



COMMENT

Multiple symbiotic partnerships are common in scleractinian corals, but not in octocorals: Comment on Goulet (2006)

Andrew C. Baker^{1,2,*}, Adrienne M. Romanski²

¹Division of Marine Biology and Fisheries, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149, USA

²Department of Ecology, Evolution and Environmental Biology, Columbia University, MC 5557, 1200 Amsterdam Avenue, New York, New York 10027, USA

ABSTRACT: The ability of reef corals to adapt or acclimatize to projected climate change is a critical, but controversial, question in contemporary coral reef science and conservation. Much research has focused on whether or not corals are able to flexibly associate with diverse symbionts ('zooxanthellae') whose different physiologies may impart greater resistance to environmental extremes. Goulet (2006; Mar Ecol Prog Ser 321:1–7) concluded that most coral species only host zooxanthellae from a single *Symbiodinium* clade, and that these symbionts do not change in response to environmental disturbance, disease, or temperature stress. We re-evaluate her data and show that: (1) almost two-thirds of the coral species investigated have been severely undersampled ($N \leq 5$); (2) more than three-quarters of the scleractinian (stony) coral species sampled more adequately ($N > 10$) host multiple *Symbiodinium* clades, or multiple types within a clade; (3) scleractinian corals are more flexible than octocorals; (4) almost all scleractinian coral families can host more than one symbiont clade. Moreover, the molecular approaches used by many studies are likely to have underestimated *Symbiodinium* diversity, because they are unable to detect symbionts at low abundance and because they cannot distinguish between closely related types. In addition, various other studies show that: (1) scleractinian corals commonly host multiple symbiont types within a *Symbiodinium* clade; (2) symbiont communities in scleractinian corals are dynamic; (3) 'cryptic' symbiont taxa found at low abundance within colonies are unlikely to be molecular artifacts. We suggest that the majority of scleractinian coral species, including virtually all of the dominant reef-building taxa, can be found hosting multiple symbiont types, even at the clade level. This flexibility is important in understanding the past evolutionary success of these species and their future survival trajectories in the face of projected climate change.

KEY WORDS: Coral · *Symbiodinium* · Symbiosis · Climate change · Bleaching · Zooxanthellae · Diversity

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Symbiont diversity within coral species is severely undersampled

Goulet (2006) analyzed data on 442 coral species from 43 studies and found that 340 species (77%) hosted *Symbiodinium* from only one clade. We compiled data from the same sources, but to avoid inflating

the species count excluded coral species reported only to the generic level ('sp.' or 'spp.'), except where they could be unambiguously assigned to a single species not otherwise represented in the dataset. We also did not include T. L. Goulet et al. (unpubl.), for which no details were provided in Goulet (2006; see her Table 1, and references therein). Our analysis contained 307

*Email: abaker@rsmas.miami.edu

species, of which 230 (75%) hosted only one clade. However, 64% (198 of 307 species surveyed) were only sampled 5 times or less, including 73% (168 of 230 species) found to host only one clade (Table 1). Goulet's conclusion that 'most corals may not change their symbionts' is therefore based on an extremely limited sampling effort not reflected in her statement that sample sizes per species 'ranged from 1 to 565 with only 18% represented by a sample size of 1' (p.3). In fact, when the analysis is restricted to the species for which sampling has been more significant ($N > 10$), over two-thirds of all coral species (and almost three-quarters of scleractinian coral species) host multiple symbiont types at the clade level or below (Table 1).

Field surveys of *Symbiodinium* have provided an overall picture of symbiont diversity on reefs at the expense of exploring diversity within host species. Fig. 1 illustrates the highly skewed distribution of sampling effort to date, and shows that it is inappropriate to draw conclusions regarding intra-specific symbiont diversity for all but the most broadly sampled coral species. Sampling of corals in unusual environments continues to reveal previously undocumented associations, even in relatively common and well-studied corals. Examples include *Symbiodinium* from Clade D in one colony of *Colpophyllia natans* sampled from a creek environment in the Florida Keys (A. C. Baker unpubl.) and an unusually deep and isolated colony of *Acropora palmata* in the Flower Gardens containing a Clade C symbiont (T. C. LaJeunesse unpubl.). Until coral species have been sampled in sufficient numbers, from diverse habitats, and across broad geographic and latitudinal ranges, only the most conservative conclusions regarding the absolute diversity of *Symbiodinium* found within single coral species can be made (Baker 2003).

Flexibility in relative, not absolute, terms

Although determining the absolute diversity of symbionts capable of associating with any particular coral species is problematic, comparisons of relative diversity among different coral taxa, when appropriately controlled for sampling effort, are still informative. These analyses should form the basis for comparing the relative flexibility of different coral

Table 1. Sampling effort per coral species from data sources listed in Goulet (2006), modified as described in the text. Almost three-quarters of the coral species found so far to contain only 1 clade have been sampled 5 times or less (Row 4), often from the same reef or habitat. Only 12% of the species found to contain only 1 clade have been sampled more than 10 times (Row 6), and of those species that have been sampled more than 10 times, the majority (60%) in fact host multiple clades (Row 7). More than three-quarters of scleractinian species sampled more than 10 times have been found to contain multiple clades or multiple types within a clade (Row 8)

Row	No. of species sampled	All corals	Scleractinian corals	Octo-corals
1	Total	307	250	57
2	Only 1 clade found	230	178	52
	% of Row 1	75	71	91
3	Only 1 clade found, with $N = 1$	63	55	8
	% of Row 2	27	31	15
4	Only 1 clade found, with $N \leq 5$	168	126	42
	% of Row 2	73	71	81
5	With $N > 10$	67	59	8
6	Only 1 clade found, with $N > 10$	27	21	6
	% of Row 2	12	12	12
7	Multiple clades found, with $N > 10$	40	38	2
	% of Row 5	60	64	25
8	Multiple clades or multiple types within a clade found, with $N > 10$	48	46	2
	% of Row 5	72	78	25

species. Rather than ascribing flexibility to those species found, so far, to contain more than one clade, and inflexibility to those that have not, we suggest that a more accurate approach for assessing host flexibility is to standardize observed diversity against sampling effort.

Fig. 1 illustrates this principle for octocorals and scleractinian corals using the data sources listed in Goulet (2006), modified as described above. As sampling effort per species increases, the number of *Symbiodinium* clades documented also increases. Although we cannot use this approach to calculate a simple estimate of absolute diversity from literature sources (because more flexible coral species also tend to have attracted more sampling effort), it is nevertheless useful in highlighting relative differences in apparent flexibility between groups. Octocorals, for example, show relatively weak increases in symbiont diversity with increased sampling effort, while diversity recorded in scleractinian corals increases relatively rapidly. This indicates that scleractinian hosts are more flexible than their octocoral counterparts, but this difference is revealed only when >10 samples per species are collected. We hypothesize that this difference may be related to octocorals' greater dependence on heterotrophy compared to scleractinian corals (Fabricius & Klumpp 1995), with octocorals consequently

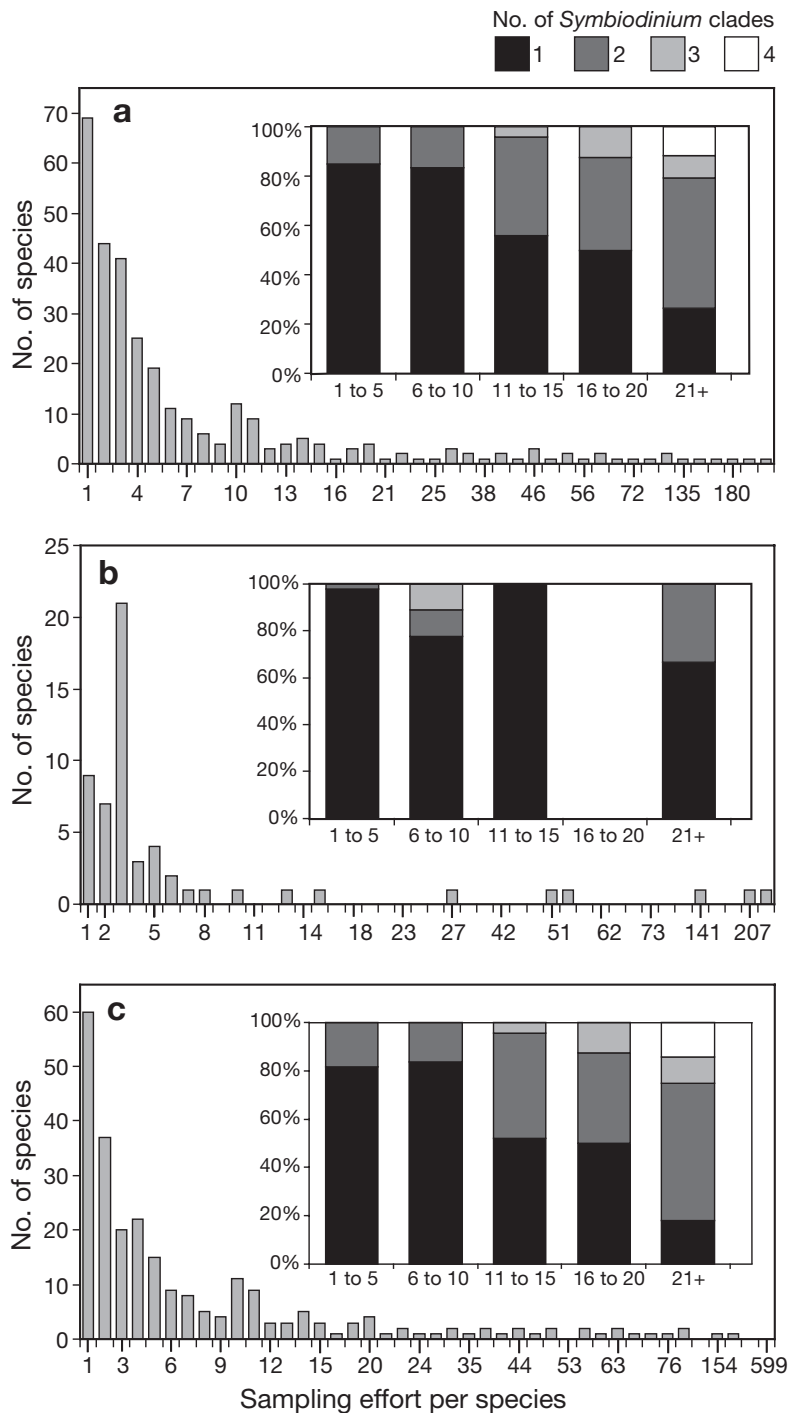


Fig. 1. Sampling effort per species for (a) all corals; (b) octocorals only; and (c) scleractinian corals only. All distributions are highly skewed to the left, revealing that most species are sampled few times. The same horizontal axis is used for all 3 panels, but tick marks and values along this axis are staggered across panels (a) to (c) to improve clarity. Inset panels show proportion of samples containing 1, 2, 3 or 4 *Symbiodinium* clades. As sampling effort increases (horizontal axis), a greater proportion of samples are revealed as hosting multiple clades. The number of clades detected increases with sampling effort faster in scleractinian corals than octocorals, indicating greater relative flexibility in the former compared to the latter

having less to gain from retaining flexibility as a symbiotic trait (van Oppen et al. 2005b). Relative differences in autotrophy vs. heterotrophy may also help explain patterns of flexibility within the scleractinian corals.

Evolutionary considerations also support our conclusion that more coral species host multiple clades of *Symbiodinium* than have been documented to date. Table 2 shows that the vast majority of scleractinian families, including all of the dominant reef-building families (e.g. Faviidae, Acroporidae, Pocilloporidae, Poritidae), are able to host more than one clade, despite low sampling effort in some groups. Goulet's (2006) analysis assumes that different coral genera within the same family, and even different coral species within the same genus, show independent patterns of symbiotic association, with some species hosting multiple clades, and other closely related species hosting a single clade. For example, in our re-analysis of the data in Goulet (2006), 13 species of *Acropora* were recorded with symbionts in multiple clades (A, C and/or D jointly), while 33 species contained symbionts in only one clade (A, C or D separately). Goulet's interpretation of species data assumes that the ability to be flexible is a discrete evolutionary trait that has been gained (and/or lost) many times within genera. We think this is unlikely, and suggest that, although species vary in their relative flexibility, the patchy distribution of different symbiont taxa within many coral genera is more likely due to our failure to document the full range of symbiont diversity as a result of limited sampling of hosts and habitats. In the example of *Acropora*, we predict that, as more data are collected, it will become apparent that the genus (comprising ~120 species) is flexible to a much greater degree than the sparse dataset currently indicates.

Many scleractinian coral species exhibit within-clade diversity

Our re-analysis of the data in Goulet (2006) revealed that 47 of the 230 species (20%) documented as hosting only one clade of *Symbiodinium* contained multiple types within that clade. However, this is again a substantial underestimate, because: (1) low sample sizes limit conclusions for many species; and

Table 2. Distribution of *Symbiodinium* clades in scleractinian coral families. All families show diversity in their associations with symbionts in different clades, despite relatively low sampling effort in several families. The only exception is the Rhizangiidae, of which only 1 species, the temperate *Astrangia danae*, has been sampled to date

Family	Clade					No. of species sampled	Median no. of samples per species
	A	B	C	D	F		
Acroporidae	×		×	×		65	5
Agariciidae		×	×	×		24	3.5
Astrocoeniidae	×	×	×	×		8	5.5
Dendrophylliidae	×		×	×		5	2
Euphylliidae			×	×		5	5
Faviidae	×	×	×	×		52	3
Fungiidae	×		×	×		12	2
Meandrinidae	×	×	×			4	2.5
Merulinidae			×	×		7	4
Mussidae		×	×	×		11	2
Oculinidae		×	×	×		4	8
Pectiniidae			×	×		6	2
Pocilloporidae	×		×	×		10	9.5
Poritidae	×	×	×	×	×	25	6
Rhizangiidae		×				1	11
Siderastreidae		×	×	×		11	5

(2) many of the studies did not use molecular markers with sufficient resolution to detect significant within-clade diversity

Goulet's (2006) meta-analysis is missing at least 10 studies on the distribution and dynamics of *Symbiodinium* (LaJeunesse et al. 2004a, van Oppen 2004, Chen et al. 2005, McClanahan et al. 2005, van Oppen et al. 2005a,b, Huang et al. 2006, Magalon et al. 2006, Pochon et al. 2006, Thornhill et al. 2006a). Together with 8 more recent studies (Banaszak et al. 2006, Berkelmans & Van Oppen 2006, Garren et al. 2006, Rotjan et al. 2006, Thornhill et al. 2006b, Ulstrup et al. 2006, Warner et al. 2006, Apprill & Gates 2007), this literature is critical to a meta-analysis of coral flexibility, because these studies involve either large sample sizes within single coral species, a high diversity of sampled coral species and/or high resolution techniques suitable for detecting intra-clade diversity.

Of these 18 studies not included in Goulet's analysis, 15 investigated symbiont diversity using a fine-scale molecular marker (the internal transcribed spacer regions of nuclear ribosomal DNA, hypervariable regions in chloroplast 23S rDNA, or microsatellites); 13 of these studies documented coral species with intracladal symbiont diversity. Because significant physiological variability exists within clades (Savage et al. 2002, Tchernov et al. 2004), we cannot ignore the potentially critical role this diversity plays in understanding the physiological capacity of reef corals in response to environmental change.

Stasis vs. change in coral species hosting one clade

Goulet (2006) concludes that the majority of coral species host a single clade of *Symbiodinium*, and that these species exhibit fidelity in their algal genotypes over time, despite transplantation, disease or temperature stress. We suggest that the majority of scleractinian corals in fact host multiple clades, and that corals which host multiple clades shuffle the relative abundance of these symbionts in response to all of the factors listed by Goulet (e.g. Baker 2001, Glynn et al. 2001, Toller et al. 2001, Baker et al. 2004, Chen et al. 2005, Berkelmans & van Oppen 2006, Thornhill et al. 2006a). Moreover, Goulet's conclusion that corals hosting only one clade exhibit algal fidelity is based on studies of only 4 scleractinian and 2 octocoral species (Goulet 2006, her Table 2). Of the scleractinian species, *Fungia scutaria* and *Porites compressa* were represented by a single

individual sampled only once, after transplantation (LaJeunesse et al. 2004b,c), and *Alveopora japonica* hosts multiple clades (Rodriguez-Lanetty et al. 2002), and should not have been included.

In fact, when we include all the available literature, only 3 scleractinian species that have been found so far to host only a single clade (*Pavona gigantea*, *Acropora millepora* and *Agaricia agaricites*) have also been the subject of monitoring studies involving more than one individual (Iglesias-Prieto et al. 2004, Berkelmans & van Oppen 2006, Thornhill et al. 2006b). These data are insufficient to support Goulet's overall conclusion that most corals are unable to change their algae. Studies of mixed-clade symbiont communities have shown these communities to be highly dynamic, and (as we argue here) these findings likely apply to the majority of scleractinian coral species.

Cryptic symbionts are not artifacts

Laboratory cultures of zooxanthellae can become dominated by types of *Symbiodinium* that are not representative of the dominant symbiont in the host from which they were originally isolated (Santos et al. 2001, LaJeunesse 2002). This indicates that algal symbiont communities *in hospite* include novel symbiont types whose relative numerical abundance is below the detection threshold of conventional PCR-based identification methods (typically 5 to 10% of the total symbiont community; Thornhill et al. 2006a). These 'cryptic

tic' symbionts may be critical in providing corals with a greater capacity for symbiont 'shuffling' in response to environmental change (Baker 2003, 2004).

However, Goulet (2006) asserts that there is little or no evidence to support the existence of 'cryptic' symbionts in corals. She argues that unusual symbionts that emerge in culture from a coral source are not evidence of 'cryptic' zooxanthellae, because these symbionts have not been found to associate with that coral in nature, but she provides no alternative explanation for the origin of these unusual symbionts.

Goulet (2006) also argues that the molecular methods that have documented cryptic symbionts are prone to artifacts, and she cites cloning as a particular example of this. However, other molecular approaches, such as denaturing gradient gel electrophoresis, also commonly produce profiles indicating the presence of various unidentified symbiont taxa at background levels (e.g. LaJeunesse et al. 2004a). Moreover, Apprill & Gates (2007) recently used cloning and sequencing to reveal dramatic background diversity in symbiont communities, and provide arguments supporting the authenticity of these findings. Finally, J. C. Mieog et al. (unpubl.) has used quantitative PCR to show that cryptic *Symbiodinium*, undetectable by conventional molecular methods, are common. These background symbionts are not in the same clade as the dominant type, and were documented even in a coral species (*Acropora tenuis*) not known to host multiple clades as an adult. Taken together, the evidence for the presence of background symbionts is overwhelming, and supports the conclusion that most field surveys published to date are extremely likely to have underestimated within-colony *Symbiodinium* diversity at all taxonomic levels.

Conclusions

Although there are a number of mechanisms by which reef corals (as symbioses between cnidarians and dinoflagellate algae in the genus *Symbiodinium*) might respond to climate change (Gates & Edmunds 1999, Coles & Brown 2003), most research has focused on whether or not corals are able to flexibly associate with diverse symbionts whose different physiologies impart greater resistance to environmental extremes (Buddemeier & Fautin 1993, Rowan et al. 1997, Baker 2003, 2004, Baker et al. 2004, Berkelmans & van Oppen 2006). Goulet (2006) has suggested that these findings are likely to apply to only a minority of coral species, but our re-analysis of the literature she cited indicates that she is incorrect to conclude that 'most corals host only one zooxanthella clade and do not change their algae, neither over time, nor after expo-

sure to elevated temperatures, disease, or following transplantation' (p. 1). In fact, although some coral species do appear very specific in their associations with *Symbiodinium* (e.g. Rodriguez-Lanetty et al. 2006), corals as a group exhibit a range of flexibility, with the majority (>>50%) of scleractinian coral species likely to be capable of hosting algal symbionts in different clades, as well as diverse symbionts within a single clade. Scleractinian corals are considerably more flexible than their octocoral counterparts, which may be related to their greater dependence on autotrophy.

There is no doubt that corals are severely threatened by the effects of climate change. However, Goulet's (2006) conclusion that 'the majority of coral species may not be able to switch symbionts and may be in greater peril than some studies imply' (p. 5) is not adequately supported by the data in her meta-analysis. We suggest that a more relativistic perspective, combined with an appreciation of the limited sampling undertaken to date, provides a more accurate picture of flexibility in coral-algal symbiosis and has important implications for understanding and predicting the future of reefs.

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