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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
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 assemblies. 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) (Houbrêque 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 Symbiodiniaceae 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 B. 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-culturabl 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 to 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 stricto* to Clade A and also defined several new genera: B as *Brevidium*, 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. thermophilum*) 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 CO₂ 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 CO₂, 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, Neptheidae and Xenidae 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 Neptheidae 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 Neptheidae 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 Neptheidae. 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 polyactyla* – 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 | Symbiodiniaceae genera | Citation                        |
|----------------|-------------|------------|----------------|------------------------|-------------------------|---------------------------------|
| Alcyoniidae    | Sarcophyton | ehrenbergi | GBR Australia  | 7-10                   | C                       | Sammarco and Strychar, 2013     |
|                |             | glaucum    | Australia      |                         | A                       | Carlos et al., 1999             |
|                |             | sp.        | Lizard Island  | 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 Red sea    | 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  | 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 |                | 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      | lacerthiensis         | 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                      | 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     | 1.5                    | C                      | Ziegler et al., 2018             |
| Family         | Genus      | Species     | Location     | Reported depth range/m | Symbiodiniaceae genera | Citation                      |
|---------------|------------|-------------|--------------|------------------------|------------------------|-------------------------------|
| Xenidae       | Cespitularia | sp.         | Australia    | <15 C                  | C                      | van Oppen et al., 2005       |
|               | Efflatounaria | sp.         | Australia    | 2-6 C                  | C                      | Goulet et al., 2008          |
|               | Heteroxenia | fuscescens  | Israel       | 2-6 C                  | C                      | Behayahu, 1991; Goulet et al., 2008 |
|               |             | sp.         | Australia    | <10 C                  | C                      | Lajeunesse et al., 2004      |
|               | Sarcothelia | sp.         | Hawaii       | <10 C                  | C                      | Lajeunesse et al., 2004      |
|               | Sympodium   | sp.         | Australia    | <15 D                  | D                      | van Oppen et al., 2005       |
|               | Xenia       | macrospiculata | Israel     | <20 C                  | C                      | Barneah et al., 2004         |
|               |             | umbellata   | Israel       | <20 C                  | C                      | Barneah et al., 2004         |
|               |             | elongata    | GBR          | 7-10 C                 | C                      | Sammarco & Strychar, 2013    |
|               |             | farauensis  | Eilat's reef | <20 C                  | C                      | Barneah et al., 2004         |

Figure 1. Frequency of each symbiodiniaceae 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 Clc and C65, and finally 3 % contain C3, Cl:i, C71a, Cl:k, Cl:5e, Cl:q, Cl:5b 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, Clc, Cl:q, 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. | Cl               | Australia| <17                    | LaJeunesse et al., 2004a |
|                 | C3j              | Australia| 2-4                    | LaJeunesse et al., 2003 |
| *Rhytisma* sp.  | C1:1             | Australia| 2-6                    | Goulet et al., 2008  |
|                 | Cl               | Australia| <17                    | LaJeunesse et al., 2004a |
|                 | C65              | Australia| <17                    | LaJeunesse et al., 2004a |
| *Sarcophyton* sp.| 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. | Clc              | Australia | 5                      | Lajeunesse et al., 2003 |
|                  | C65              | Australia | 10-17                  | Goulet et al., 2008 |
| **Nephthea** sp. | Cl               | New Zealand | 10                   | Goulet et al., 2008 |
|                  | C3               | New Zealand | 10                   | Wicks et al., 2010 |
|                  | C3j              | Australia | <10                   |          |
|                  | C1z              | New Zealand | 5-10                 |          |
| **Paralemnalia digitiformis** | Cl1:2            | Australia | 2-6                   | Goulet et al., 2008 |
|                  | C64              | Australia | 2-6                   |          |
| **Paralemnalia thyroidea** | Cl1:2           | Australia/Israel | 2-6       | Goulet et al., 2008 |
| **Stereonephthya** sp. | Cl15             | Australia/ Fiji | 2-6        | Goulet et al., 2008 |
| **Anthelia** sp. | C64              | Australia | 10-17                  | Lajeunesse et al., 2004a |
| **Sarcothelia** sp. | C84a             | Australia | 2-6                   | Goulet et al., 2008 |
| **Asterospicularia laurae** | Cl15             | Australia | 2-6                   | Goulet et al., 2008 |
| **Cespitularia** sp. | Cl15             | Australia | 2-6                   | van Oppen et al., 2005 |
|                  | Cl1q             | Australia | <15                   | Goulet et al., 2008 |
| **Efflatounaria** sp. | Clc              | Australia | 2-6                   | Goulet et al., 2008 |
|                  | Clc:3a           | Australia | 2-6                   |          |
| **Heteroxenia** sp. | Cl15             | Australia | 10-17                  | Lajeunesse et al., 2004a |
|                  | Cl15e            | Australia | 1-17                  |          |
|                  | C64              | Australia | 1-17                  | van Oppen et al., 2005 |
|                  | Cl               | Australia | <18                   |          |
| **Xenia** sp.    | Clk              | Australia | 15                    | Lajeunesse et al., 2003 |
|                  | C64              | Australia | 3-17                  |          |
|                  | Cl15             | Israel    | 2-6                   | Goulet et al., 2008 |
Discussion

Soft corals form an integral part of the coral reef community worldwide, yet very little research has focused on the Symbiodiniaceae 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 Symbiodiniacea; 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 (Gaullet, 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
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 Nephthidae (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 dominance 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 Cl5 and C64 (Table 2) (LaJeunesse et al., 2004). Numerous host-specific, regionally endemic and/or rare types have radiated from the ancestral Types Cl and C3 symbionts (LaJeunesse et al., 2004). As per the data collected, Cl was the most prevalent symbiont among soft corals. Similarly, type Cl has been reported to be common in many hard corals. For example,
A. cytherea, A. nasuta, Pavona sp., Leptttastrea 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 dominance 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 Anthealia sp. (Xenidae), while C8j was mostly associated with the alcyonarian 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, Cladocium, 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 Cladocium. 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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