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FEATURE ARTICLE

Most corals may not change their symbionts

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ABSTRACT: Many corals (stony corals and octocorals) rely on their symbiotic algae (zooxanthellae) for survival. Under stress, zooxanthellae are expelled, resulting in coral bleaching. The hypothesis that corals may survive climate change by exchanging algal types is shown here to be potentially applicable only to a minority of corals. Data on 442 coral species from 43 studies reveal that only a few coral species may be able to change their symbionts. The ability to change symbionts seems to be linked to whether a coral species can host multiple zooxanthella clades, either at different depths on the same reef, on different reefs or at different geographic locations, or concurrently within the same colony. The combined data set shows that only 23% of coral species host multiple zooxanthella clades. Most coral species (77%) exhibit fidelity to a narrow subset of a single zooxanthella clade, some even to specific algal genotypes within a clade. These specific algal genotypes in coral species hosting a single algal clade do not change over time. Furthermore, no algal change occurs when a coral colony is either transplanted to different environments, or subjected to stressors such as disease or increased temperatures. For the majority of corals, therefore, algal switching does not appear to occur. These coral species will survive only if the existing host–symbiont combination withstands the changing conditions. If climate warming continues, coral reefs may undergo a change in biodiversity such that only a subset of symbiotic corals may persist.

KEY WORDS: Zooxanthella · Coral · Bleaching · Global warming · Clade · Symbiosis · Adaptive bleaching hypothesis

Most corals host only one zooxanthella clade and do not change their algae, neither over time, nor after exposure to elevated temperatures, disease, or following transplantation.

Photo: Denis Goulet

INTRODUCTION

Many stony corals and octocorals (collectively referred to hereafter as corals) form an obligatory mutualism with unicellular algae (zooxanthellae). Under stressful environmental conditions, such as elevated water temperatures, there is a loss of zooxanthellae and/or their photosynthetic pigments, a phenomenon commonly called coral bleaching (Glynn 1996). According to the adaptive bleaching hypothesis, bleaching may enable corals to adopt zooxanthellae better suited for a new environment (Buddemeier & Fautin 1993). These algae may enter the symbiosis from exogenous sources (symbiont 'switching') or, if multiple zooxanthellae already concurrently exist within the host, a shift in symbiont dominance may occur (symbiont 'shuffling') (Baker 2003).

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The possibility of zooxanthella turnover is particularly appealing in light of global warming and the predictions that coral symbioses, as we know them, are reaching their thermal limits (Hoegh-Guldberg 1999). Numerous recent studies on zooxanthella genotypes in corals have focused on zooxanthella turnover (Rowan et al. 1997, Baker 2001, Baker et al. 2004, Lewis & Coffroth 2004, Little et al. 2004, Rowan 2004, Berkelmans & van Oppen 2006). It has been suggested that corals may survive global climate change by switching their symbiotic algae (Buddemeier & Fautin 1993, Little et al. 2004, Rowan 2004). Fautin & Buddemeier (2004) even stated that adaptive bleaching is a general phenomenon. The possibility of algal switching or shuffling, however, relies on the assumption that a coral species can host multiple algal genotypes, either sequentially or simultaneously.

The distinction between zooxanthella genotypes is based on different parts of the zooxanthella genome such as nuclear genes encoding either the small subunit (SSU) or the large subunit (LSU) of the ribosomal RNA, internal transcribed spacers (ITS1 and ITS2), 5.8S regions and large subunit chloroplast rDNA (cprDNA). The various genome regions have yielded a relatively robust division of zooxanthellae into 8 clades (A–H). These clades are found in a variety of host phyla such as Cnidaria (e.g. corals, octocorals, sea anemones), Mollusca (e.g. clams), Porifera (e.g. sponges), and Protozoa (e.g. foraminiferans) (Stat et al. 2006, their Table 1). Each clade includes multiple zooxanthella 'types' (see reviews by Baker 2003, Coffroth & Santos 2005, Stat et al. 2006).

In the 15 yr since the cladal division of zooxanthellae was first introduced, numerous researchers have reported the cladal identity of zooxanthellae in 442 coral species from multiple geographic locations. The objective of this study was to use this large dataset to reach conclusions about coral–algal symbioses and the possibility and generality of symbiont turnover in times of global climate change.

METHODS

Since 1991, 43 studies included data on the zooxanthella genetic identity in 442 scleractinian corals and octocoral species (Table 1). In this study these data were pooled into 1 large data set, using only data published from field-collected samples, and not from zooxanthella cultures, since culturing is highly selective (Goulet & Coffroth 1997, Santos et al. 2001, LaJeunesse 2002). Most reports identified zooxanthellae at the cladal level, with a few reporting resolution within-clades. Comparison of zooxanthella types is hampered by the fact that researchers use different parts of the genome for the within-clade division and there is no generally accepted nomenclature of the zooxanthella types. Data analysis was therefore conducted at the cladal level with further comparisons at the within-clade level as the data permitted.

A coral species was defined as hosting multiple zooxanthella clades if that coral species hosted >1 zooxanthella clade at different depths, in different geographic locations, at different sampling times, or within the same colony. A coral species was classified as hosting multiple zooxanthella clades with no distinction being made as to whether the multiple clades were a result of algal 'switching' or algal 'shuffling' (internal turnover as described in Baker 2003).

To determine if a geographic pattern existed, data was entered in tabular format in order to create a GIS (Geographic Information System) map using ArcMap (v8.3, ESRI). The GIS includes a world map as the primary base layer. A geographic coordinate system was used for the spatial component of the samples. The latitude and longitude coordinates of the samples were converted to decimal format. The data were plotted to reveal any spatial patterns in the distribution of coral species hosting single versus multiple zooxanthella clades.

RESULTS AND DISCUSSION

In a changing environment, such as that encountered in times of global climate change, not all coral species fare the same (Loya et al. 2001, Douglas 2003). Differential survival of corals can be attributed to a coral colony's tolerance (Brown et al. 2002, Bhagooli & Hidaka 2004), the zooxanthellae's tolerance (Rowan et al. 1997), or both.

Table 1. Data sources for the meta-analysis on coral symbionts

Baker (1999, 2001)
Baker & Rowan (1997)
Baker et al. (1997, 2004)
Barneah et al. (2004)
Billinghurst et al. (1997)
Chen et al. (2005)
Darius et al. (1998, 2000)
Diekmann et al. (2002, 2003)
Fabricius et al. (2004)
Goulet & Coffroth (2004)
Goulet et al. (unpubl.)
Iglesias-Prieto et al. (2004)
Karako-Lampert et al. (2004)
LaJeunesse (2002)
LaJeunesse et al. (2003, 2004, 2005)
Loh et al. (1997, 2001)
McNally et al. (1994)
Rodriguez-Lanetty & Hoegh-Guldberg (2003)
Rodriguez-Lanetty et al. (2000, 2003, 2004)
Rowan & Knowlton (1995)
Rowan & Powers (1991a,b)
Rowan et al. (1997)
Santos et al. (2001, 2003a,b)
Savage et al. (2002)
Toller et al. (2001b)
Ulstrup & van Oppen (2003)
van Oppen et al. (2001)
Visram & Douglas (2006)
Wilcox (1997, 1998)
Yang et al. (2002)

Association between corals and zooxanthella genotypes

Recombination of coral–zooxanthella genotypic combinations may be advantageous (Buddemeier & Fautin 1993) and a way for the slowly evolving corals to adapt or acclimate to the rapidly changing conditions (Baker et al. 2004). Different coral–zooxanthella genotypic combinations may display different physiologies. For example, in *Pocillopora* spp. 32°C causes photoinhibition in Clade C containing colonies, while causing photoprotection in colonies hosting Clade D zooxanthellae (Rowan 2004). Similarly, *Acropora millepora* hosting Clade D zooxanthellae exhibit a higher thermal tolerance compared to colonies hosting Clade C zooxanthellae (Berkelmans & van Oppen 2006). Physiologies dependent on the host–symbiont combination are also seen in the sea anemone *Aiptasia pallida*, in which 2 natural and 1 artificial host–symbiont combinations (with Clade A and B zooxanthellae) yielded 3 different physiological responses to elevated temperatures (Goulet et al. 2005). In all of these examples, the host naturally associates with zooxanthellae from several clades.

A key assumption of algal symbiont change is that corals can host multiple zooxanthella genotypes, either concurrently or sequentially. Combining data published from 1991 to 2006 generated a data set of zooxanthella identity from 442 coral species (both scleractinian corals and octocorals, Table 1). Sample sizes for number of colonies sampled from a particular coral species ranged from 1 to 565 with only 18 % represented by a sample size of 1. Many genera were represented by multiple species. In many instances, the same species was sampled from multiple reefs and multiple geographic locations, during multiple years, at different times throughout the year, and by different researchers. The current data demonstrate that, as adults, most coral species may not be able to change their zooxanthella population. Coral–algal recombination, therefore, may not be a viable option for most coral species. Four lines of evidence support this conclusion.

(1) Most corals host a single zooxanthella clade. Analyzing coral–zooxanthella symbioses at the cladal level reveals that coral species fall into 2 categories. The first category contains coral species that can host multiple zooxanthella clades either over depth on the same reef, in different geographic areas, or within the same colony. Coral species in this category are in the minority, since only 23 % of the coral species sampled hosted multiple zooxanthella clades (Fig. 1). The second category includes the majority of coral species (77 %). These coral species host only 1 zooxanthella clade. A global comparison demonstrated that hosting

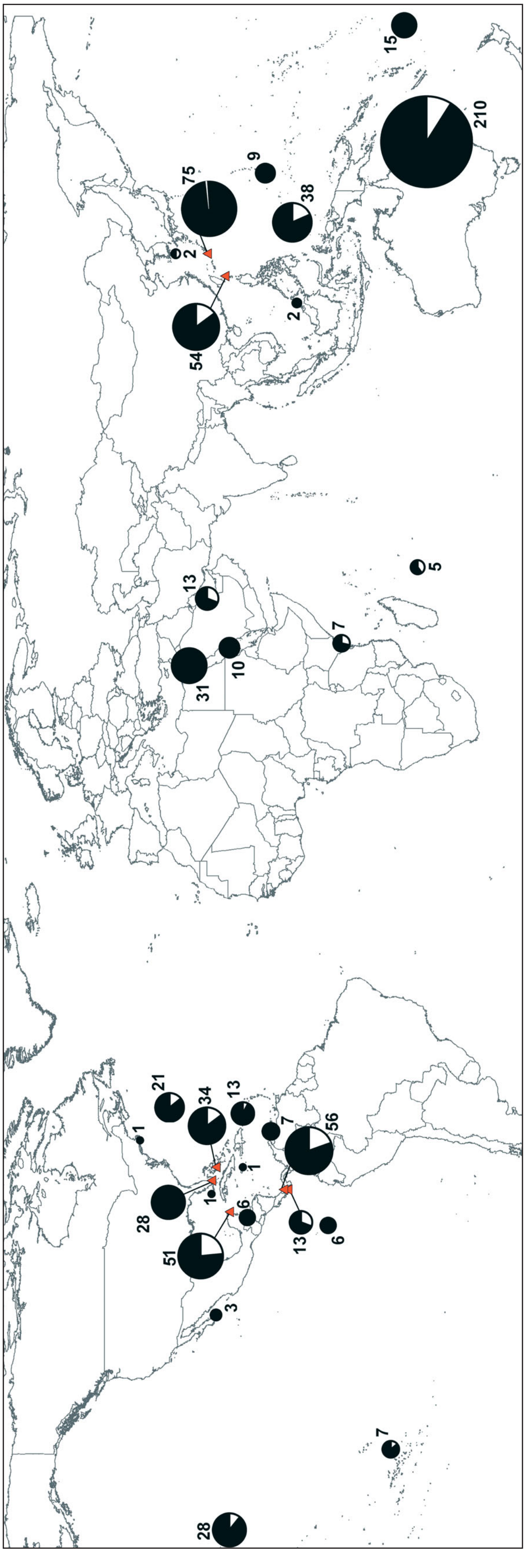

Fig. 1. Global distribution of stony coral and octocoral species hosting single (black) versus multiple (white) zooxanthella clades. A species was classified as hosting multiple zooxanthella clades if multiple clades occurred either within the same colony or in different colonies. Pie charts denote percentage of species. Pie chart size indicates the number of species sampled at a given site (listed by each pie chart). For example, in Australia n = 210 species; 91 % with a single zooxanthella clade and 9 % with multiple clades. Data sources are given in Table 1

a single zooxanthella clade is prevalent worldwide (Fig. 1). Although the fact that most coral species host 1 zooxanthella clade has been noted previously (LaJeunesse 2002, Baker 2003), the implications of the existence of multiple versus single zooxanthella clades within a coral species have not been discussed.

All documented instances of long-term change in symbiont populations, for example, have been reported from corals that naturally host multiple zooxanthella clades (Baker 2001, Baker et al. 2004, Berkelmans & van Oppen 2006). In a 12 mo transplant experiment, 7 out of the 8 scleractinian coral species sampled displayed a change in their zooxanthella clade (Baker 2001). These species, however, naturally host zooxanthellae of different clades. Coral colonies in the genus *Pocillopora* host both Clade C and D zooxanthellae, and following a bleaching event, most colonies hosted Clade D (Baker et al. 2004). *Acropora millepora* colonies transplanted for 9 mo shifted between the 2 zooxanthella clades found in this species, Clades C and D, while other colonies of *A. millepora* from another site did not change their Clade C zooxanthellae during a 14 mo transplant (Berkelmans & van Oppen 2006). Corals hosting multiple clades may demonstrate a shift or switch in algal clades, but they may be the exception rather than the norm.

(2) Coral species that host a single zooxanthella clade do not demonstrate algal turnover even at the within-clade level. Long-term studies (>6 mo) of coral species hosting a single algal clade reveal that zooxanthella genotypic fidelity even exists at the within-clade level (Goulet & Coffroth 2003a,b, Rodriguez-Lanetty et al. 2003, Iglesias-Prieto et al. 2004, LaJeunesse et al. 2004, 2005, Kirk et al. 2005), and down to the level of individual zooxanthella genotype (Goulet & Coffroth 2003b). This is found when comparing coral colonies within a species over time, after transplantation to novel environments, exposure of coral colonies to disease, or elevated temperatures (Table 2).

Table 2. Coral species hosting a single zooxanthella clade for which data is available at the sub-cladal level monitoring over time, after transplantation to novel environments, exposure of coral colonies to disease, or elevated temperatures. ITS1 = internal transcribed spacer region 1; LSU = large subunit ribosomal RNA; ITS2 = internal transcribed spacer region 2; cprDNA = partial LSU chloroplast rDNA; SSU = small subunit ribosomal RNA

Host species	Genetic marker used	Source
Alveopora japonica	ITS1, LSU	Rodriguez-Lanetty et al. (2003)
Fungia scutaria	ITS2	LaJeunesse et al. (2005)
Gorgonia ventalina	cprDNA, SSU	Kirk et al. (2005)
Pavona gigantea	ITS2	Iglesias-Prieto et al. (2004)
Plexaura kuna	Multilocus DNA fingerprinting, SSU	Goulet & Coffroth (2003a,b)
Porites compressa	ITS2	LaJeunesse et al. (2004)

Rodriguez-Lanetty et al. (2003) sampled zooxanthellae in the scleractinian coral *Alveopora japonica* in different seasons throughout the year. Using sequences of LSU and ITS1 rDNA, they determined that *A. japonica* in all instances hosted zooxanthellae belonging to Clade F. Using DNA fingerprinting to distinguish among zooxanthella genotypes, Goulet & Coffroth (2003b) followed colonies of the octocoral *Plexaura kuna* over a 10 yr period that included a bleaching event. The *P. kuna* colonies retained the original individual zooxanthella genotype in all samples collected over this 10 yr period (Goulet & Coffroth 2003b). In addition, all *P. kuna* clonemates, a reflection of the octocoral genotype over time, exhibited the same individual zooxanthella genotype (Goulet & Coffroth 2003b).

Transplantation of colonies of coral species that host a single algal clade also did not induce an algal turnover, neither at the cladal nor sub-cladal level. The same zooxanthella genotype persisted after transplanting *Plexaura kuna* colonies to novel environments for 20 mo (Goulet & Coffroth 2003b). *Pavona gigantea* kept its specific sub-clade of zooxanthellae (Clade C1c) a year after transplantation to a shallow depth (Iglesias-Prieto et al. 2004). A *Porites compressa* colony collected below 10 m and transplanted to a shallow patch reef maintained its deep-water zooxanthella type (C15b) even 10 yr after being transplanted (LaJeunesse et al. 2004). *Fungia scutaria* retained its original zooxanthella type (C1b) for 35 yr after being transplanted from the Indo-Pacific to the Caribbean, (LaJeunesse et al. 2005). This finding is of particular interest since Clade C1b is not found in the Caribbean.

A comparison of a hypervariable region within the large subunit of the choloroplast ribosomal gene in zooxanthellae in healthy and diseased *Gorgonia ventalina* revealed that all *G. ventalina*, regardless of their health, hosted a single Clade B sub-clade (Kirk et al. 2005). Furthermore, in laboratory experiments, where *G. ventalina* colonies were subjected to elevated temperature for varying times, *G. ventalina* did not switch its zooxanthella sub-clade (Kirk et al. 2005).

In summary, all studies on coral species that host a single zooxanthella clade show no algal turnover at the clade or sub-clade level.

(3) No study has demonstrated that coral species hosting a single zooxanthella clade form new symbiotic combinations with 'cryptic zooxanthellae'. It has been suggested that the algal genotypes identified from specific coral hosts are actually an underestimation of the genotypes that exist within the host species

(Baker 2003). Proponents for these undetected (cryptic) multiple genotypes base their suggestion on results obtained with either: (1) zooxanthella cultures, or (2) from working with particular molecular techniques. Considering (1), in some instances zooxanthella clades are cultured from a coral that are not known to associate with that coral in nature (Goulet & Coffroth 1997, Santos et al. 2001, LaJeunesse 2002). (2) Using a cloning approach, for instance, algal genotypes have been described that have not surfaced from surveying zooxanthellae extracted from corals in the wild. Some of the presumed variability in zooxanthella genotypes, however, may be an artifact of the molecular technique used. For example, cloning may generate sequences that do not represent zooxanthellae (Toller et al. 2001a, Baker 2003).

The role and importance of 'cryptic zooxanthellae', if they exist and are not an artifact of a technique, has not been demonstrated. There is no evidence that the additional algal genotypes obtained via culturing or a molecular technique are in symbiosis with the host; they might be 'transient' or 'opportunistic contaminant' algal cells found externally or internally, but without constituting part of the symbiosis (Santos et al. 2001, LaJeunesse 2002, LaJeunesse et al. 2004). Furthermore, if a coral species is known to host multiple clades, then background levels of the multiple clades may occur. In coral species that host a single algal clade, 'cryptic zooxanthellae' have not surfaced in any of the long-term studies.

(4) Can early ontogeny provide a window to acquiring new zooxanthella genotypes in those coral species where the adults do not change zooxanthella genotypes? The few studies on zooxanthellae in newly settled polyps of coral species that host only 1 zooxanthella clade as adults suggest that the primary polyp stage is more flexible to hosting multiple zooxanthella genotypes, even from different algal clades (Coffroth et al. 2001). For example, newly settled polyps of the octocoral *Pseudoplexaura porosa* host either Clade A, B, C or a mixture of A and B algae (Coffroth et al. 2001). Newly settled polyps of *Plexaura kuna* either host Clade A, Clade B, or a mixture of both algae (Coffroth et al. 2001). On the other hand, all juvenile *P. porosa* and *P. kuna* colonies (≥3 cm) sampled in nature host only Clade B (Coffroth et al. 2001). Adult *P. porosa* and *P. kuna* colonies also only host Clade B zooxanthellae (Goulet & Coffroth 2003a,b, 2004).

The adult colonies' zooxanthella complement may arise by at least 2 processes: (1) Newly settled polyps that acquire a zooxanthella clade not found in the adults may die. Consequently, only polyps hosting the clade found in the adults will survive to the juvenile and adult stage. (2) Competition among zooxanthellae may occur in newly settled coral polyps. The zooxanthellae belonging to the clade characteristic of the adults may outcompete all other zooxanthellae, resulting in all adult colonies hosting only one zooxanthella clade. In *Plexaura kuna*, all adult colony clonemates host the same specific individual genotype within Clade B, demonstrating a lack of zooxanthella turnover even at the within-clade level (Goulet & Coffroth 2003a,b). Therefore, from the few studies comparing zooxanthellae in newly settled polyps and adult colonies in coral species where the adults host a single zooxanthella clade, it does not appear that switching of clades or of types within a clade occurs.

Conclusions

Given the data available today, the majority of coral species host a single zooxanthella clade. Coral species that are in symbiosis with only 1 zooxanthella clade may host several types within a clade, but an individual coral colony does not switch its type over time, when transplanted to different environments or when subjected to stressors such as disease or increased temperatures.

In the context of global climate change, the majority of coral species may not be able to switch symbionts and may be in greater peril than some studies imply. How the remaining 23% of coral species are capable of hosting multiple zooxanthella clades remains to be determined. For the majority of corals, the question is not whether symbiont change is possible, but under which conditions the existing symbiosis may survive. If global climate change continues, coral reefs may undergo a significant change in biodiversity, as only a small subset of symbiotic stony coral and octocoral species may survive.

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