. *Symbiodinium C7* is a low-light adapted species, and colonies with this symbiont may perform better under lower irradiances relative to these other partner combinations. Pooled comparisons, whereby the rates of the native symbioses (*A3*, *B17*, and *C7*) were compared with *S. trenchii* alone, show that colonies with *S. trenchii* calcify at a significantly lower rate than do colonies with native symbiont species (*P* = 0.0015).

Discussion

Invasion of an Alien Endosymbiont. The concordance of these population genetic data with phylogenetic, biogeographic, and ecological evidence compels us to conclude that *S. trenchii* was introduced into the Greater Caribbean by human-related

Table 1. Summary statistics by location, including number of colonies sampled, number of host taxa (genera) sampled, number of unique MLGs of *S. trenchii*, clonal richness (R), number of private alleles, information index (I), and observed (H_o) and expected (H_e) heterozygosity

Location	No. of samples	No. of host taxa	Unique MLGs	Clonal richness (R)	Private alleles	Information index (I)	Observed (H_o)	Expected (H_e)
Greater Caribbean	112	8	29	0.25	0	0.70 (0.15)	0.65 (0.13)	0.40 (0.08)
Indian Ocean (Thailand)	57	22	52	0.91	16	1.42 (0.21)	0.76 (0.06)	0.66 (0.05)
Pacific (Palau)	76	29	66	0.87	16	1.24 (0.20)	0.78 (0.08)	0.59 (0.06)

Numbers in parenthesis represent the SE for a particular statistic.

activities (possibly multiple times and as recently as several decades ago). *S. trenchii* is part of an adaptive radiation of clade D centered in the Indo-West Pacific proposed to have occurred during the Pleistocene, which produced many genetically and ecologically distinct (i.e., host-specialized) species (20). Consistent with this epoch timeline, the high frequency of rare alleles and high genotypic diversity in populations of *S. trenchii* from the Indo-Pacific indicate a temporal existence lasting hundreds of thousands to millions of years (Table 1 and Fig. 2 *A* and *B*) (24, 25). Other members of this group, including *Symbiodinium "glynni"* (nomen nudum = type *D1*), also exhibit high allelic and genotypic diversity in the Indo-Pacific (20, 22) (Fig. S2D).

The widespread clonality exhibited by *S. trenchii* across the entire Western Atlantic is highly unusual in light of population genetic evidence from other *Symbiodinium* spp. (Fig. S2), and not merely a characteristic of *Symbiodinium* populations from the Greater Caribbean region. Diversity (allele and MLGs) in these *S. trenchii* populations was a fraction of what was recovered from minimal host sampling over small areas of Indo-Pacific reefs (less than 50 m²) (Fig. 1). It could be argued that the low genetic diversity in the Atlantic may have arisen from the recent expansion of a small, resident population that was subjected to a severe bottleneck in response to regional environmental degradation (26, 27). However, populations recovering from acute natural selection and reduction in population size should retain relatively high amounts of neutral allelic diversity (28). Additionally, the emergence from one small native population does not account for the lack of alleles unique to the Atlantic, which should exist in a population isolated for millions of years. The most parsimonious explanation is that *S. trenchii* was introduced to the Greater Caribbean in recent decades from the Indo-Pacific and has rapidly proliferated over the entire region.

S. trenchii possesses many of the physiological and ecological characteristics commonly attributed to successful biological invaders

(6). It is common as a host–generalist in a broad diversity of stony coral taxa living in warm, turbid, low-pH Indo-Pacific habitats (20). Furthermore, populations of this *Symbiodinium* exhibit high genetic connectivity over thousands of kilometers (15). *S. trenchii*, therefore, is predisposed for ecological opportunism, especially during times of severe stress, or in coral colonies persisting in marginal environments.

Environmental instability brought on by global climate change favors the successful invasion of species with physiological or life history traits that incline them to respond opportunistically (1, 8). The coral reef ecosystems of the Greater Caribbean are among the most impacted in the world from warming climate, elevated $p\mathrm{CO_2}$, overfishing, and pollution (27). The rate of climate warming and large-scale environmental degradation in recent decades may have conditioned coral communities to opportunistic invasion by *S. trenchii*. Several species of symbiotic cnidarians have been introduced to the Greater Caribbean from the Indo-Pacific, yet there is no evidence that the *Symbiodinium* spp. they carried have become established in native hosts (29, 30). Similarly, the brown sea anemone, *Exaiptasia* (= *Aiptasia*), has spread successfully via human transport to locations around the Indo-Pacific (31). However, its symbiont, *Symbiodinium minutum*, while continually released to the new environments where this animal now persists, does not seem to be compatible with Indo-Pacific cnidarians (32).

Marine pathogens and introduced species have taken only a few years to disperse across the Greater Caribbean (33, 34), supporting the feasibility that a successfully introduced *Symbiodinium* could spread rapidly. The earliest introductions may have occurred at southern Caribbean ports (Panama, Barbados, and Curaçao) where populations of *S. trenchii* possess greater genotypic diversity, relative to other Greater Caribbean locations (Fig. 1E). The first documentation of this species in the Atlantic Ocean Basin was from Panama in the mid-to-late 1990s (21, 35). Microorganisms, including dinoflagellates, are transported
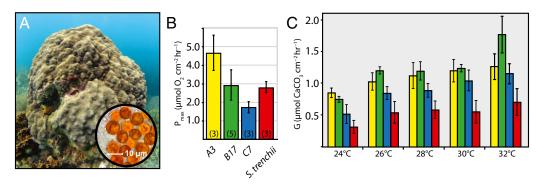

Fig. 3. Comparison of photosynthetic rates and instantaneous calcification among different coral-*Symbiodinium* combinations. (*A*) In the Greater Caribbean, *S. trenchii* associates with reef building colonies of *Orbicella* spp. living in warm and/or turbid environments, or in colonies recovered from episodes of severe bleaching (photo by Dustin Kemp). (*Inset*) Magnified *Symbiodinium* that measure about 8–12 μm in cell diameter. (*B*) In hospite *S. trenchii* photosynthesizes (P_{max}) at rates statistically indistinguishable from host–typical symbionts (undescribed species *A3*, *B17*, and *C7*) (Table S3) but (*C*) can significantly reduce rates of coral calcification measured over a broad range of temperatures. Calcification rates (under an irradiance of ~400 μmol quanta m⁻²·s⁻¹) in colonies with *S. trenchii* were statistically different (up to 50% less) than colonies with *A3* and *B17* at all temperatures (Table S4 and Fig. S4). All error bars were drawn as ± SE.

globally through the ballast water of cargo ships (36), and shipping traffic through the Panama Canal alone may be the source of this introduction. Recent Caribbean-wide surveys have detected *S. trenchii* at background concentrations in numerous coral genera (37–39), and, as environmental conditions worsen, its prevalence and persistence may increase, especially in corals that are the most sensitive to stress (13, 16).

Under stressful conditions *S. trenchii* can displace native symbiont populations and dominate a host colony for periods of time lasting a few years, or more (13, 19). It remains unknown what biotic or abiotic factors ultimately drive this competitive outcome. When native symbiont populations decline in hospite during coral bleaching, increases in inorganic nitrogen from partial tissue necrosis may promote the proliferation of low abundance background populations of *S. trenchii* (40). Therefore, it may be a better competitor when inorganic nitrogen concentrations are high (41). Conversely, its resilience to thermal stress may allow it to assimilate available nitrogen when other dominant symbiont species have physiologically lost this capacity, leading to increased proliferation of this species while other symbionts decline.

Ecosystem Implications. The long-term effect of a nonnative symbiont on native coral communities may have significant consequences (42). The introduction of *S. trenchii* to a distinct Atlantic fauna with no coevolutionary history generates associations that are probably suboptimal (i.e., maladapted). Although colonies with this symbiont may cope with increasingly unstable environmental conditions, significant physiological trade-offs may persist that diminish functional performance (43–47). Indeed, our measurements showed that calcification rates were affected in colonies of *Orbicella* harboring *S. trenchii* in comparison with native *Symbiodinium* spp. (when subjected to the environmental conditions of our experiment).

Coral reef accretion requires positive carbonate budgets in which constructive processes, mainly by coral calcification, are larger than the destructive processes of physical, chemical, or biological erosion (48). Some heat-tolerant symbionts have depressed rates of CO_2 fixation (44) and may limit the relative amount of photosynthates translocated to the host, which are necessary for calcification (49). Our P_{max} and calcification data indicate that *S. trenchii* may fix amounts of carbon similar to native symbionts (Fig. 3B) but retain a larger portion of these photosynthetic products for its own use. Reduced nutrient translocation in symbioses with *S. trenchii* would ultimately deprive the host of energy and therefore limit maximum rates of calcification. If extrapolated across large numbers of coral colonies, severe reductions in calcification may be sufficient to influence a coral's ability to compete successfully for space and ultimately affect reef growth (43, 50). However, additional investigations are needed to determine whether the presence of *S. trenchii* also imposes limitations in calcification when occurring in other species of Caribbean coral.

The establishment of *S. trenchii* in the Greater Caribbean highlights a critical need to better understand the consequences of microbial introductions on ecosystem stability and function (6). The responses of coral–dinoflagellate symbioses to climate change are often discussed from the standpoint of the host controlling its partnerships with thermally tolerant symbionts. The behavior of *S. trenchii* counters such host-centric perspectives by indicating that ecological opportunism and the range expansion by only a few, or one, symbiont species can drive the dynamic response of reef coral symbioses to climate change. These de novo mutualisms open another dimension of research into the functional ecology and evolutionary genetics of coral–dinoflagellate symbioses (51). The ecological opportunism of *S. trenchii*, for better or worse, will likely affect the regional response of Atlantic coral communities to continued ocean warming.

Materials and Methods

Sample Collections. Samples of *S. trenchii* (initially called type *D1a*, or *D1-4*) (15) analyzed in this study were originally obtained during large regional investigations of *Symbiodinium* diversity in the Atlantic (e.g., ref. 52) (Dataset S1), the eastern Indian Ocean, and the western Pacific Ocean (e.g., ref. 20). Small specimens obtained from Cnidarians (mostly scleractinians) were collected by self-contained underwater breathing apparatus (SCUBA) from reefs at eight locations around the Greater Caribbean and included Barbados, Belize, Curaçao, Florida Keys, Flower Garden Banks, Mexico, Panama and St. Croix. *S. trenchii* was also obtained from two locations in the eastern Indian Ocean (Andaman Sea, Thailand) and two locations in the western Pacific Ocean (Palau) (Fig. 1 B and C). Small (1–2 cm²) fragments with tissue were preserved in either a high salt, 20% DMSO buffer (53) or 95% ethanol and stored at −20 °C until DNA extraction. Collection totals and range of dates for each location are as follows: Greater Caribbean (GC; n = 112, recovered from the screening of over 1,500 samples) from 1999 to 2013, Andaman Sea in the Indian Ocean (IND; n = 57) in 2007, and Palau in the west Pacific (PAC; n = 76) in 2009 (Dataset S1).

Genetic and Physiological Analyses. Additional methods, along with supporting tables, figures, and access to source codes, are available in *Supporting Information*.

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ECOLOGY

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