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*Review Article*

# Clade D *Symbiodinium* in Scleractinian Corals: A "Nugget" of Hope, a Selfish Opportunist, an Ominous Sign, or All of the Above?

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Clade D *Symbiodinium* are thermally tolerant coral endosymbionts that confer resistance to elevated sea surface temperature and bleaching to the host. The union between corals and clade D is thus important to management and coral conservation. Here, we review the diversity and biogeography of clade D *Symbiodinium*, factors linked to increasing abundances of clade D, and the benefits and drawbacks of associating with clade D for corals. We identify clade D *Symbiodinium* as uncommon pandemically distributed generalists found in higher abundances on reefs exposed to challenging sea surface temperatures and local stressors or with a history of bleaching. This distribution suggests that clade D *Symbiodinium* are mostly opportunistic endosymbionts, whereby they outcompete and replace optimal symbionts in health-compromised corals. We conclude by identifying research gaps that limit our understanding of the adaptive role clade D *Symbiodinium* play in corals and discuss the utility of monitoring clade D *Symbiodinium* as indicators of habitat degradation in coral reef ecosystems.

## 1. Introduction

Scleractinian corals form obligate endosymbioses with unicellular photosynthetic dinoflagellates in the genus *Symbiodinium* [1, 2]. The *Symbiodinium* translocates newly fixed organic carbon to the host coral and, in return, receive inorganic waste metabolites from host respiration and an environment free from predators [3]. This mutually beneficial symbiosis contributes to the productivity of coral reef ecosystems, promotes deposition of calcium carbonate skeletons, and creates the structural framework that protects coastlines and serves as habitat for the extraordinary biodiversity found in coral reef ecosystems [4]. A consortium of bacteria, archaea, viruses, and fungi also forms close associations with corals and contributes collectively to the overall function and environmental thresholds of corals (e.g., [5–8]). These coral-microorganism communities are collectively described as the coral holobiont.

Climate change and other anthropogenic impacts have already damaged an estimated 30% of the world's coral reefs, and further declines in the integrity of coral reef ecosystems are projected for the near future [9]. A suite of often synergistic factors are contributing to the declining health of corals including global stressors such as elevated sea water temperatures and ocean acidification and local stressors like increased nutrient loading, sedimentation, and pollution [9]. The best documented and arguably most acutely damaging environmental conditions for corals are anomalously high surface seawater temperatures (SSTs) [10, 11]. Corals live close to their thermal maxima, and when ocean temperatures elevate beyond a normal range for a given region, the thermal tolerance of the coral-*Symbiodinium* symbiosis can be exceeded [12, 13]. This deleteriously impacts the functional integration of the symbiosis, and the dinoflagellates are expelled or lost from the host tissues [14]. The breakdown of the symbiosis

reflects in a paling of coral tissues, the phenomenon known as coral bleaching [13]. Depending on the duration and severity of the environmental disturbance and the extent of bleaching, a coral will either be repopulated with *Symbiodinium* and return to its characteristic brown coloration or die. However, corals that survive thermal challenges show a reduction in reproductive capacity, exhibit reduced growth rates and increased susceptibility to disease [15]. The thermal challenges for corals are predicted to intensify with climate change and will be compounded by ocean acidification [16, 17]. The latter, caused by the dissolution of atmospheric carbon dioxide into seawater, has the potential to reduce or inhibit calcification completely, effects that have profound implications for corals and reef accretion. In addition to these global stressors, local stressors such as sedimentation and pollution from coastal runoff, overfishing, bacterial infection, and salinity changes all impact coral health and is contributing to the deterioration of reef integrity worldwide [18–20].

Given the serious threat that climate change and local anthropogenic impacts pose to the world's coral reefs [9], management and conservation efforts are currently focused on understanding and monitoring the responses of coral reef ecosystems to these stressors with the ultimate goal of developing action strategies aimed at mitigating their damaging effects on coral health (e.g., [21]). The monitoring clearly shows that corals exhibit variation in their responses to stress with some species, and individuals within species, being more resistant (e.g., [22]). One factor that contributes to this resistance is the genetic identity of the endosymbionts hosted by a coral. Members of the genus *Symbiodinium* show variation in physiological characteristics that contribute to the overall performance of the coral holobiont [23]. For example, *Symbiodinium* clade D is thermally tolerant and increases the resistance of corals that harbor them to elevated SSTs [24, 25]. Given this context, it is not surprising that the jurisdiction-wide NOAA Coral Reef Research Plan highlights "the potential for coral reefs to adapt to future bleaching events through changes in clades of zooxanthellae in individual species and shifts in taxonomic composition of symbiotic organisms," as a key research area with the potential to contribute to the management objective of "minimizing the effects of climate change on coral reef ecosystems" [26]. The "changes in clades of zooxanthellae" described in the plan refers specifically to the ability of corals to acquire *Symbiodinium* clade D. Here, we synthesize the literature pertaining to clade D *Symbiodinium* to provide context for this research agenda. Specifically, we organize the discussion around six key themes: (1) the diversity and distribution of clade D *Symbiodinium*; (2) coral species known to associate with clade D; (3) reef environments and abiotic factors linked with increased abundances of clade D; (4) benefits and drawbacks of harboring clade D for corals; (5) research gaps limiting our understanding of the adaptive role that clade D *Symbiodinium* play in corals; and (6) advantages of using clade D *Symbiodinium* as a tool for monitoring coral reefs.

## 2. The Diversity and Distribution of Clade D *Symbiodinium*

*Symbiodinium* diversity is generally characterized using molecular markers because there is very little morphological differentiation within the genus [27]. Given their morphological uniformity, it is perhaps surprising that genetic distances among members of the genus *Symbiodinium* are comparable to different taxonomic orders in free-living dinoflagellate groups [28, 29]. *Symbiodinium* is currently divided into 9 divergent phylogenetic clades, named A-I [30], with each containing subclade genetic sequence types distinguished using faster evolving gene markers. In order to further resolve the taxonomy of *Symbiodinium* to species, molecular markers that clearly resolve genotypes correlated to biogeography, host, environment, or physiology need to be employed and, ideally, the putative species available in culture. The latter has proven very difficult for *Symbiodinium*, and the majority of diversity remains unculturable to date. In addition, the Internal Transcribed Spacer 2 (ITS2), a molecular marker frequently used to distinguish subclade sequence types for *Symbiodinium* is multicopy and intragenomically variable, and there are two major interpretational problems that stem from these characteristics. First, more than one ITS2 sequence can be found in an individual *Symbiodinium* cell and the differences among sequence types within a cell are often greater within a cell than between different *Symbiodinium* cells. As such, the relationship between individual *Symbiodinium* cells and the ITS2 sequences is not 1 : 1 [31, 32]. Second, a particular ITS2 sequence may be dominant (or abundant) in one *Symbiodinium* cell but represent a minor (or rare) sequence type in another *Symbiodinium* cell. These two issues combine to make it difficult to quantify the number of individual *Symbiodinium* cells present in a sample based on retrieval of ITS2 sequences alone and hence impossible to accurately delineate the number of species present.

*Symbiodinium* clade D is considered to be a relatively rare but pandemically distributed endosymbiont of corals (Figure 1), generally representing less than 10% of the endosymbiotic community in the host population (see Section 4 for exceptions) [33]. This contrasts with *Symbiodinium* clade C, which is the dominant lineage in corals throughout the Great Barrier Reef and other Pacific coral reef ecosystems [32, 34–38] and is codominant with clade B in corals from the Atlantic [35, 39]. Consistent with their very different abundances on reefs, clade C has over 100 subclade sequence types (based on the ITS2) and clade D just 10 [33, 34, 40]. In this paper we consider all available data on clade D *Symbiodinium* and discuss these data at the level of clade rather than the individual subclade sequence types. Our rationale for this approach is twofold: first, the different genetic markers used to identify clade D *Symbiodinium* subclade sequence types provide different levels of taxonomic resolution, making it difficult to identify parallels among studies (e.g., partial large ribosomal subunit DNA [41], versus the internal transcribed spacer 1 [42], versus ITS2 [33], versus cytochrome oxidase B [43]); second, no study has yet examined whether different clade D subclade

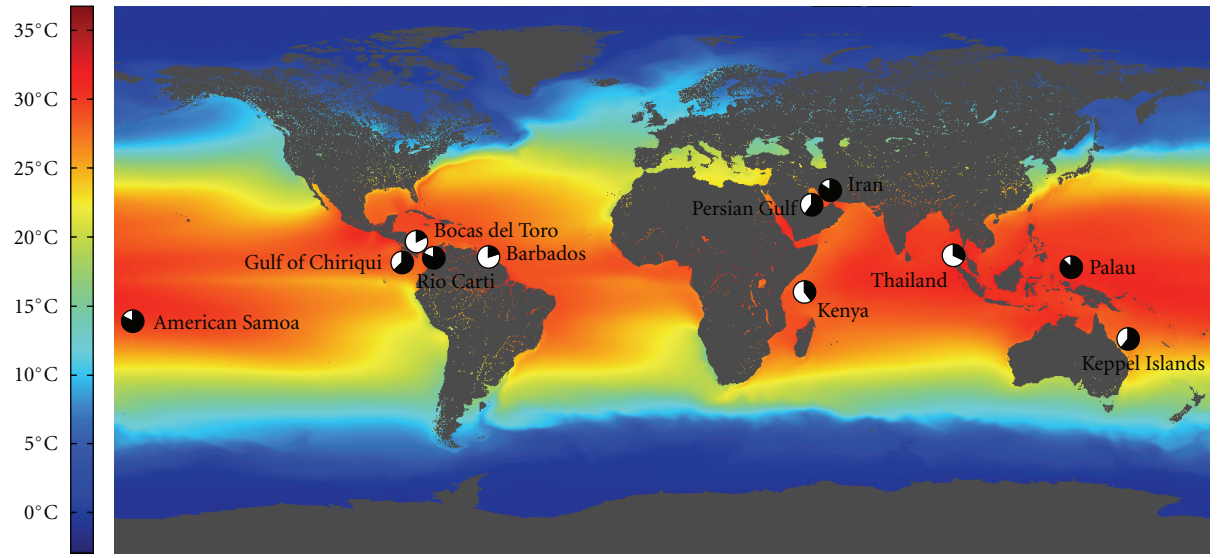


Figure 1: Global map showing mean sea surface temperatures between 1985–2005 from CoRTAD [47]. Black and white sections of pie charts represent the frequency of clade D and C, respectively, from the corresponding studies in Table 1.

sequence types exhibit differences in basic physiology or in their capacity to interact with coral hosts. Therefore, even though some studies have provided preliminary evidence for within clade D delineation (e.g., [33]), the ecological significance of these designated subclade D *Symbiodinium* is unknown.

## 3. Species of Coral Known to Associate with Clade D *Symbiodinium*

Clade D *Symbiodinium* are found in endosymbioses with a diverse range of coral species that encompass a variety of characteristics common in corals. For example, hosts include fast-growing branching coral species (e.g., *Acropora, Stylophora and Pocillopora*), slow-growing massive species (e.g., *Montastraea*), encrusting forms (e.g., *Montipora*) and solitary corals (e.g., *Fungia*) [25, 37, 41, 44–46]. Depending on the coral host, clade D *Symbiodinium* can be acquired vertically (passed from parent coral to offspring, e.g., *Pocillopora*, *Stylophora* and *Montipora*) or horizontally (acquired from the ocean environment, e.g., *Montastraea*, *Acropora* and *Fungia*). It is important to note that clade D *Symbiodinium* also associate with a taxonomically diverse group of other organisms including foraminiferans, soft coral, bivalves, and sponges [27]. Given their capacity to interact with such a broad array of hosts, Clade D *Symbiodinium* are described as generalist endosymbionts.

Although clade D *Symbiodinium* are considered relatively rare in comparison to clades B or C, they are the dominant endosymbionts in some host species, such as *Pocillopora* from the Gulf of California (Eastern Pacific), *Montipora patula* from Johnston atoll (Central Pacific), and *Oulastrea crispata* from Japan (Western Pacific) [32, 46, 48]. Interestingly, some of these hosts exclusively associate with other clades of *Symbiodinium* at different locations. For example, *Pocillopora* harbors clade C in the southern Great Barrier Reef [49, 50]. Further, the endosymbiotic communities of juvenile *Acropora tenuis* are dominated by clade D *Symbiodinium*, but the dominance hierarchy in these endosymbiont communities shifts during development to ones dominated by clade C *Symbiodinium* in adults [51]. The reason why corals show differences in the composition of their endosymbiotic communities among locations or with ontogeny of the host is not clearly understood but is attributed to some combination of local adaptation of the holobionts to abiotic conditions [27], delayed onset of symbiont specificity in juveniles [51] and, genetic radiation by both the host and *Symbiodinium* [34].

## 4. Reef Environments and Abiotic Factors Linked with Increased Abundances of Clade D *Symbiodinium*

Clade D *Symbiodinium* are present in higher abundances on some reefs than others, and these are often reefs exposed to relatively high levels of SSTs or local stressors such as sedimentation or reefs with a history of coral bleaching (Table 1, Figure 1). For example, clade D *Symbiodinium* are the most common endosymbionts in the Persian Gulf, where they associate with a wide range of coral genera [41, 52]. Corals in this region typically experience ocean temperatures exceeding 33°C [41], representing some of the warmest waters where corals are found in the world. This region also experiences high salinities (up to 40 ppt) and water temperatures as cool as 14°C [53, 54]. Clade D *Symbiodinium* are also more abundant in Acroporid corals from back-reef environments in American Samoa, where the SSTs reach higher maximum temperatures than the neighboring fore-reef environments, where *Acropora* primarily hosts clade C [43]. Likewise in Palau, corals in the lagoonal environment of Heliofungia Lake experience higher SSTs than the neighboring fringing and platform reefs and

Table 1: Distribution and factors associated with relatively high abundances of *Symbiodinium* clade D in corals.

| Location | Host corals | Factors | References |
|---|---|---|---|
| American Samoa | *Acropora* | High Temperature | [43] |
| Thailand | *Fungia* | High temperature (mean, ≈29 –32°C) | [33] |
| | *Platygyra* | High turbidity (≈0.4 –0.6 mg/m$^2$ Chl a) | |
| | *Symphyllia* | Coastal habitat | |
| | *Favites* | | |
| | *Goniastrea* | | |
| | *Pavona* | | |
| | *Goniopora* | | |
| | *Montipora* | | |
| | *Oulastrea* | | |
| | *Pocillopora* | | |
| Barbados | *Agaricia* | Bleaching | [56] |
| | *Montastraea* | | |
| Gulf of Chiriqui | *Pocillopora* | Bleaching | [41] |
| Kenya | *Acropora* | Bleaching | [41] |
| | *Astreopora* | | |
| | *Pocillopora* | | |
| | *Stylophora* | | |
| | *Galaxea* | | |
| | *Porites* | | |
| | *Coeloseris* | | |
| | *Pavona* | | |
| | *Hydnophora* | | |
| | *Echinopora* | | |
| | *Favia* | | |
| | *Goniastrea* | | |
| | *Leptoria* | | |
| | *Montastraea* | | |
| | *Platygyra* | | |
| Keppel Islands | *Acropora* | Bleaching | [42] |
| Palau | *Hydnophora* | High temperature (mean, 28.5–31.8°C) | [45] |
| | *Echinophyllia* | Lagoonal habitat | |
| | *Echinopora* | | |
| | *Favites* | | |
| | *Goniastrea* | | |
| | *Montastrea* | | |
| | *Fungia* | | |
| | *Heliofungia* | | |
| | *Merulina* | | |
| | *Lobophyllia* | | |
| | *Pectinia* | | |
| | *Porites* | | |
| Boca del Toro | *Montastraea* | High turbidity (sedimentation) | [55] |
| | | Coastal habitat | |
| Rio Carti | *Montastraea* | Coastal habitat (sedimentation) | [44] |

Table 1: Continued.

| Location | Host corals | Factors | References |
|---|---|---|---|
| Persian Gulf | *Acropora* | High temperature (summer >33°C) | [41] |
| | *Pocillopora* | Bleaching (temperature >38°C) | |
| | *Goniopora* | | |
| | *Pavona* | | |
| | *Oxypora* | | |
| | *Acanthastrea* | | |
| | *Cyphastrea* | | |
| | *Favites* | | |
| | *Platygyra* | | |
| | *Turbinaria* | | |
| Iran (Persian Gulf) | *Acropora* | High temperature (summer, mean: 33°C, max: 33°C) | [52] |
| | *Cyphastrea* | Low temperature (winter, 13.2°C) | |
| | *Favia* | | |
| | *Turbinaria* | | |
| | *Pavona* | | |
| | *Platygyra* | | |
| | *Porites* | | |
| | *Psammocora* | | |

exclusively harbor clade D *Symbiodinium* [45]. Further, a diverse range of coral species host clade D *Symbiodinium* in coastal reef habitats in Thailand that experience higher levels of sedimentation, and warmer waters than offshore reefs [33]. In addition, the coral genus *Montastraea* associates with clade D *Symbiodinium* on reefs exposed to high levels of sedimentation where thermal stress is absent [44, 55]. Collectively, these data confirm that clade D *Symbiodinium* associate with a diverse range of coral species found in conditions that range from thermally challenging to polluted.

Mass coral bleaching events are often driven by higher than normal SSTs. For corals that survive the stress event, bleaching, or the loss of endosymbionts from host tissues, provides a potential opportunity for the host to modify its endosymbiotic communities by acquiring new *Symbiodinium* during recovery that are better optimized to the environment [57]. Given the range of challenging environments that clade D *Symbiodinium* are found in naturally, the repopulation of recovering bleached coral hosts with clade D *Symbiodinium* is thought to represent a survival mechanism or a "nugget of hope" for corals facing ocean warming with climate change [25]. Several studies have shown increases in the abundance of clade D *Symbiodinium* in corals following bleaching events (Table 1, Figure 1) [41, 42, 56]. For example, Baker et al. [41] showed a higher incidence of clade D in a diversity of hosts sampled from reefs with a history of bleaching. In more targeted studies aimed at understanding the timing of changes in *Symbiodinium* communities, a shift in the dominance hierarchy from clade C to D in endosymbiotic communities in *Acropora millepora* occurred within 3 months of a bleaching event [42] but leading up to bleaching as ocean temperatures increased in *Montastraea annularis* [56]. In contrast to these reports of change, a number of studies have also shown that the endosymbiotic communities of corals exposed to episodes of thermal stress remain stable and dominated by *Symbiodinium* belonging to clades other than D [58–61]. For example, clade D *Symbiodinium* have not yet been found in Fiji, a location that has had frequent thermal stress anomalies [43], and clade D is rare on offshore reefs in the Great Barrier Reef, a region where there have been a number of coral bleaching events [35, 36, 50]. The detection of clade D *Symbiodinium* in recovering bleached corals is, however, complicated by the fact that the endosymbiotic communities in these corals often revert to their original dominant *Symbiodinium* at some point during recovery (over 2-3 years postbleaching) [59]. Recent evidence suggests that these shifts in dominance hierarchy reflect changes in the relative abundance of endosymbiotic types found in the host colony (shuffling) rather than the acquisition of clade D *Symbiodinium* from the water column or sediments [25, 56]. The latter infers that only those corals that initially harbor cryptic clade D in their *Symbiodinium* community have the capacity to become dominated by them during or after a stress event. Such a scenario could help explain the patchy distribution of clade D and the inconsistencies in the literature that pertain to the composition of *Symbiodinium* in post-stressed corals (i.e., stable versus shift to clade D dominance). It is unknown what circumstances allow for the initial uptake of clade D in individual corals, but evidence points to life-stage and environmental conditions as important factors. Perhaps it takes several generations for clade D to integrate into a host endosymbiotic community, and it is an event that only occurs when stressful conditions occur at a specific point during the integration process.

## 5. Benefits and Drawbacks of Harboring *Symbiodinium* Clade D for Corals

The increased thermal tolerance of clade D *Symbiodinium* relative to the other *Symbiodinium* clades has understandably received a lot of attention. Rowan [24] showed that clade D *Symbiodinium* isolated from *Pocillopora damicornis* in Guam showed evidence of photoprotection at 32°C, while clade C isolated from the same host showed photoinhibition. These results provided the context to explain the thermal sensitivity and propensity of corals harboring clade C *Symbiodinium* to bleaching and the higher resistance of corals hosting clade D [41]. A shift in dominance to clade D *Symbiodinium* in *Acropora millepora* has since been shown to result in an acquired tolerance of 1–1.5°C [25].

These aforementioned studies clearly demonstrate that clade D *Symbiodinium* have a higher thermal tolerance than other clades of *Symbiodinium* and confer a higher level of resistance to thermal stress to the corals that host them. Although this is a very positive attribute, there are also drawbacks of harboring endosymbiotic communities dominated by clade D *Symbiodinium* for corals. For example, they grow more slowly than conspecifics harboring clade C *Symbiodinium* [62, 63]. Indeed, *Acropora millepora* harboring clade D grow 38% slower than colonies harboring clade C and bleaching reduces growth by 50% in this species regardless of the *Symbiodinium* clade hosted [63]. In reality, many of the circumstances where clade D *Symbiodinium* are found represent conditions that are stressful for the host and it is plausible that these conditions render the host more susceptible to invasion by opportunistic *Symbiodinium* present in the environment that exploit the host as a habitat rather than engage in an interactive and mutually beneficial partnership. In the short term, a coral may benefit from harboring clade D *Symbiodinium* allowing them to survive current bleaching conditions, but there are clearly fitness trade-offs associated with these shifts that may have major implications for the long-term growth and survival of coral reefs.

## 6. Research Gaps Limiting Our Understanding of the Adaptive Role That Clade D *Symbiodinium* Play in Corals

There are a number of significant gaps in our knowledge of clade D *Symbiodinium* and their interactions with corals. First, although the thermal tolerance of clade D *Symbiodinium* as a group has received a lot of attention, no information is available on the relative thermal tolerances of subclade sequence types within clade D. It is clear, however, that some subclade C *Symbiodinium* sequence types show evidence of increased thermal tolerance over others [42, 60, 64], and thus it is probable that variation also exists in clade D.

Second, our understanding of the endosymbiotic and free-living diversity and biogeography of *Symbiodinium* in general, and clade D specifically, is incomplete, with no information available from the majority of the world's reefs. A handful of studies have characterized *Symbiodinium* diversity in a wide range of marine invertebrates at a select location using a "snapshot" approach that most often distinguishes the dominant endosymbionts in corals (e.g., [32, 35–39]). More detailed analyses of corals at these locations often reveal additional *Symbiodinium* diversity and new patterns in their distribution [49]. The bulk of evidence suggests that clade D becomes more abundant in coral hosts via changes in the relative abundance of different *Symbiodinium* clades within existing endosymbiotic communities. As such, documenting the presence of clade D *Symbiodinium* as cryptic members of coral endosymbiont communities is important to predicting which corals have the innate capacity to potentially use this mechanism to survive thermal anomalies and bleaching events. Studies that have specifically addressed this issue show that there is considerable complexity in coral *Symbiodinium* communities and that clade D is often a cryptic member of endosymbiotic communities in corals [56, 65, 66].

Third, we have no information about the suite of biological and environmental characteristics that combine to initiate a shift in the dominance hierarchy to clade D. For example, no studies to date have evaluated whether corals have the ability to acquire *Symbiodinium* clade D from the environment as adults or examined the distribution and diversity of clade D *Symbiodinium* in the water column and sediments. If adult corals can acquire clade D *Symbiodinium* from the environment, this represents a mechanism to increase the pool of corals that can increase thermal resistance on the short term.

Lastly, the interactive physiology and fitness benefits/trade-offs for corals that host endosymbiotic communities dominated by clade D *Symbiodinium* are poorly understood. Only three studies focusing on a single coral genus (*Acropora*) at one location have compared the fitness of corals with endosymbiotic communities dominated by either clade C or D *Symbiodinium*, and these studies suggest that corals dominated by clade D *Symbiodinium* have reduced growth rates [23, 62, 63]. It is unknown how these changes in growth play out in terms of the long-term survival and reproductive fitness of the host colony, but understanding these trade-offs across host species and environments is critical to interpreting the overall contribution that shifts towards clade D will contribute to the long-term survival of coral reef ecosystems.

## 7. Advantages of Using Clade D *Symbiodinium* as a Tool for Monitoring Coral Reefs

Clade D *Symbiodinium* are useful from a management perspective because they are often found in increased abundance on coral reefs that are exposed to some combination of environmental stressors (challenging thermal regimes and/or land-based pollutants) that compromise coral health. As such, the presence of clade D *Symbiodinium* may represent a powerful biological indicator of negative changes in coral health that are driven by suboptimal conditions on reefs. Monitoring the abundance of *Symbiodinium* in corals in the field for shifts towards clade D provides valuable information on dynamic and sublethal changes in coral health states that

reflect the condition of the ecosystem. The monitoring itself is relatively straightforward and cost effective and can be achieved by tagging colonies at the site to be monitored, taking small biopsies of coral tissues and surrounding ocean water on an annual or rapid response basis during/after bleaching events, and detecting *Symbiodinium* clade D using standard and quantitative PCR. Such monitoring systems can be implemented to follow corals in their environment and evaluate their responses to acute and/or chronic stressors, identify corals in populations and communities that are health compromised and susceptible to stress, and as an early indication of stress in the absence of bleaching or other visible signs of compromised health. Monitoring the occurrence of clade D *Symbiodinium* in corals, therefore, represents an additional tool that complements the current ecological methods used to monitor coral reef ecosystem health.

## 8. Conclusion

Clade D *Symbiodinium* are relatively uncommon pandemically distributed endosymbionts that associate with a diversity of coral and invertebrate hosts. *Symbiodinium* clade D generally occurs in higher abundance in corals from thermally challenging environments and/or reefs impacted by land-based pollution. In the short term, corals associating with clade D benefit from higher thermal tolerance and resistance to bleaching. However, corals hosting clade D exhibit lower growth rates than conspecifics harboring clade C *Symbiodinium*. In most cases, clade D *Symbiodinium* appear to be opportunistic and are found or become dominant in corals exposed to stressful abiotic conditions that negatively impact coral health. Increased abundance on reefs and/or shifts towards *Symbiodinium* communities dominated by clade D potentially represents a tool with which to monitor the health of a coral reef ecosystem with respect to changes in reef environments.

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## References

[1] H. Freudenthal, "*Symbiodinium* gen. nov. and *Symbiodinium microadriaticum* sp. nov., a zooxanthella: taxonomy, life cycle, and morphology," *Journal of Protozoology*, vol. 9, pp. 45–52, 1962.

[2] R. Trench, "Diversity of symbiotic dinoflagellates and the evolution of microalgal-invertebrate symbioses," in *Proceedings of the 8th International Coral Reef Symposium*, vol. 2, pp. 1275–1286, 1997.

[3] L. Muscatine, "Glycerol excretion by symbiotic algae from corals and tridacna and its control by the host," *Science*, vol. 156, no. 3774, pp. 516–519, 1967.

[4] L. Muscatine and J. Porter, "Reef corals: mutualistic symbioses adapted to nutrient-poor environments," *Bioscience*, vol. 27, pp. 454–460, 1977.

[5] C. J. Bentis, L. Kaufman, and S. Golubic, "Endolithic fungi in reef-building corals (order: Scleractinia) are common, cosmopolitan, and potentially pathogenic," *Biological Bulletin*, vol. 198, no. 2, pp. 254–260, 2000.

[6] F. Rohwer, V. Seguritan, F. Azam, and N. Knowlton, "Diversity and distribution of coral-associated bacteria," *Marine Ecology Progress Series*, vol. 243, pp. 1–10, 2002.

[7] L. Wegley, Y. Yu, M. Breitbart, V. Casas, D. I. Kline, and F. Rohwer, "Coral-associated Archaea," *Marine Ecology Progress Series*, vol. 273, pp. 89–96, 2004.

[8] N. L. Patten, P. L. Harrison, and J. G. Mitchell, "Prevalence of virus-like particles within a staghorn scleractinian coral (*Acropora muricata*) from the Great Barrier Reef," *Coral Reefs*, vol. 27, no. 3, pp. 569–580, 2008.

[9] T. P. Hughes, A. H. Baird, D. R. Bellwood et al., "Climate change, human impacts, and the resilience of coral reefs," *Science*, vol. 301, no. 5635, pp. 929–933, 2003.

[10] O. Hoegh-Guldberg, "Climate change, coral bleaching and the future of the world's coral reefs," *Marine and Freshwater Research*, vol. 50, no. 8, pp. 839–866, 1999.

[11] O. Hoegh-Guldberg, P. J. Mumby, A. J. Hooten et al., "Coral reefs under rapid climate change and ocean acidification," *Science*, vol. 318, no. 5857, pp. 1737–1742, 2007.

[12] J. W. Porter, W. K. Fitt, H. J. Spero, C. S. Rogers, and M. W. White, "Bleaching in reef corals: physiological and stable isotopic responses," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 86, no. 23, pp. 9342–9346, 1989.

[13] O. Hoegh-Guldberg and G. J. Smith, "The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana," *Journal of Experimental Marine Biology and Ecology*, vol. 129, no. 3, pp. 279–303, 1989.

[14] W. K. Fitt and M. E. Warner, "Bleaching patterns of four species of Caribbean reef corals," *Biological Bulletin*, vol. 189, no. 3, pp. 298–307, 1995.

[15] J. F. Bruno, E. R. Selig, K. S. Casey et al., "Thermal stress and coral cover as drivers of coral disease outbreaks," *PLoS Biology*, vol. 5, no. 6, pp. 1220–1227, 2007.

[16] J. A. Kleypas, J. W. McManu, and L. A. B. Mene, "Environmental limits to coral reef development: Where do we draw the line?" *American Zoologist*, vol. 39, no. 1, pp. 146–159, 1999.

[17] J. C. Orr, V. J. Fabry, O. Aumont et al., "Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms," *Nature*, vol. 437, no. 7059, pp. 681–686, 2005.

[18] P. W. Glynn, "Coral reef bleaching: ecological perspectives," *Coral Reefs*, vol. 12, no. 1, pp. 1–17, 1993.

[19] T. P. Hughes, "Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef," *Science*, vol. 265, no. 5178, pp. 1547–1551, 1994.

[20] A. Kushmaro, Y. Loya, M. Fine, and E. Rosenberg, "Bacterial infection and coral bleaching," *Nature*, vol. 380, no. 6573, p. 396, 1996.

[21] NOAA, *Coral Reef Conservation Program Goals & Objectives 2010–2015*, NOAA Coral Reef Conservation Program, Silver Spring, Md, USA, 2009.

[22] Y. Loya, K. Sakai, K. Yamazato, Y. Nakano, H. Sambali, and R. Van Woesik, "Coral bleaching: the winners and the losers," *Ecology Letters*, vol. 4, no. 2, pp. 122–131, 2001.

[23] J. C. Mieog, J. L. Olsen, R. Berkelmans, S. A. Bleuler-Martinez, B. L. Willis, and M. J. H. van Oppen, "The roles and interactions of symbiont, host and environment in defining coral fitness," *PLoS ONE*, vol. 4, no. 7, article e6364, 2009.

[24] R. Rowan, "Thermal adaptation in reef coral symbionts," *Nature*, vol. 430, no. 7001, p. 742, 2004.

[25] R. Berkelmans and M. J. H. Van Oppen, "The role of zooxanthellae in the thermal tolerance of corals: a "nugget of hope" for coral reefs in an era of climate change," *Proceedings of the Royal Society B*, vol. 273, no. 1599, pp. 2305–2312, 2006.

[26] K. A. Puglise and R. Kelty, *NOAA Coral Reef Ecosystem Research Plan for Fiscal Years 2007–2011*, NOAA Coral Reef Conservation Program, Silver Spring, Md, USA, 2007.

[27] M. Stat, D. Carter, and O. Hoegh-Guldberg, "The evolutionary history of *Symbiodinium* and scleractinian hosts—symbiosis, diversity, and the effect of climate change," *Perspectives in Plant Ecology, Evolution and Systematics*, vol. 8, no. 1, pp. 23–43, 2006.

[28] R. Rowan and D. A. Powers, "Ribosomal RNA sequences and the diversity of symbiotic dinoflagellates (zooxanthellae)," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 89, no. 8, pp. 3639–3643, 1992.

[29] M. Stat, E. Morris, and R. D. Gates, "Functional diversity in coral-dinoflagellate symbiosis," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 105, no. 27, pp. 9256–9261, 2008.

[30] X. Pochon and R. D. Gates, "A new *Symbiodinium* clade (Dinophyceae) from soritid foraminifera in Hawai'i," *Molecular Phylogenetics and Evolution*, vol. 56, no. 1, pp. 492–497, 2010.

[31] D. J. Thornhill, T. C. Lajeunesse, and S. R. Santos, "Measuring rDNA diversity in eukaryotic microbial systems: how intragenomic variation, pseudogenes, and PCR artifacts confound biodiversity estimates," *Molecular Ecology*, vol. 16, no. 24, pp. 5326–5340, 2007.

[32] M. Stat, X. Pochon, R. O. M. Cowie, and R. D. Gates, "Specificity in communities of *Symbiodinium* in corals from Johnston Atoll," *Marine Ecology Progress Series*, vol. 386, pp. 83–96, 2009.

[33] T. C. LaJeunesse, D. T. Pettay, E. M. Sampayo et al., "Long-standing environmental conditions, geographic isolation and host-symbiont specificity influence the relative ecological dominance and genetic diversification of coral endosymbionts in the genus *Symbiodinium*," *Journal of Biogeography*, vol. 37, no. 5, pp. 785–800, 2010.

[34] T. C. LaJeunesse, ""Species" radiations of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the Miocene-Pliocene transition," *Molecular Biology and Evolution*, vol. 22, no. 3, pp. 570–581, 2005.

[35] T. C. LaJeunesse, W. K. W. Loh, R. Van Woesik, O. Hoegh-Guldberg, G. W. Schmidt, and W. K. Fitt, "Low symbiont diversity in southern Great Barrier Reef corals, relative to those of the Caribbean," *Limnology and Oceanography*, vol. 48, no. 5, pp. 2046–2054, 2003.

[36] T. C. LaJeunesse, R. Bhagooli, M. Hidaka et al., "Closely related *Symbiodinium* spp. differ in relative dominance in coral reef host communities across environmental, latitudinal and biogeographic gradients," *Marine Ecology Progress Series*, vol. 284, pp. 147–161, 2004.

[37] T. C. LaJeunesse, D. J. Thornhill, E. F. Cox, F. G. Stanton, W. K. Fitt, and G. W. Schmidt, "High diversity and host specificity observed among symbiotic dinoflagellates in reef coral communities from Hawaii," *Coral Reefs*, vol. 23, no. 4, pp. 596–603, 2004.

[38] D. Abrego, M. J. H. Van Oppen, and B. L. Willis, "Highly infectious symbiont dominates initial uptake in coral juveniles," *Molecular Ecology*, vol. 18, no. 16, pp. 3518–3531, 2009.

[39] T. C. LaJeunesse, "Diversity and community structure of symbiotic dinoflagellates from Caribbean coral reefs," *Marine Biology*, vol. 141, no. 2, pp. 387–400, 2002.

[40] X. Pochon, L. Garcia-Cuetos, A. C. Baker, E. Castella, and J. Pawlowski, "One-year survey of a single Micronesian reef reveals extraordinarily rich diversity of *Symbiodinium* types in soritid foraminifera," *Coral Reefs*, vol. 26, no. 4, pp. 867–882, 2007.

[41] A. C. Baker, C. J. Starger, T. R. McClanahan, and P. W. Glynn, "Corals' adaptive response to climate change," *Nature*, vol. 430, no. 7001, p. 741, 2004.

[42] A. M. Jones, R. Berkelmans, M. J. H. Van Oppen, J. C. Mieog, and W. Sinclair, "A community change in the algal endosymbionts of a scleractinian coral following a natural bleaching event: field evidence of acclimatization," *Proceedings of the Royal Society B*, vol. 275, no. 1641, pp. 1359–1365, 2008.

[43] T. A. Oliver and S. R. Palumbi, "Distributions of stress-resistant coral symbionts match environmental patterns at local but not regional scales," *Marine Ecology Progress Series*, vol. 378, pp. 93–103, 2009.

[44] W. W. Toller, R. Rowan, and N. Knowlton, "Zooxanthellae of the *Montastraea annularis* species complex: patterns of distribution of four taxa of *Symbiodinium* on different reefs and across depths," *Biological Bulletin*, vol. 201, no. 3, pp. 348–359, 2001.

[45] K. E. Fabricius, J. C. Mieog, P. L. Colin, D. Idip, and M. J. H. Van Oppen, "Identity and diversity of coral endosymbionts (zooxanthellae) from three Palauan reefs with contrasting bleaching, temperature and shading histories," *Molecular Ecology*, vol. 13, no. 8, pp. 2445–2458, 2004.

[46] T. C. LaJeunesse, H. R. Bonilla, M. E. Warner, M. Wills, G. W. Schmidt, and W. K. Fitt, "Specificity and stability in high latitude eastern Pacific coral-algal symbioses," *Limnology and Oceanography*, vol. 53, no. 2, pp. 719–727, 2008.

[47] B. S. Halpern, S. Walbridge, K. A. Selkoe et al., "A global map of human impact on marine ecosystems," *Science*, vol. 319, no. 5865, pp. 948–952, 2008.

[48] Y.-T. Lien, Y. Nakano, S. Plathong, H. Fukami, J.-T. Wang, and C. A. Chen, "Occurrence of the putatively heat-tolerant *Symbiodinium* phylotype D in high-latitudinal outlying coral communities," *Coral Reefs*, vol. 26, no. 1, pp. 35–44, 2007.

[49] E. M. Sampayo, L. Franceschinis, O. Hoegh-Guldberg, and S. Dove, "Niche partitioning of closely related symbiotic dinoflagellates," *Molecular Ecology*, vol. 16, no. 17, pp. 3721–3733, 2007.

[50] M. Stat, W. K. W. Loh, O. Hoegh-Guldberg, and D. A. Carter, "Symbiont acquisition strategy drives host-symbiont associations in the southern Great Barrier Reef," *Coral Reefs*, vol. 27, no. 4, pp. 763–772, 2008.

[51] D. Abrego, M. J. H. Van Oppen, and B. L. Willis, "Onset of algal endosymbiont specificity varies among closely related species of *Acropora* corals during early ontogeny," *Molecular Ecology*, vol. 18, no. 16, pp. 3532–3543, 2009.

[52] P. G. Mostafavi, S. M. R. Fatemi, M. H. Shahhosseiny, O. Hoegh-Guldberg, and W. K. W. Loh, "Predominance of clade D *Symbiodinium* in shallow-water reef-building corals off Kish and Larak Islands (Persian Gulf, Iran)," *Marine Biology*, vol. 153, no. 1, pp. 25–34, 2007.

[53] N. Downing, "Coral reef communities in an extreme enviornment: the northwest Arabian Gulf," in *Proceedings of the 5th International Coral Reef Congress*, C. Gabrie, B. Salvat, C. Lacroix, and J. Toffart, Eds., vol. 6, pp. 343–348, Antenne Museum-EPHE, Moorea, Tahiti, French Polynesia, 1985.

[54] S. L. Coles and Y. H. Fadlallah, "Reef coral survival and mortality at low temperatures in the Arabian Gulf: new species-specific lower temperature limits," *Coral Reefs*, vol. 9, no. 4, pp. 231–237, 1991.

[55] M. Garren, S. M. Walsh, A. Caccone, and N. Knowlton, "Patterns of association between *Symbiodinium* and members of the *Montastraea annularis* species complex on spatial scales ranging from within colonies to between geographic regions," *Coral Reefs*, vol. 25, no. 4, pp. 503–512, 2006.

[56] T. C. LaJeunesse, R. T. Smith, J. Finney, and H. Oxenford, "Outbreak and persistence of opportunistic symbiotic dinoflagellates during the 2005 Caribbean mass coral "bleaching" event," *Proceedings of the Royal Society B*, vol. 276, no. 1676, pp. 4139–4148, 2009.

[57] R. Buddemeier and D. Fautin, "Coral bleaching as an adaptive mechanism," *Bioscience*, vol. 43, pp. 320–325, 1993.

[58] D. J. Thornhill, W. K. Fitt, and G. W. Schmidt, "Highly stable symbioses among western Atlantic brooding corals," *Coral Reefs*, vol. 25, no. 4, pp. 515–519, 2006.

[59] D. J. Thornhill, T. C. LaJeunesse, D. W. Kemp, W. K. Fitt, and G. W. Schmidt, "Multi-year, seasonal genotypic surveys of coral-algal symbioses reveal prevalent stability or post-bleaching reversion," *Marine Biology*, vol. 148, no. 4, pp. 711–722, 2006.

[60] E. M. Sampayo, T. Ridgeway, P. Bongaerts, and O. Hoegh-Guldberg, "Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 105, pp. 10444–10449, 2008.

[61] M. Stat, W. K. W. Loh, T. C. LaJeunesse, O. Hoegh-Guldberg, and D. A. Carter, "Stability of coral-endosymbiont associations during and after a thermal stress event in the southern Great Barrier Reef," *Coral Reefs*, vol. 28, no. 3, pp. 709–713, 2009.

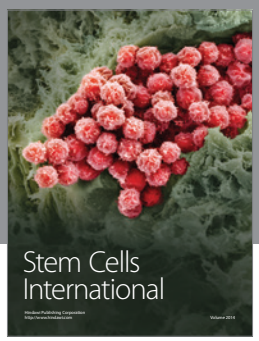
[62] A. F. Little, M. J. H. Van Oppen, and B. L. Willis, "Flexibility in algal endosymbioses shapes growth in reef corals," *Science*, vol. 304, no. 5676, pp. 1492–1494, 2004.

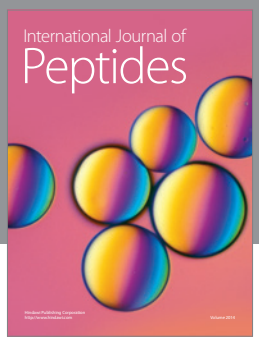
[63] A. Jones and R. Berkelmans, "Potential costs of acclimatization to a warmer climate: growth of a reef coral with heat tolerant vs. sensitive symbiont types," *PloS One*, vol. 5, no. 5, article e10437, 2010.

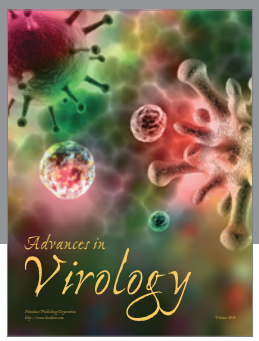
[64] D. Tchernov, M. Y. Gorbunov, C. De Vargas et al., "Membrane lipids of symbiotic algae are diagnostic of sensitivity to thermal bleaching in corals," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 101, no. 37, pp. 13531–13535, 2004.

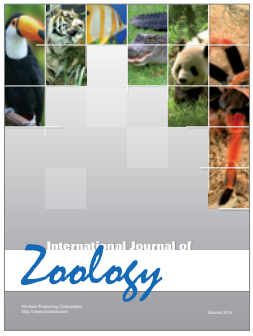
[65] J. C. Mieog, M. J. H. Van Oppen, N. E. Cantin, W. T. Stam, and J. L. Olsen, "Real-time PCR reveals a high incidence of *Symbiodinium* clade D at low levels in four scleractinian corals across the Great Barrier Reef: implications for symbiont shuffling," *Coral Reefs*, vol. 26, no. 3, pp. 449–457, 2007.

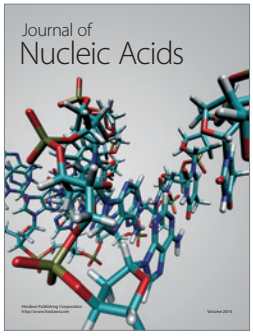
[66] A. M. S. Correa, M. D. McDonald, and A. C. Baker, "Development of clade-specific *Symbiodinium* primers for quantitative PCR (qPCR) and their application to detecting clade D symbionts in Caribbean corals," *Marine Biology*, vol. 156, no. 11, pp. 2403–2411, 2009.

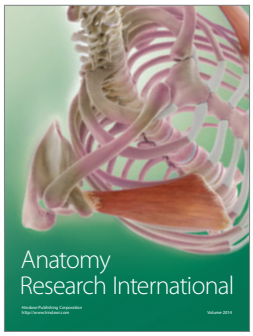


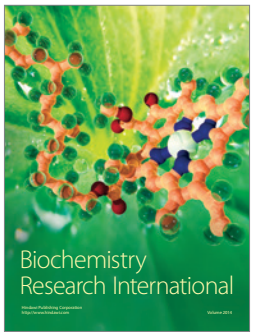


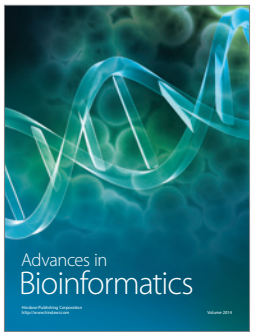


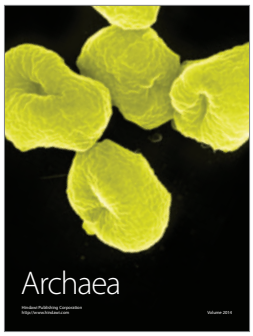


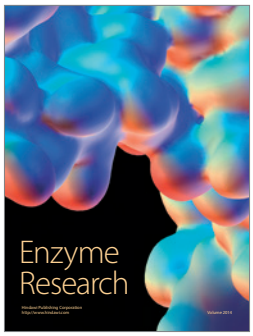


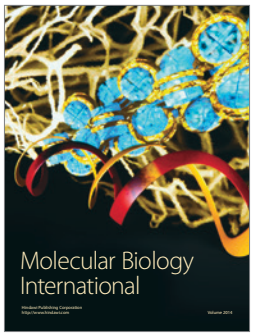












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