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A review of soft corals (Octocorallia: Alcyonacea) and their symbionts: Distribution of clades and functionality

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Abstract

Even though soft corals are an integral part of the coral reef ecosystem, very little research has focused on their endosymbiotic association with the zooxanthellae (Symbiodiniaceae). Symbiotic algae appear in soft corals from both the tropical seas as well as temperate regions across the world. The present study provides a list of soft corals along with their associated zooxanthellae using published data. By combining all the data, 52 soft coral species belonging to 21 genera were identified and their corresponding specific Symbiodiniaceae genera were analysed. It was important to initially compare soft corals and distinguish zooxanthellae at clade level to find any host specificity. The vast majority (75 %) of soft corals predominantly hosted the genus *Cladocopium* (Clade C) and therefore the focus of this study was to evaluate its geographical distribution. The genus *Cladocopium* consists of many species which are classified as subclades in this study, exhibiting high intra-clade diversity. For 40 of the 52 soft corals reviewed, 18 % had the same clade type C1 (considered as generalists and ancestral) and 13 % contained the clades C15, C64 and C1:3a, respectively. Analysis showed that some clades (C71a, C15b and C64) were confined to specific geographical regions while clade C1 was distributed worldwide. Understanding the distribution of endosymbionts may enable predictions of which symbioses will survive and exist under future climate change scenarios.

Keywords: soft corals, zooxanthellae, symbiodiniaceae, endosymbiosis, *Cladocopium*

Introduction

Global coral communities have been severely damaged as a result of natural and anthropogenic disasters (Dar *et al.*, 2012), and soft corals which occupy up to 25 % of the primary space (Benayahu, 1995) have been equally affected. About 107 species of soft corals have been reported in Brazilian waters (Almeida *et al.*, 2014), 80 species in the inshore zone of the Red Sea (Dar *et al.*, 2012), and 70 species in Taiwanese reefs (Banayahu *et al.*, 2004). They may also be found in many colder regions such as Antarctica, southern Africa, the Pacific Northwest coast of North America, and the North Atlantic (Haverkort-Yeh *et al.*, 2013). Sesoko Island, Japan, is best known for soft coral coverage of as high as 34.4 % (Loya *et al.*, 2001). The presence of octocorals in most benthic habitats under the influence of various environmental factors, indicates the adaptive nature of this taxonomic group (van de Water *et al.*, 2018).

The most conspicuous feature of soft corals is the polyps which contain eight tentacles (hence octocorals) that are invariably pinnate (Janes and Lee, 2007). For some genera, the tentacles contain sensory cells which are filled with zooxanthellae, unicellular photosynthetic microalgae belonging to the Symbiodiniaceae (Order Suessiales, Class Dinophyceae) (Fournier, 2013).

These symbiotic types of soft corals have a tendency to be found in shallow tropical and subtropical waters (Cooper *et al.*, 2014). The host and the symbiont hold a mutualistic relationship, where the symbiont receives inorganic nutrients from the host and in-turn provides translocated photosynthetic products necessary for host functions (Muscatine, 1990) such as calcification and reproduction (Farag *et al.*, 2018). Farag *et al.* (2018) further stated that the formation of the modern

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coral reef ecosystem and the contributions to global carbon and biogeochemical cycles is due to the mutualistic exchange of metabolites between the host, the zooxanthellae and their associated microbial assemblages. Unlike hard corals, soft corals exhibit mostly a mixotrophic nature (Fabricius and Klumpp, 1995; Slattery *et al.,* 2019). Depending on symbiont diversity, the host trophic mode can be autotrophic or heterotrophic (Baker *et al.,* 2015). Similar to scleractinian corals, heterotrophic feeding in soft corals is also increased by the energy provided by the Symbiodiniaceae (Slattery *et al.,* 2019) and allow corals to thrive in oceanic deserts (nutrient-poor environments) (Houlbrèque and Ferrier-Pagès, 2009). Both hard and soft corals acquire their symbionts by vertical and horizontal transfer. The diversity of symbionts is higher in hard corals but at the same time the association of Symbiodiniacea in soft corals is more stable than that of the hard corals (Poland and Coffroth, 2016). Compared to zooxanthellate octocorals, azooxanthellate (absence of dinoflagellates) octocorals populate deep and dark environment where they rely solely on heterotrophic feeding (Fabricius and Klumpp, 1995).

Research on different soft corals such as the genera *Sarcophyton, Sinularia, Xenia* and *Lobophytum* has demonstrated that a similar endosymbiotic relationship exists between the zooxanthellae and the soft coral hosts (Sammarco and Strychar, 2013). Extensive studies over the past 60 years on the physiological contribution of the zooxanthellae to symbiosis unveiled their major role in the nutrition of the host (Santos *et al.,* 2002). Furthermore, some reviews highlighted that depending on the local environment as well as the microhabitats within a host, some adult coral species can couple with different dinoflagellates from the genera of Symbiodiniaceae (Little *et al.*, 2004). In tropical reefs, an increase in the diversity of symbiotic Symbiodiniaceae may improve the adaptability of coral to climate change (Qin *et al.,* 2019). This particular form of association, termed polymorphic, implies that corals from the same species may not be physiologically similar and the presence of a particular zooxanthellae may play a role in determining the physiology of the host-symbiont endosymbiosis association (Toller *et al.* 2001). The ability of the host to acquire multiple symbiont phylotypes depends also on the host age (Poland and Coffroth, 2016). The work carried out by Poland and Coffroth (2016) has shown that the octocoral *Briareum asbestinum* can easily harbour up to 11 symbiont phylotypes, with single polyps capable of harbouring at least 6 phylotypes simultaneously in its juvenile state of life, while the adult colonies are in symbiotic association with only 1 or 2 symbiont phylotypes.

Rowan and Powers (1992), who spearheaded phylogenetic work on *Symbiodinium*, used nuclear ribosomal small subunit (nr18s) sequences to obtain 3 key clades (A-C). Various nuclear ribosomal large subunit (nr28s) sequences were assigned to different host taxa as well as larger geographic parameters (Santos *et al.*, 2002) to ultimately obtain 9 *Symbiodinium* lineages, with suggestions that many more genetic variations exist within the clades (Davis *et al.*, 2017). Some questions have been raised on the phylogenetic techniques used in the study of zooxanthellae. Rowan *et al.* (1996) addressed, and Santos *et al.* (2001) questioned, the un-established culture techniques used for zooxanthellae and the dilemma of excluding un-culturable microalgae. This exclusion led to a lack of crucial data and a limited sample size for the phylogenetic studies. Additionally, Rowan (1998) mentioned that some of the members of the zooxanthellae still remain uncultured and lack description. The presence of many morphological characters and the lack of sexual reproduction in this algal group has not allowed the evolutionary groups within the zooxanthellae to be adequately described (Wilcox, 1998). Consequently, it has been suggested that these techniques have limited use in phylogenetics (Schoenberg and Trench, 1980). Despite the comprehensive body of physiological knowledge, the understanding on the phylogenetics of zooxanthellae remains unresolved.

Previously, researchers assumed that all zooxanthellae were associated with a single accepted species, *Symbiodinium microdriaticum* (Freudenthal) (Taylor, 1974). The heterogeneity of zooxanthellae in response to different hosts was addressed by various researchers (eg. Santos *et al.*, 2002; Trench, 1993; Rowan, 1998; Schoenberg and Trench, 1980). The existence of a single genus comprising of hundreds of both closely and distantly related species is most likely to generate confusion (LaJeunesse *et al.*, 2018). Interestingly, recent in-depth research by LaJeunesse *et al.* (2018) explained the evolutionary divergence of *Symbiodinium,* previously referred as to as 'clades', as being analogous to the genera in the family Symbiodiniaceae. Systematic revision was needed due to low transcript similarity (<20 % orthologous gene loci) between the Symbiodiniaceae clade recognized by Bayer *et al.* (2012). Moreover, high species diversity among Symbiodiniaceae distributed across highly diverse marine organisms, and ecologically diverge lineages, increased the importance for a systematic revision (LaJeunesse *et al.,* 2018). LaJeunesse *et al.* (2018) redefined the genus *Symbiodinium sensu strictu* to Clade A and also defined several new genera: B as *Brevidum*, C as *Cladocopium*, D as *Durusdinium*, E as *Effrenium*, F as *Fugacium* and G as *Gerakladium*. Additionally, the lineage encompasses multiple distinct genetic types which are highly variable (LaJeunesse *et al.,* 2018).

Increase in temperature and loss of Symbiodiniaceae in soft corals: a reality or a myth?

It is no more a myth that worldwide coral bleaching, due to loss of zooxanthellae, is a heat stress response to an increase of sea surface temperature above the mean yearly maximum or elevated above 30 °C (Brown, 1990). Several reports have documented that corals are affected by long term temperature exposure above 30 °C and that they usually condition themselves to global heat stress (Strychar *et al.*, 2005). Adaptive bleaching hypothesis (Fautin and Buddemeier, 2004) proposed that bleaching provides an opportunity for corals to change their algal communities to acquire more heat-resistant algal species. High mortality rates due to bleaching episodes have been reported and there is now good evidence to show that in response, zooxanthellae communities may change following bleaching in at least a few coral species. The soft coral host and the zooxanthellae display different degrees of adaptation to rising sea surface water temperature (Sammarco and Strychar, 2013). Barshis *et al.* (2014) explained how the host usually has a stronger transcriptional response to stress changes, while the Symbiodiniaceae is deprived of this transcriptional response. Lack of transcriptional responses was identified in Symbiodiniaceae D2 and C3k when exposed to heat stress, which differ generally from the transcriptional shifts in coral hosts (Barshis *et al.,* 2014). Fitt *et al.* (2000) monitored the growth rate of several Symbiodiniaceae and found that temperature plays a vital role in their optimal growth and photosynthetic rate. Moreover, zooxanthellae can display optimal growth rates at temperatures between 26 °C – 32 °C, with some growing best at 26 °C with death occurring at 32 °C (Fitt *et al.,* 2000). Yet exceptions exist, such as in the Persian Gulf where some zooxanthellae (mainly the thermotolerant lineage *S. thermophilium*) have adapted to temperatures as low as 13 °C and as high as 38 °C (Sammarco and Strychar, 2013). The density of zooxanthellae in soft corals usually varies seasonally (Fitt *et al.,* 2000), but after abnormal seasonal change, it is vital that they become re-established within a few days or weeks to prevent the corals from dying (Sammarco and Strychar, 2013). The re-establishment of zooxanthellae is time dependant and this process can be hindered by factors such as salinity, pollution, ocean acidification and diseases. The 'layered cell' hypothesis describes how the Symbiodiniaceae population increases within the layers of soft corals, with the outer layer having a higher zooxanthellae density than the inner layers. The cells located deeper within the soft corals are exposed to lower light intensity and are less adapted to resist thermal and UV fluctuation than the resistant cells located in the upper layers. When loss of upper layer zooxanthellae cells occurs due to a rise in temperature above the tolerant value, the less-resistant inner layer cells are exposed to temperature and UV differences, making them more vulnerable and causing dissociation from the soft corals. This explains the concept of the 'two large bursts' of Symbiodiniaceae loss in soft corals elucidated by Strychar *et al.* (2005). Corals in general, and mainly octocorals, have an obligate association with the zooxanthellae, which even after an overproduction of reactive oxygen species (ROS), do not expel the symbionts, which instead migrate to the stolon (Parrin *et al.*, 2016). The symbionts still possess photosynthesis power after full migration to the stolons (van de Water *et al.,* 2018).

Extreme storm events as reported by Emanuel (2013) can cause serious damage to coral reefs, and ocean acidification undoubtedly affects physiological processes in corals (Doney *et al.,* 2009). The drop in pH limits the capacity to produce calcium carbonate structures and limits algal photosynthetic productivity (Sogin *et al.,* 2016). The work by Farag *et al.* (2018) clearly demonstrated that an increase in CO_2 levels results in a change in both polar and non-polar metabolism in soft corals. However, the change in metabolic reaction varies depending on the species. Interestingly, when exposed to an increase in CO_2, nicotinic acid was released from *S. glaucum* but not from *S. ehrenbergi* (Farag *et al.,* 2018). Farag *et al.* (2018) suggested that the release of nicotinic acid may account for the increased stress resistance of *S. glaucum* compared to *S. ehrenbergi*, however no further published records are available. Alteration of metabolites (amino acids, polyamines, nitrogenous compounds) can act as biomarkers for predicting the impact of stress.

The objective of this review is to understand the distribution of different type of endosymbionts in soft corals (Octocorallia:Alcyonacea). The soft corals and their associated symbionts were listed demonstrating that the majority of the soft corals form an endosymbiotic association with *Cladocopium.* The specificity of the genus *Cladocopium* and its geographical distribution was also reviewed.

Methods

Data from various reports were compiled into one large data set. The Symbiodiniaceae data were taken from field-collected soft corals and not from zooxanthellae culture due to the probability of overlooking non-culturable Symbiodiniaceae (Goulet and Coffroth, 1997; Santos *et al.,* 2001; LaJeunesse, 2002). Most reports identified zooxanthellae at the genus level, with some reporting within-clades resolution. If a soft coral was not identified to the species level, the genus was noted with a 'sp.' notation. To be more explicit, each genus level (soft corals) was treated as a different species. Such an approach diminishes misinterpreting the species hosting a single Symbiodiniaceae. Furthermore, the latest systematic revision of the zooxanthellae (LaJeunesse *et al.,* 2018) was taken into account while pooling the various data on soft corals and their particular endosymbionts. Using the compiled data set, a dendrogram was generated using the SPSS statistics 20 programme. Particularly, Average Linkage (between groups) was used to generate the phylogenetic tree based on the Symbiodiniaceae possessed by the soft corals. Less emphasis was given to the collection depth of the soft corals while constructing the dendrogram. A combined data set of soft corals with the specific genus *Cladocopium* type from various geographic locations was evaluated.

Results

Soft corals and their associated zooxanthellae

Fifty-two soft coral species belonging to 21 genera from the families Alcyoniidae, Nephteidae and Xeniidae obtained from various research works as well as their corresponding Symbiodiniaceae genera were studied. The depth from which the soft corals were collected ranged from 1 m to a maximum depth of 40 m. Moreover, 60 % of the soft corals were from Australia (Great Barrier Reef and Lizard Island), while the rest were from the Red Sea, Hawaii, Fiji, Guam and China. Most reports identified the soft corals up to species level, yet some were limited to genus level. The Symbiodiniaceae genera reported in the soft corals were *Symbiodinium* (Clade A), *Breviolum* (Clade B), *Cladocopium* (Clade C), *Durusdinium* (Clade D) and *Gerakladium* (Clade G) (Table 1). Interestingly, it can be inferred that the majority of the soft corals form an endosymbiotic association with *Cladocopium* (Clade C) (Fig. 1). Soft corals in multiple sites from the Great Barrier Reef (GBR), Guam, Fiji, Japan, Red Sea and Hawaii hosted predominantly clade C zooxanthellae (Table 1). Genus *Symbiodinium* was found in soft corals sampled from Hawaii, Israel, and the GBR, while *Breviolum, Durusdinium* and *Gerakladium* were only found in GBR.

The results from the dendrogram (Fig. 2) clearly show that all soft corals hosting the genus *Cladocopium* clustered together, irrespective of the depth from where they were collected. Similar results were obtained for soft corals hosting the genus *Durusdinium* and *Symbiodinium*. *Nephthea* sp. from the family Nephtheidae were found in the different clusters due to the presence of distinct zooxanthellae. They hosted different zooxanthella clades at different geographic locations (LaJeunesse and Trench, 2000); namely genus *Cladocopium* from Israel, *Durusdinium* and *Breviolum* from Australia, and *Symbiodinium* from the Red Sea. It can also be inferred that cladal specificity does not occur at the family level of soft corals. In the family Alcyoniidae, all 20 species host genus *Cladocopium*, with two species also hosting genus *Durusdinium* and genus *Symbiodinium*. In the 15 Nephtheidae species, 7 hosted the genus *Cladocopium,* 2 hosted genus *Durusdinium,* 3 hosted genus *Symbiodinium,* 1 hosted the genera *Breviolum* and *Gerakladium*, and one hosted multiple zooxanthella (A, C). The greater diversity of zooxanthellae clades was observed in the family Nephtheidae. In the family Xenidae, 12 species hosted genus *Cladocopium*, and 1 hosted the genera *Durusdinium* and *Symbiodinium,* respectively. Furthermore, specific zooxanthellae genera were distributed globally while others exhibited a restricted distribution. Genus *Cladocopium* was globally distributed while genus *Symbiodinium* was very common in soft coral species in Australia, the Red Sea and Hawaii., based on data that are available. Interestingly, the genera *Durusdinium, Breviolum* and *Gerakladium* were restricted in soft corals from Australia. Aside from geographical location, the depth the soft corals were sampled from also defines the cladal specificity. The majority of the soft corals hosting the genus *Cladocopium* were obtained from a wide depth range from 1 m to 40 m (*Sarcophyton* sp. - 1.5 m; *Sinularia polydactyla* – 2-6 m, *Sinularia lochmodes* - 7-10 m, *Klyxum* sp. – 10-17 m, *Rhytisma fulvum fulvum* - 3-40 m) while the genera *Durusdinium, Symbiodinium* and *Gerakladium* were mostly found in soft corals at a depth of <20 m. The genus *Breviolum* was collected from soft corals at a depth of 3 m.

Table 1. List of soft corals and their associated Symbiodiniaceae genera from tropical and temperate regions. GBR: Great Barrier Reef, NA: Not available.

Family	Genus	Species	Location	Reported depth range/m	Symbiodi-niaceae genera	Citation
Alcyoniidae	*Sarcophyton*	*ehrenbergi*	GBR Australia	7-10	C	Sammarco and Strychar, 2013
		glaucum	Australia	NA	A	Carlos *et al.*, 1999
		sp.	Lizard Island Australia	1.5	C	van Oppen *et al.*, 2005
		sp.	South China Sea	5	C	Gong *et al.*, 2018
		trocheliophorum	Eilat's reef Red sea	<20	C	Barneah *et al.*, 2004
	Sinularia	*lochmodes*	GBR Australia	7-10	C	Sammarco and Strychar, 2013
		gardinen	Eilat's reef Red sea	<20	C	Barneah *et al.*, 2004
		querciformis	Eilat's reef Red sea	<20	C	Barneah *et al.*, 2004
		polydactyla	Australia	2-6	C	Goulet *et al.*, 2008
		abrupta	Hawaii	2-6	C	Goulet *et al.*, 2008
		erecta	Fiji	2-6	C	Goulet *et al.*, 2008
		flexibilis	Australia	2-6	C	Goulet *et al.*, 2008
		gyrosa	Fiji	2-6	C	Goulet *et al.*, 2008
		maxima	Guam	2-6	C	Goulet *et al.*, 2008
	Lobophytum	sp.	Lizard Island Australia	1.5	C	van Oppen *et al.*, 2005
		compactum	Australia	2-6	C	Goulet *et al.*, 2008
	Cladiella	*pachyclados*	Eilat's reef Red sea	<20	C	Barneah *et al.*, 2004
		tuberculoides	Israel	<20	C	Barneah *et al*, 2004
		sp.	Australia	2-6	C	Goulet *et al.*, 2008
		sp.	Australia	<18	D	van Oppen *et al.*, 2005
	Rhytisma	*fulvum fulvum*	Australia Israel	3-40	C	Barneah *et al.*, 2004
	Klyxum	sp.	Australia	10-17	C	LaJeunesse *et al.*, 2004 ; van Oppen *et al.*, 2005
		sp.	Australia	<18	D	van Oppen *et al.*, 2005

Family	Genus	Species	Location	Reported depth range/m	Symbiodiniaceae genera	Citation
Nephtheidae	*Capnella*	*lacerthliensis*	Northern GBR Australia	2-6	C	Goulet *et al.*, 2008
		sp.	Northern GBR Australia	<18	A,C	van Oppen *et al.*, 2005
		sp.	GBR Australia	<15	D	van Oppen *et al.*, 2005
	Lemnalia	sp.	Australia	<15	C	Goulet *et al.*, 2008; van Oppen *et al.*, 2005
	Litophyton	*arboreum*	Australia Israel	<20	A	Goulet *et al.*, 2008; Barneah *et al.*, 2004
	Nephthea	sp.	Eilat's reef Red sea	<20	A	Barneah *et al.*, 2004
		sp.	Israel	<20	C	Goulet *et al.*, 2008
		sp.	Australia	3	B	LaJeunesse *et al.*, 2003
		sp.	Australia	>3	D	LaJeunesse *et al.*, 2003
	Paralemnalia	*thyrsoides*	Red sea	<20	C	Barneah *et al.*, 2004; Goulet *et al.*, 2008
		digitiformis	Australia	2-6	C	Goulet *et al.*, 2008
		eburnea	Australia	<20	C	Barneah *et al.*, 2004
	Stereonephth-ya	*cundabiluensis*	Red sea	<20	A	Barneah *et al.*, 2004
		sp.	Australia	<15	G	van Oppen *et al.*, 2005
		sp.	Fiji	2-6	C	Goulet *et al.*, 2008
Xenidae	*Anthelia*	*edmondsoni*	Hawaii	2-6	A	Goulet *et al.*, 2008
		glauca	Israel	<20	C	Barneah *et al.*, 2004
	Asterospicularia	*laurae*	Australia	2-6	C	Goulet *et al.*, 2008
	Bayerxenia	sp.	Lizard Island Australia	1.5	C	Ziegler *et al.*, 2018

Family	Genus	Species	Location	Reported depth range/m	Symbiodiniaceae genera	Citation
Xenidae (continued)	Cespitularia	sp.	Australia	<15	C	van Oppen *et al.*, 2005
	Efflatounaria	sp.	Australia	2-6	C	Goulet *et al.*, 2008
	Heteroxenia	*fuscescens*	Israel	2-6	C	Behayahu, 1991; Goulet *et al.*, 2008
		sp.	Australia	<10	C	LaJeunesse *et al.*, 2004
	Sarcothelia	sp.	Hawaii	<10	C	LaJeunesse *et al.*, 2004
	Sympodium	sp.	Australia	<15	D	van Oppen *et al.*, 2005
	Xenia	*macrospiculata*	Israel	<20	C	Barneah *et al.*, 2004
		umbellata	Israel	<20	C	Barneah *et al.*, 2004 Behayahu, 1991
		elongata	GBR Australia	7-10	C	Sammarco & Strychar, 2013
		farauensis	Eilat's reef Red sea	<20	C	Barneah *et al.*, 2004

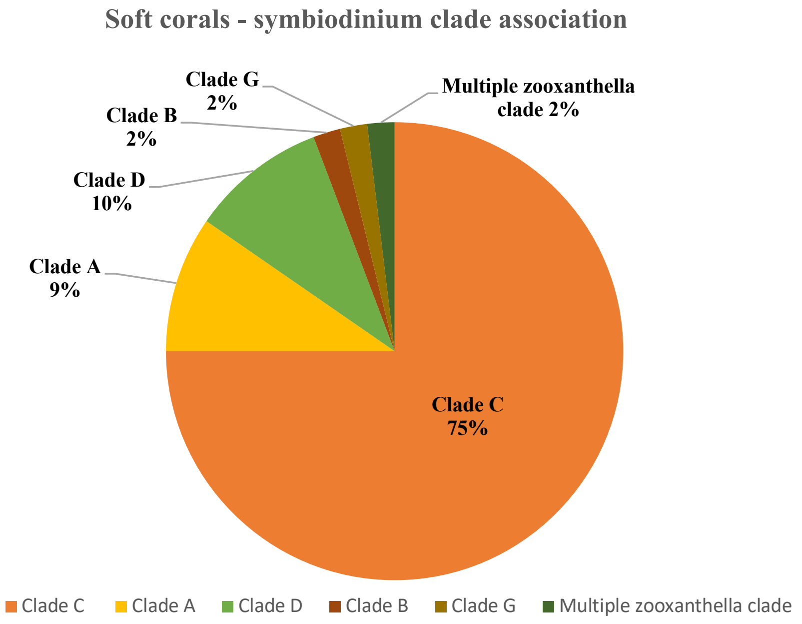

Figure 1. Frequency of each symbiodiniacea genus in the soft corals from the regions mentioned above (Table 1). The species were classified as hosting multiple genera when occurring in either the same or different colonies.

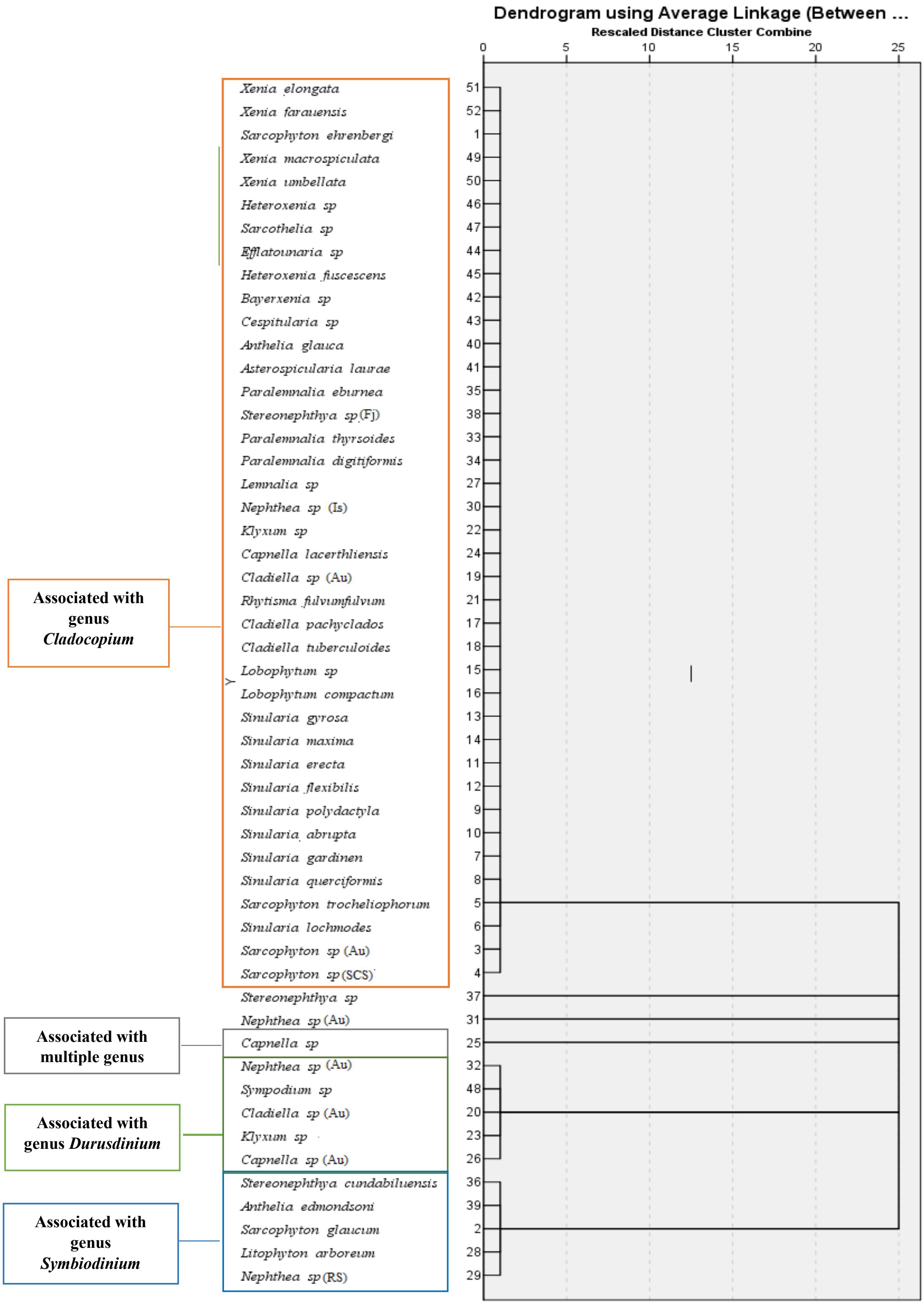

Figure 2. Dendrogram based on the average linkage (between group) method using the different Symbiodiniaceae associated with the different soft corals. Au: Australia; SCS: South China Sea; Fj: Fiji; RS: Red Sea

Soft corals and genus *Cladocopium* (clade C) specificity

Forty out of the 52 soft corals reviewed were found to be associated with *Cladocopium* (clade C). The results from Table 2 summarise how different soft corals have the ability to host multiple *Cladocopium* subclades at different collection depths. For example, *Paralemnalia digitiformis* from Australia has been found to harbour C1:2 and C64, and *Heteroxenia* sp. from Australia is associated with C15, C15e and C64 (Table 2). The data showed that the all the genus *Cladocopium* subclade was obtained from soft corals sampled from a depth of less than 20 m. Furthermore, Fig. 3, constructed from 40 soft corals, illustrates that 18 % have the same type C1 (considered as generalists and ancestral), 13 % contain the C15, C64 and C1:3a respectively, 8 % harbour C3j and C1:2, 5 % have C1c and C65, and finally 3 % contain C3, C1:1, C71a, C1k, C15e, C1q, C15b and C84a, respectively.

The results shown in Fig. 4 illustrate the global distribution of genus *Cladocopium* type in soft corals. Specialized symbionts (such as C71a, C1:2, C15b, C15, C1z) displayed limited ranges in geographic distribution. C71a is dominant in soft corals in the region of Japan and C15b only in Hawaii. Soft corals from the tropical zone are more likely to host a wide variety of Clade C type. Australia, being partially in the sub-tropical zone, hosts various Clade C types (C1, C64, C1:3a, C1c, C1q, and many more). C1 (generalist) is known to be distributed worldwide in various hosts, but due to limited research having been conducted on soft corals and their symbionts, it is difficult to show the generalist nature of C1. From Fig. 4, it can be seen that C1 was present in various soft coral species from Australia and New Zealand.

Table 2. List of soft corals and their associated Clade C subclade.

Soft corals Host	Clade C subclade	Location	Reported depth range/m	Citation
Klyxum sp.	C1	Australia	<18	van Oppen *et al*, 2005
	C64	Australia	10-17	LaJeunesse *et al.*, 2004a
Lobophytum compactum	C1:3a	Australia	2-6	Goulet *et al.*, 2008
Lobophytum sp.	C1	Australia	<17	LaJeunesse *et al.*, 2004a
	C3j	Australia	2-4	LaJeunesse *et al.*, 2003
Rhytisma sp.	C1	Australia	<18	van Oppen *et al.*, 2005
	C1:1	Australia	2-6	Goulet *et al.*, 2008
Sarcophyton sp.	C1	Australia	<17	LaJeunesse *et al.*, 2004a
	C65	Australia	<17	LaJeunesse *et al.*, 2004a
	C71a	Japan	<10	LaJeunesse *et al.*, 2004a
	C1:3a	Australia	2-6	Goulet *et al.*, 2008
	C3j	Australia	<10	LaJeunesse *et al.*, 2003
Sinularia flexibilis	C1:3a	Australia	2-6	Goulet *et al.*, 2008
Sinularia polydactyla	C1:3a	Australia	2-6	Goulet *et al.*, 2008

Soft corals Host	Clade C subclade	Location	Reported depth range/m	Citation
Sinularia sp.	C1c	Australia	5	LaJeunesse *et al.*, 2003
	C65	Australia	10-17	Goulet *et al.*, 2008
	C1	New Zealand	10	Wicks *et al.*, 2010
	C3	New Zealand	10	
	C3j	Australia	<10	
	C1z	New Zealand	5-10	
Nephthea sp.	C1 C1:2	Australia	2-6	Goulet *et al.*, 2008
Paralemnalia digitiformis	C1:2 C64	Australia	2-6	Goulet *et al.*, 2008
Paralemnalia thyrsoidea	C1:2	Australia/ Israel	2-6	Goulet *et al.*, 2008
Stereonephthya sp.	C15	Australia/ Fiji	2-6	Goulet *et al.*, 2008
Anthelia sp.	C64	Australia	10-17	LaJeunesse *et al.*, 2004a
	C84a	Australia	2-6	Goulet *et al*, 2008
Sarcothelia sp.	C15b	Hawaii	10-20	LaJeunesse *et al.*. 2004b
Asterospicularia laurae	C15	Australia	2-6	Goulet *et al.*, 2008
Cespitularia sp.	C15 C1q C1	Australia	<15	van Oppen *et al.*, 2005 Goulet *et al.*, 2008
Efflatounaria sp.	C1c C1:3a	Australia	2-6	Goulet *et al.*, 2008
Heteroxenia sp.	C15	Australia	10-17	LaJeunesse *et al.*, 2004a
	C15e			
	C64		1-17	
Xenia sp.	C1	Australia	<18	van Oppen *et al.*, 2005
	C1k C64	Australia	15 3-17	LaJeunesse *et al.*, 2003
	C15	Israel	2-6	Goulet *et al.*, 2008

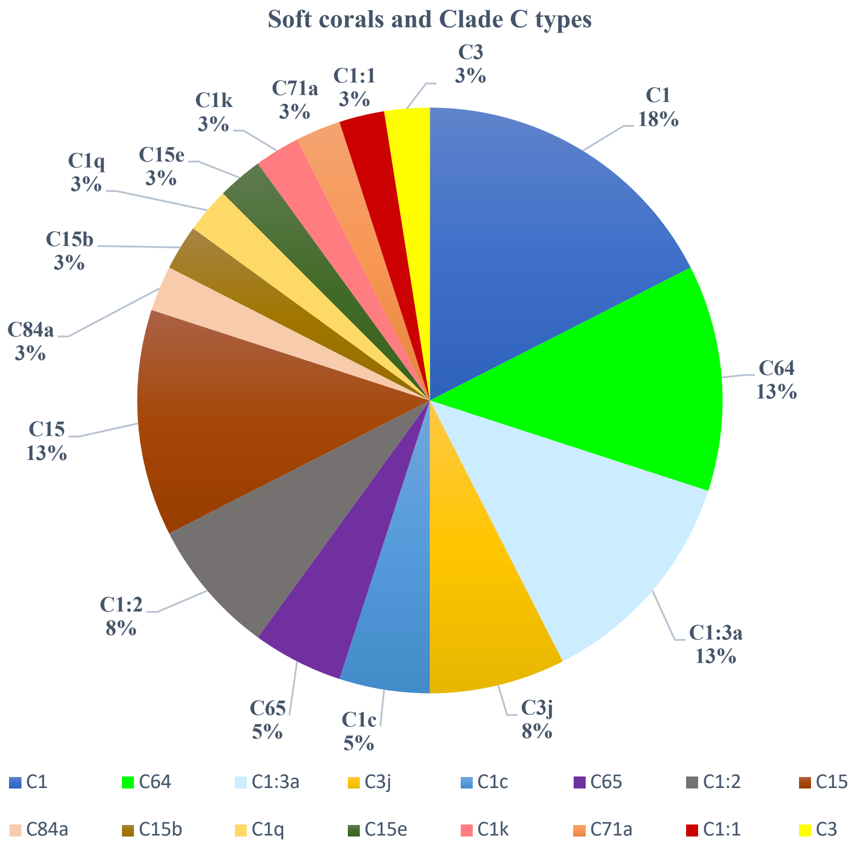

Figure 3. Frequency of each Clade C (*Cladocopium*) subclade in the soft corals mentioned above in Table 2.

Discussion

Soft corals form an integral part of the coral reef community worldwide, yet very little research has focused on the Symbiodiniacea genera they possess (Goulet *et al.*, 2008; Barneah *et al.*, 2004; van Oppen *et al.*, 2005). The data compiled in this study revealed the array of Symbiodiniacea associated with tropical and temperate soft coral species. Three main factors were reported to play a role in the specificity of Symbiodiniaceae; namely the ability to host multiple clades (Goulet *et al.,* 2008), the mode of acquisition of zooxanthellae (Barneah *et al.,* 2004), and finally geographical location / bathymetric distribution (Iglesias-Prieto *et al.*, 2004).

Specificity of Symbiodiniaceae clades hosted by soft corals

The diversity and complexity of the Symbiodiniacea genera has prompted researchers to explore cladal specificity. The specificity of the host and associated symbionts can explain the difference in coral physiology (growth rate, photophysiology, thermal stress resistance, bleaching and disease susceptibility) (Stat *et al.*, 2009). Several hypotheses have been proposed to explain the degree of specificity of Symbiodiniacea genera.

Ability to host single/multiple zooxanthellae and zooxanthellae density

One of the proposed theories holds that the specificity of a Symbiodiniacea genus is defined by the ability of some soft corals (eg. *Sinularia* sp., *Lobophytum* sp. and *Xenia* sp.) to host a single zooxanthellae clade at a time (Goulet *et al.,* 2008). These types of soft corals may not change their symbionts even if a change in environmental condition occurs (Gaulet, 2006). A change such as a rise in sea surface temperature will cause bleaching and eventually death of the corals if they fail to acquire the same symbionts again in a specific time period (Sammarco and Strychar, 2013). However, octocorals hosting a single clade are found to be more stable over time and space when subjected to different thermal stresses as compared to the scleractinian corals (Tamar and Marie Alice, 2003).

It is interesting to note that some soft corals such as the *Capnella sp.* may host more than one zooxanthellae

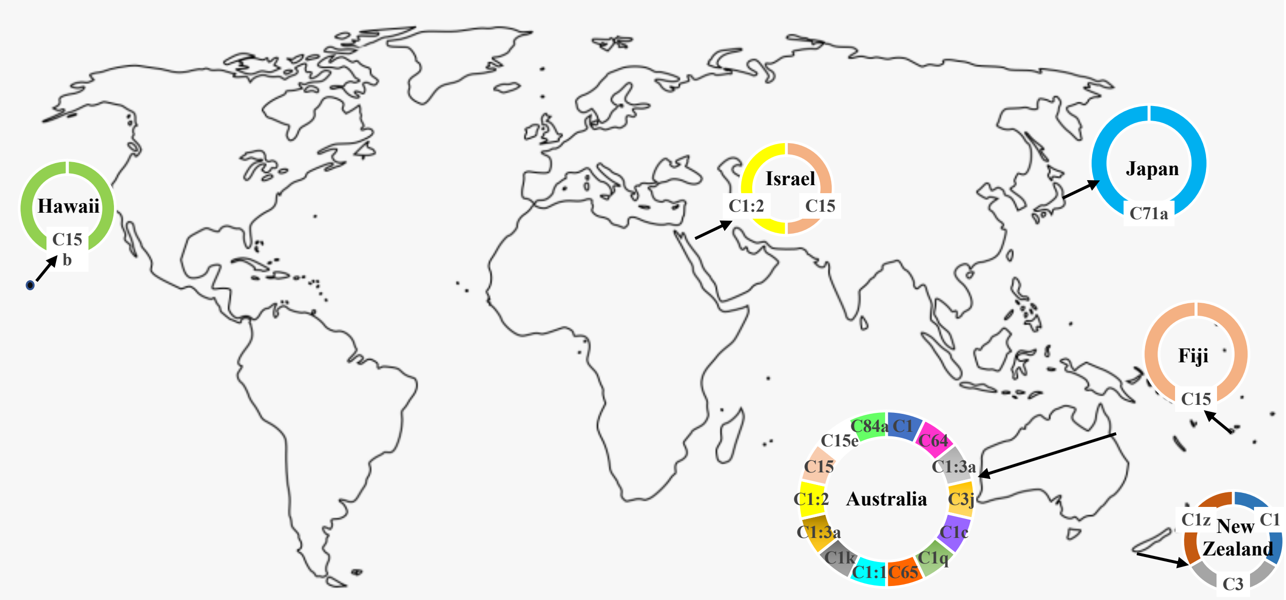

Figure 4. Global distribution of genus *Cladocopium* type in soft corals. Pie charts represent the percentage of each genus *Cladocopium* type at each geographic location.

genus at a time (van Oppen *et al.,* 2005). One possible explanation is that before one of the genera gets outcompeted, a change in the climatic condition may result in a change in the dominancy of a particular zooxanthellae genus (Carlos *et al.,* 2000). Intraspecific zooxanthellae diversity on a single host is not confined to soft corals communities, and has also been found in scleractinian corals (Baker, 1999, 2001; Baker *et al.*, 1997; Glynn *et al.*, 2001; LaJeunesse, 2001, 2002; LaJeunesse *et al.*, 2003; Pawlowski *et al.*, 2001; Pochon *et al.*, 2001; Santos *et al.,* 2001; Van Oppen, 2001, Howells *et al.,* 2013), foraminiferans (Pawlowski *et al.*, 2001; Pochon *et al.*, 2001), gorgonians (Coffroth *et al.*, 2001; Santos *et al.*, 2003; Goulet and Coffroth, 1999, 2003a, b), hydrocorals (Baker, 1999; LaJeunesse 2002) and anemones (Santos *et al.,* 2003). Scleractinian corals hosting multiple symbionts have been known for decades. For example, Baker and Romanski (2007) reported that 38 of 59 (64 %) of hard corals surveyed contained multiple symbionts.

Contrarily, the type and ability to host different/single clades defines the potential of a coral to withstand thermal stress, but zooxanthellae density (ZD) in the host also plays an important role (Xu *et al.*, 2016). For example, hard corals such as massive *Favia* and *Porites* with high ZDs are less vulnerable to thermal bleaching as compared to branching *Acropora* corals with a low ZD (Li *et al.*, 2008; Li *et al.*, 2011). Further research and evidence is needed to confirm the effect of zooxanthellae density on the host and thermal tolerance (Qin *et al.,* 2019).

Mode of acquisition

Barneah *et al.* (2004) worked on cladal specificity and explained how this to some extent depends on the mode of acquisition of zooxanthellae. Soft corals hosting the genus *Cladocopium* 'clade C' mainly acquire their symbionts through horizontal acquisition from the environment, while those hosting the genus *Symbiodinium* acquire theirs directly from their parents (Barneah *et al.*, 2004). Horizontal transmission patterns are advantageous for both hard and soft corals to form associations with Symbiodiniaceae which are heat-tolerant (Boulotte *et al.*, 2016). The mode of acquisition may not always explain the distinct Symbiodiniacea genera in soft corals as exemplified by *Stereonephthya* sp. belonging to the family Nephtheidae (Goulet *et al.*, 2008). Van Oppen *et al.* (2005) stated that the symbionts associated with *Stereonephthya* are facultative as most members of that particular group are azooxanthellate. Several studies (Barneah *et al.,* 2004; Goulet *et al.,* 2008; van Oppen *et al.,* 2005) showed that *Stereonephthya* sp. form an endosymbiotic association with different zooxanthellae in distinct environments. *Stereonephthya cundabiluensis* from the Red Sea (Barneah *et al.,* 2004) host the genus *Symbiodinium*, while the other *Stereonephthya* sp. from Australia (van Oppen *et al.,* 2005) and Fiji (Goulet *et al.,* 2008) host the genus *Gerakladium* and *Cladocopium,* respectively. Barneah *et al.* (2004) mentioned that the reason for *Stereonephthya cundabiluensis* hosting *Symbiodinium* is due to the fact that the symbionts are obtained vertically. It is currently unclear as to how the other

Stereonephthya sp. have a variety of symbionts. Poor correlation between transmission mode and zooxanthellae type was also observed in the scleractinian corals *Montipora* sp. and *Acropora* sp. (van Oppen, 2004).

Geographical location/bathymetric distribution

Geographical location plays a role in clade distribution within the soft corals. Van de Water *et al.* (2018) emphasized the dominancy of some genera based on their geographical location. Red Sea and Pacific Ocean octocorals are dominated by *Cladocopium,* Mediterranean octocorals by *Symbiodinium*, while those in the Caribbean are dominated by *Breviolum.* However, the lack of high resolution spatial and temporal biological and environmental data has resulted in many fundamental gaps in the understanding of zooxanthellae biogeography (Cooper *et al.,* 2011). Latitudinal variations in coral-algal symbiosis have been reported by Baker (2003). Studies on scleractinian corals have documented that *Symbiodinium*, *Breviolum* and *Fugacium* are more common at higher latitudes, while *Cladocopium* tends to be more common in the tropics (Rodriguez-Lanetty *et al.,* 2001, 2002; Savage *et al*., 2002; reviewed in Baker, 2003). However, all these studies concluded that the clade distributions which vary worldwide are governed by temperature and light factors (Rowan and Knowlton, 1995; Baker, 2003; Toller *et al*., 2001; Ulstrup and van Oppen, 2003; Fabricius *et al.,* 2004; Rowan, 2004).

Another factor that determines the clade specificity is location (i.e. depth). Light intensity is directly proportional to depth, and soft corals will likely host distinct genotypes or species of zooxanthellae dependant on depth (Iglesias-Prieto *et al.*, 2004). In the case of *Nephthea* sp. in Australia (LaJeunesse *et al.,* 2003) specimens collected from a depth of 3 m harboured the genus *Breviolum* while those collected at a depth of >3 m hosted the genus *Durusdinium.* However, the evidence for this is not conclusive as LaJeunesse *et al.* (2018) indicated that the genus *Breviolum* occurs in hosts found at depths ranging from 5-30 m. Moreover, soft corals hosting the genus *Cladocopium* were obtained from a wide depth ranging from 1 m to 40 m. LaJeunesse *et al.* (2018) identified this particular genus as being symbiotic with soft corals across depths ranging from the intertidal to the mesophotic zone. Additionally, the genus *Symbiodinium* are adapted to high light intensity (LaJeunesse *et al.,* 2018) explaining why most soft corals harbouring this genus were all from a depth of less than 20 m. In addition, the genus *Durusdinium* reported from marginal reef environments can tolerate stressful environments and are resistant to coral bleaching, thus explaining their presence in soft corals at depths of less than 18 m (Table 1). Furthermore, the genus *Durusdinium* has been reported to occur in areas where turbidity is high (Chen *et al.,* 2003).

Increasingly frequent and harsh episodes of coral bleaching and mortality have been reported in recent decades. An increase of sea surface temperature above 30°C (Brown, 1990) (usually occurring at 20 m below the sea surface) causes the soft corals to dissociate from their symbionts, and the specificity of particular zooxanthellae genera defines the degree to which bleaching takes place. Soft corals hosting genus *Durusdinium* (extremophile) are more likely to increase the thermal tolerance of the coral (Ulstrup and van Oppen, 2003) compared to those hosting genus *Cladocopium*. Hosts harbouring genus *Symbiodinium* and *Breviolum* are considered more susceptible to bleaching compared to the other genera (Baker *et al.,* 1997). Therefore, it can be concluded that corals hosting unique or multiple symbiotic Symbiodiniaceae have varying abilities to deal with environmental stress (Sampayo *et al.*, 2008; Silverstein *et al.*, 2015).

Specificity of genus Cladocopium in soft corals

From 40 soft corals sampled, association was highest with the genus *Cladocopium* (Clade C). Similarly, the work by Leveque *et al.* (2019) showed *Cladocopium* as being the most abundant endosymbiont identified in all the Merulinidae corals, accounting for 78.2 % of sequences retained. Clade C strains exhibited more within-clade diversity as compared to the other functional clades (Lesser *et al.,* 2013). Savage *et al.* (2002) mentioned that the comparison of zooxanthellae physiology within a clade from various hosts revealed as much variability within a clade as between clades. The phenomenon of specificity, where the symbiont type forms a partnership with individual hosts with some degree of selectivity (depending on the depth and geographical location) is important for the understanding of the symbiotic association (LaJeunesse, 2001). Host species that are in symbiosis with a sole zooxanthella clade may host several types within that clade (Gaulet, 2006). For example, a single colony of *Heteroxenia* sp. hosts C15 and C64 (Table 2) (LaJeunesse *et al.,* 2004). Numerous host-specific, regionally endemic and/or rare types have radiated from the ancestral Types C1 and C3 symbionts (LaJeunesse *et al.,* 2004). As per the data collected, C1 was the most prevalent symbiont among soft corals. Similarily, type C1 has been reported to be common in many hard corals. For example, *A. cytherea, A. nasuta, Pavona* sp., *Lepttastrea* sp., *Fungi* sp. and *Pocillopora* sp. have all been reported to be associated with type C1 (Stat *et al.,* 2009). Additionally, types C15, C64 and C1:3a were among the most common symbionts. Specialized symbionts (such as C71a, C1:2, C15b, C15, C1z) displayed limited ranges in geographic distribution as shown in Fig. 4. C71a is dominant in soft corals in the region of Japan and C15b in Hawaii, and both are from the temperate zone. Soft corals from the tropical zone are more likely to host a wide variety of Clade C type. Australia being partially in the sub-tropical zone, hosts various Clade C type (C1, C64, C1:3a, C1c, C1q and many more). The work of LaJeunesse *et al.* (2004) confirmed that specific/rare forms of symbionts tend to have narrow geographic ranges and express endemicity. Similarly, biogeographic patterns in symbiont type was reported in scleractinian corals (Stat *et al.,* 2009). According to Stat *et al.* (2008), *Acropora cytherea* in Hawaii associates with C1, C3 and C3b while *A. cytherea* from the GBR harbours C3 only (LaJeunesse *et al.,* 2003). However, it is also possible that a rare symbiont specialized to live in a particular host in a specific region displayed more generalized associations at another geographical location (LaJeunesse *et al.,* 2003).

Apart from the presence of a variety of Symbiodiniaceae species, the type of endosymbionts present in the host can change in response to environmental conditions. Jones *et al.* (2008) reported that after a bleaching event, the hard coral *Acropora millepora*, which predominantly hosted *Cladocopium* C3, acquired more C1 or *Durusdinium* endosymbionts. Furthermore, shuffling of symbionts in *A. millepora* from C1 to C2 due to temporal change has been documented by Cooper *et al.* (2011).

Symbionts that are acquired from the environment are usually dependant on the particular environment and latitude where they occur which affects the dominancy of certain zooxanthellae (LaJeunesse *et al.,* 2004). Some more specialist subclades such as C15 (present in soft corals from Australia, Fiji and Israel) can survive in different waters at different depths and are thus considered resistant to thermal stress. The variance in thermal tolerance highlights the fact that the genus *Cladocopium* type is ecologically and physiologically distinct and the sequence divergence is low (LaJeunesse *et al.,* 2003).

The complex nature of Clade C type has been explored by various researchers. From the data collected, it can be inferred that some specific symbionts are limited to specific host tissues (LaJeunesse *et al.,* 2003), while others are diversely present irrespective of the soft coral family. C64 was found in soft corals from the 3 different families; namely *Klyxum* sp. (Alcyoniidae), *Paralemnalia digitiformis* (Nephtheidae), and *Anthelia* sp. (Xenidae), while C3j was mostly associated with the alcyonacian soft corals (*Lobphytum* sp., *Sinularia* sp. and *Sarcophyton* sp.) (LaJeunesse *et al.,* 2003). This evidence confirms that certain host tissues act as an individual habitat that is specialised to host a specific type of zooxanthellae (LaJeunesse, 2002). Similar data was found for scleractinian corals where specific symbionts were limited to specific hosts, and sometimes to a specific genus. *Porites lobota* was found to associate solely with C15 irrespective of the biogeographical location (Hawaii and Japan) and the type of molecular marker used (ITS2 sequence and chloroplast 23S sequence) (Stat *et al.,* 2009). In addition, from Table 2 it can be seen that no particular trend was observed in the genus *Cladocopium* type composition based on the different collection depths. Most of the genus *Cladocopium* subclade was obtained from soft corals sampled from a depth of less than 20 m. However, some aspects remain unclear, as shown in the work by LaJeunesse *et al.* (2003) who showed that some zooxanthellae types are associated selectively with a specific host, at times at certain depths, and are adapted to that host's intracellular environment.

These specific zooxanthellae are functionally different from others that share almost identical rDNA-ITS sequences. Increasing knowledge on the full ecological significance of symbiont diversity, host-symbiont specificity, and soft coral physiology, is crucial for predicting how endosymbiotic association may respond to environmental changes in different geographical regions (LaJeunesse *et al.*, 2003).

Conclusions

Using the data available, this review summarises the existing symbionts associated with soft corals in the temperate and tropical regions around the globe. The majority of soft coral species host a single zooxanthella clade. Soft corals associate with 5 different zooxanthellae genera; namely *Symbiodinium*, *Breviolum, Cladocopium, Durusdinium* and *Gerakladium*. The host-symbiont specificity and diversity are influenced by factors such as the geographical location, sea depth as well as the ability of the symbionts to survive in particular environments. The most prevalent endosymbiotic association was noted between soft corals and the genus *Cladocopium*. Additionally, more within-clade diversity was observed in the genus *Cladocopium* as compared to the other functional clades. Deciphering similarities and differences between the soft corals hosting the different symbionts may aid in predicting soft coral survivorship in the face of global climate change. Furthermore, from the research reviewed, it is apparent that no data are available on the different soft corals and their associated symbionts from the Indian Ocean tropical islands such as Mauritius, Rodrigues and the Maldives, which are known to have extensive coral reefs. Thus, research work involving these small islands is of high priority.

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