The Diversity of the Giant Clams and Their Associated Symbiodiniaceae Algae in the Red Sea

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Abstract The Red Sea is host to one of the world's largest reef systems where invertebrates make up the majority of the diversity. Of those marine invertebrates, those that host microscopic algae or zooxanthellae are of the utmost importance in climate change research. Giant clams are photosymbiotic organisms and are protected under Appendix II of CITES. However, overfishing, habitat destruction, and climate change threaten their populations. The Red Sea is home to 3 of the 12 species of giant clams, *Tridacna maxima*, *Tridacna squamosa*, and *Tridacna squamosina*. *Tridacna squamosina* has the smallest geographical range, limited to the northern Red Sea, and is only present in low abundance. Overfishing in the past and present has been the main contributor to the loss of species in the Red Sea and globally. Climate change also threatens this symbiotic relationship between the giant clam and zooxanthellae in the family Symbiodiniaceae. Giant clams in the Red Sea have only been found to harbor *Symbiodinium* type A1 as their dominant type. However, as genetic techniques improve, the classification system of Symbiodiniaceae will improve and allow for better detection of diverse species within a host, which will allow for better understanding of the future of these organisms.

Keywords Giant clam · Red Sea · Symbiodiniaceae · *Tridacna* · Zooxanthellae

1 Introduction to the Red Sea

The Red Sea lies between Africa (on the West) and the Arabian Peninsula (on the East). The Gulf of Aqaba and the Gulf of Suez create narrow connections to the Mediterranean Sea in the North and the Bab-el-Mandeb strait connects to the Gulf of Aden in the South (see Fig. 1). Although the Red Sea is located on the northernmost

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Fig. 1 Map of the Red Sea

boundary of the tropics, it hosts one of the largest coral reef systems in the world (Berumen et al. 2013). It is home to a diverse array of marine organisms, some of which are still waiting to be discovered, and many of which are endemic (Berumen et al. 2013; DiBattista et al. 2016). The Red Sea is considered to be an extreme environment due to its high sea surface temperatures (SST) and higher than normal salinity (Ngugi et al. 2012; Raitsos et al. 2013). Parts of the reef ecosystem here regularly experience water temperatures as high as 33 °C in the summer months with trends showing a continuous increase of the maximum SST (Chaidez et al. 2017). The salinity of the Red Sea, although differs slightly across latitudes, is approximately 37–40 psu (practical salinity units) as measured by the NOAA National Virtual Ocean Data System. The arid environment of the Arabian Peninsula causes high evaporation over the Red Sea, leaving behind a high salt content in the marine environment. The lack of heavy rainfall and access to other bodies of water add to the high salinity of the Red Sea (Raitsos et al. 2013). With these oceanographic parameters, marine organisms have adapted to this unique environment, which has created an abundance of endemic species (DiBattista et al. 2016). The Red Sea, with its high SST, has been seen as a living laboratory for reef systems. We may see Red Sea temperatures present in other reef systems in the future as the climate continues to warm (see Voolstra et al. 2015). The importance of studying the marine organisms in the Red Sea is evident especially when looking to find heat tolerant reef species. However, the Red Sea reef is overall an understudied region when compared to the Great Barrier Reef and the Caribbean. Furthermore, of all studies from the Red Sea, the majority are from the Gulf of Aqaba, which makes up less than 2% of the entire region (Berumen et al. 2013). Representing the most understudied organisms of the Red Sea and of marine organisms in general are the invertebrates. However, as they constitute the majority of the diversity in the ocean, and more specifically in coral reef ecosystems, they are of the utmost importance.

Table 1 Giant clam species list and geographical region. Adapted from Neo et al. 2017

Species name	First described	Geographic region
Hippopus hippopus	Linnaeus, 1758	Indo-Pacific except Red Sea and West Indian Ocean
Hippopus porcellanus	Linnaeus, 1758	Sulu Archipelago and Palawan (Philippines), Sabah (Malaysia), Sulawesi and Raja Ampat (Indonesia), Palau and Milne Bay Province (Papua New Guinea)
Tridacna gigas	Linnaeus, 1758	Myanmar to the Republic of Kiribati, and the Ryukus (Japan) to Queensland (Australia)
Tridacna derasa	Röding, 1798	Cocos Islands to Tonga, China to Queensland
Tridacna squamosa	de Lamarck, 1822	Red Sea, Eastern Africa, Pitcairn Islands, South Japan, Australia
Tridacna squamosina	Sturany, 1899	Northern Red Sea
Tridacna maxima	Röding, 1798	Red Sea, Africa, Australia, China
Tridacna mbalavuana	Ladd, 1934	Fiji, Tonga, New Caledonia, Australia
Tridacna rosewateri	Sirenko & Scarlato, 1991	Saya de Marha Banks (Mauritius)
Tridacna crocea	de Lamarck, 1822	Australia to Japan, east to Palau, and from Vanatua to the Andaman Islands
Tridacna noae	Röding, 1798	Papua New Guinea, Fiji, Western Australia, Pacific Islands
Tridacna lorenzi	Monsecour, 2016	Cargados Carajos Archipelago (St. Brandon), Mascarene Piateau (Mauritius)

1. Giant Clam Diversity

One of the most conspicuous and unique invertebrates present in the reef system of the Red Sea and reefs around the world is the giant clam. Bivalves in the family of *Tridacnidae* are the largest living bivalves with some species reaching up to a meter or more in length (Neo et al. 2017). There are twelve species of giant clams in the family *Tridacnidae*, two of which are in the genus *Hippopus* and ten of which are in the genus *Tridacna* (Neo et al. 2017) (Table 1). The diverse color morphologies of these clams have allowed for uncertainty in species descriptions that are only resolved by genetic analysis. Due to this, the species list of giant clams has and will continue to be modified (see Richter et al. 2008; Huber and Eschner 2010; Penny and Willan 2014; Su et al. 2014; Borsa et al. 2015a, b; Neo et al. 2017). Giant clams are spread throughout the Pacific and Indian Oceans with the northernmost boundary in the Red Sea (see Table 1). As they are brightly colored and easily accessible from reef tops, these bivalves have received interest from fishermen and researchers alike (Fig. 2).

The morphological diversity of giant clam species gives rise to the possibility of inaccurate species distinctions. However, the most recent species described have been cryptic species, which were separated from previously described species by molecular genetics techniques (see Richter et al. 2008; Borsa et al. 2015a, b; Su et al.

Fig. 2 Photographs of giant clams being fished (**a**), consumed (**b**), and studied (**c**)

2014). Many species diversity studies have utilized genetic markers to resolve putative species distinctions among morphologically ambiguous organisms (see Palumbi 1997; Knowlton 2000; Warner et al. 2015; Johnson et al. 2015). For example, *Tridacna noae* was believed to be conspecific with *Tridacna maxima* based on basic morphology. However, with the use of genetic markers (16 s rRNA, 18 s rRNA, 28 s rRNA, and COI), two genes revealed separation between *Tridacna maxima* and the cryptic species *Tridacna noae*. Genetic results encouraged a more thorough morphological examination, which recognized small differences among shell shape and color pattern and allowed for an accurate description of the new species (Su et al. 2014). There is a possibility that there are more cryptic species of giant clams, and genetic techniques have been the most recent to resolve these distinctions accurately (see Richter et al. 2008; Naguit 2009; Huelsken et al. 2013; Su et al. 2014; Pappas et al. 2017). Genetic techniques can also give very detailed information on the evolution of species' populations, movement ecology, and genetic diversity between individuals (see Ayala et al. 1973; Benzie and Williams 1997; Kochzius and Nuryanto 2008; Hui et al. 2017). Studies of giant clams in the Red Sea that utilized genetic markers provide phylogenetic trees to show the separation among species. Those studies show that three species are present in the Red Sea, *Tridacna maxima*, *Tridacna squamosa*, and *Tridacna costata* (later synonymized with *Tridacna squamosina* (Huber and Eschner 2010) (Richter et al. 2008; Pappas et al. 2017)). Genetic techniques prove to be useful when describing the diversity in the algal partners of giant clams as well (see Carlos et al. 1999; Baillie et al. 2000; DeBoer et al. 2012; Lee et al. 2015; Pappas et al. 2017).

2. Giant Clam Symbiosis

Giant clams are unique bivalves due to their symbiotic relationship with microscopic algae or zooxanthellae in the family Symbiodiniaceae. This relationship is similar to corals in that the host animal's major food source comes from the photosynthate of the algal partner and is the main contributor to the clams' giant size (Yonge 1975; Klumpp and Lucas 1994). This relationship has both changed the

Fig. 3 Photos of *Tridacna maxima* (**a**), *Tridacna squamosa* (**b**), and *Tridacna squamosina* (**c**)

anatomy and habitat of the giant clam from that of any other bivalve (Fitt et al. 1986). For photosynthesis to be possible, giant clams live on shallow reef tops with their mantle tissue exposed upwards to receive sunlight (see Fig. 3). The umbo of the giant clam faces downwards and the shells are partially open through which the enlarged mantle tissue extends (Fig. 4a, c).

The Symbiodiniaceae cells are stored in tubules that extend from the clam's stomach to the mantle tissue (Fig. 4b, d). To obtain these cells, the clam will ingest them from the water column through the incurrent siphon where they will enter the stomach. From the stomach, the clam transports Symbiodiniaceae cells through the tubule system from the primary tubules to the secondary tubules to the tertiary tubules (see Fig. 4d). The Symbiodiniaceae cells are stacked in tertiary tubules perpendicular to the surface of the mantle tissue (Mansour 1946; Norton and Jones 1992). Specialized reflective cells called iridocytes in the mantle tissue act as mirrors and reflect light to stacked Symbiodiniaceae in the tubules to allow for the most efficient photosynthesis (Nishi 2001; Sweeney et al. 2012; Holt et al. 2014). A full description on the morphology of the giant clam due to the relationship with zooxanthellae can be found in literature (see Copland and Lucas 1988; Norton and Jones 1992; Venn et al. 2008).

3. Diversity of Symbiodiniaceae

Previously, the algae that form symbioses with marine invertebrates have been classified into a cladal system (A through I) (see Pochon and Gates, 2010) of one genus, *Symbiodinium*. However, it has been discovered that the genetic diversity within and among these clades is greater than the genetic diversity seen in other dinoflagellate genera, families, and sometimes orders (Rowan and Powers 1992; Stern et al. 2010, 2012). To better capture the diversity of these algae and to better identify potential species and functional diversity, LaJeunesse et al. (2018) have proposed a new classification system which has created each clade into a genus (currently 6 defined), and each type into a species all belonging to the family Symbiodiniaceae. This system better exemplifies the diversity within the previous clade system. For example, species in both *Cladocopium*, previously known as Clade C, and *Durusdinium*, previously known as Clade D, are extremely diverse in ecological function, especially in thermal stress tolerance (LaJeunesse et al. 2010, 2014; Hume et al. 2015). Further, in just the genus *Symbiodinium*, previously known as Clade A, there have been 18 diverse types or species described with more being discovered (see LaJeunesse et al. 2015). Some types of Symbiodiniaceae within the genus *Symbiodinium* exhibit entirely different characteristics and ecological

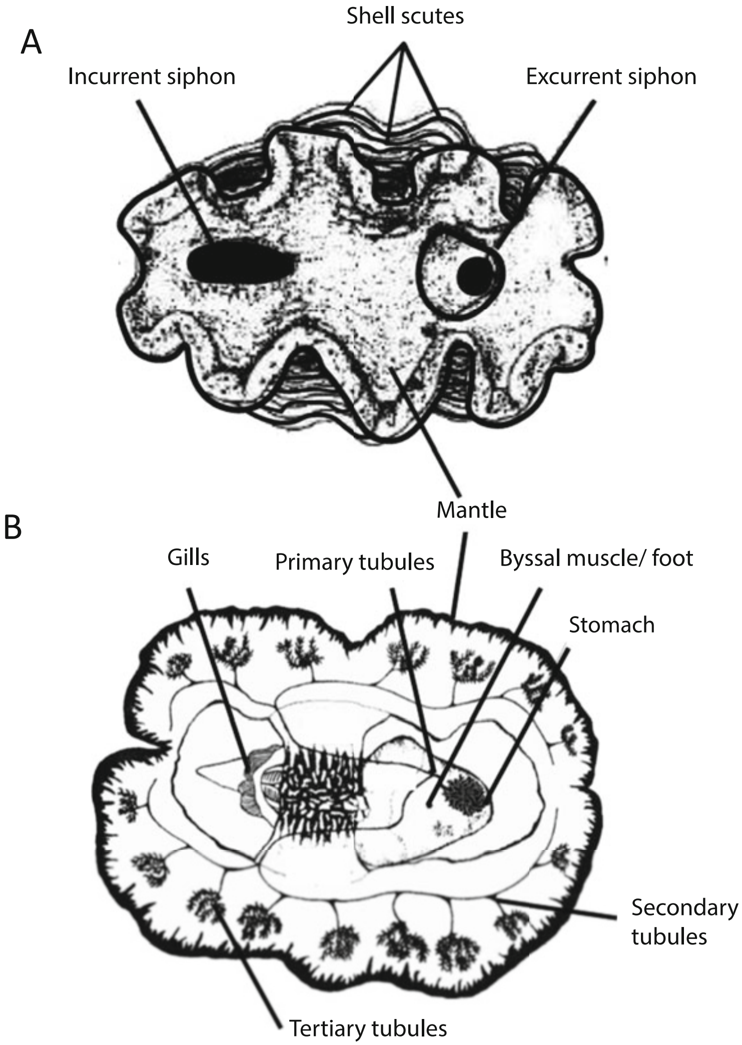

Fig. 4 Anatomical sketch of a giant clam. Aerial view (**a**, **b**) and side view (**c**, **d**) show both organs and zooxanthellae tubule system. Adapted from Norton et al. 1995

functions. *Symbiodinium* of type A1, A3, and A4 have been found to be essential partners of reef building corals (Baums et al. 2014), anemones, jellyfish, and zooanthids (LaJeunesse 2002; Finney et al. 2010; Lee et al. 2015). However, another species, *Symbiodiniaceae necroappetens,* has been described as an opportunistic and parasitic symbiont that becomes more abundant in bleached or diseased tissue of host animals (LaJeunesse et al. 2014). Although these types are of the same genus, they have different functions, which further emphasizes the need for a more precise classification system.

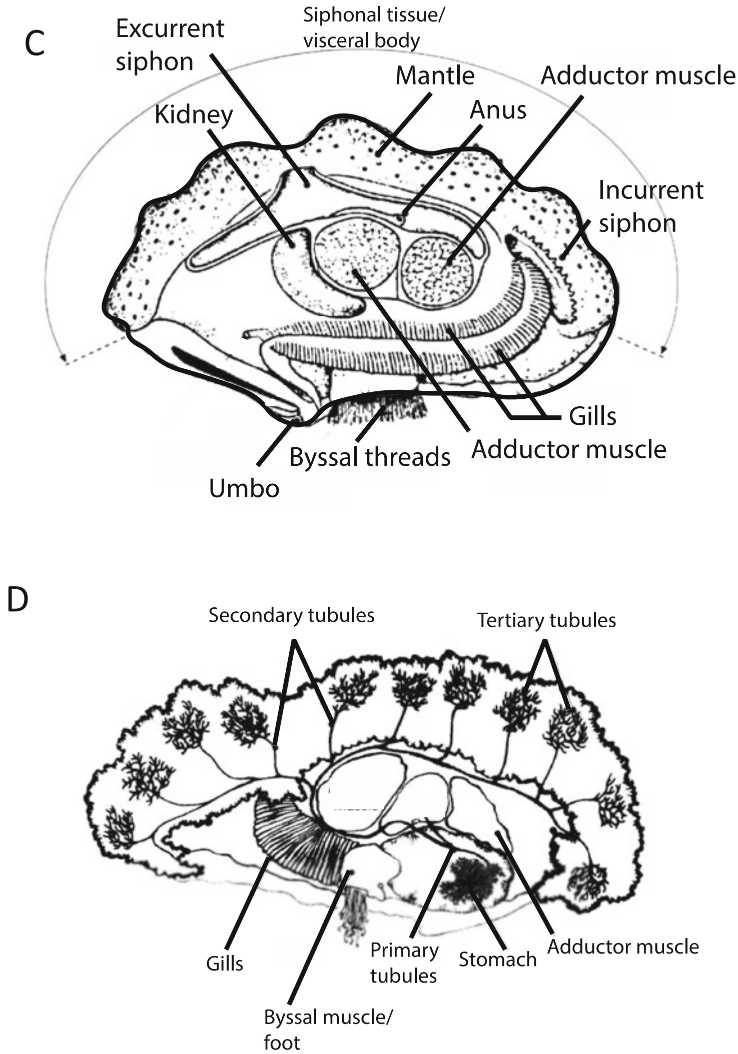

Fig. 4 (continued)

Identification of differences in Symbiodiniaceae genera and species are strongly supported by genetic differences. The most common gene region used to distinguish differences in Symbiodiniaceae is the ITS region, or the internal transcribed spacer region (LaJeunesse 2001). With current genetic technologies, scientists are able to determine Symbiodiniaceae down to type or species within a genus and can identify multiple species within an individual host animal (see Rowan et al. 1997; Baker 2001; Glynn et al. 2001; Pochon et al. 2001; Van Oppen 2001; LaJeunesse 2001; 2002; LaJeunesse et al. 2003; Jones et al. 2008). Further, studies examine the ability of host animals to shift or shuffle Symbiodiniaceae species when different species are better suited for the environment (see Baker et al. 2004; Baker and Romanski 2007; Jones et al. 2008; Stat and Gates 2011; Kemp et al. 2014; Davies et al. 2017).

Giant clams have been found to harbor Symbiodiniaceae in the genera *Symbiodinium*, *Cladocopium*, and *Durusdinium* (formerly Clades A, C, and D) (Baillie et al. 2000; DeBoer et al. 2012; Ikeda et al. 2017; Pappas et al. 2017; LaJeunesse et al. 2018). Giant clams in the Red Sea have only been found to harbor *Symbiodinium*, specifically type A1, as the dominant symbiont (Pappas et al. 2017). However, further research on Symbiodiniaceae diversity in giant clams of the Red Sea show that, although *Symbiodinium* may dominate, there are other background genera present in all giant clam hosts (Pappas unpublished). Changes in the dominant species type did occur when clams underwent thermal stress in a bleaching experiment, which may indicate potential for shifting to tolerate natural bleaching events or other changes in the environment (Pappas unpublished). As genetic technology progresses, the diversity of the family will most likely be greater than expected (see LaJeunesse et al. 2018). The new information on diversity and functional ecology of certain types of Symbiodiniaceae will be essential for understanding the potential of host animals to survive through increasing SSTs due to climate change.

4. Red Sea Species

The Red Sea hosts three species of giant clams in the genus *Tridacna*: *Tridacna maxima*, *Tridacna squamosa*, and *Tridacna squamosina* (see Richter et al. 2008; Pappas et al. 2017). The major difference between members of the giant clam group are size, shell shape, and depth. *Tridacna maxima* grows to approximately 30 to 40 cm in length and has about four to five rounded shell scutes on each side (Fig. 2a). Further, *Tridacna maxima* has been found in shallower depths than *Tridacna squamosa*, which can also be used to help identify the species in situ. *Tridacna squamosa*, also known as the fluted clam, can grow up to 40 cm in length with large, leaf-like fluted scutes that distinguish it from *Tridacna maxima* (Fig. 2b). *Tridacna squamosina* is the smallest of the three giant clams in the Red Sea, only measuring up to 32 cm in length. The shell shape of *Tridacna squamosina* is distinguishable by the zigzag pattern and more angular scutes (Fig. 2c). *Tridacna squamosina* occupies the shallowest of depths, making them easy to remove from reef tops (reviewed in Neo et al. 2017).

The most common of these species present in the Red Sea and globally is *Tridacna maxima* (Roa-Quiaoit 2005; Richter et al. 2008; bin Othman et al. 2010; Mekawy and Madkour 2012; Pappas et al. 2017). *Tridacna squamosina* has the smallest geographical range in the Red Sea; it is only found in the Northern Red Sea in very low abundance (Richter et al. 2008). *Tridacna squamosina* occupies the shallowest reef tops, no deeper than 2 meters. Making up greater than 80% of the fossil record but less than 2% of the living stock, Richter et al. (2008) suggests that *Tridacna squamosina* was heavily overfished earlier in history, which has led to its present threatened status. In the Red Sea, *Tridacna maxima* have been found to occupy water depths between 2 and 10 m, while *Tridacna squamosa* can be found at depths between 5 and 20 m (Pappas et al. 2017). Although some species live at deeper depths, all tridacnids are threatened by human harvesting (see Lucas 1994; Gladstone 2000; Ashworth et al. 2004; Van Wynsberge et al. 2016). This is clearly a major threat to the populations of giant clams in the Red Sea and globally as some species may go extinct as a result of human collection and consumption (Richter et al. 2008; Larson 2016).

5. Giant Clam Conservation

All giant clams are protected under Appendix II of CITES (2017), which indicates that, although not necessarily faced with extinction, proper management and conservation practices need to be in place so as to not threaten their populations. The IUCN Red List of Threatened Species (2017) includes eight giant clam species with four listed as vulnerable. Further, seven giant clam species are candidates for the Endangered Species Act (ESA, 2017) protection, which prohibits trade, commerce, and habitat destruction. Despite being protected, threats such as overfishing, habitat destruction, and climate change still exist (reviewed in Mies 2019; Neo et al. 2017). Giant clams have been fished for their meat and decorative purposes in the Indo-Pacific and the Red Sea throughout history (Bodoy 1984; Lewis et al. 1988; Heslinga 1996; Venkatesan 2010; Nijman et al. 2015). Aside from this direct human impact on giant clam populations, the more complicated threat to these bivalves is climate change (Pappas et al. 2017; Neo et al. 2017).

6. Climate Change and Bleaching

It is already evident that climate change is a threat to the symbiotic relationship between zooxanthellae and their host animal; increasing SST has already devastated many reefs around the world (Hughes et al. 2017). As water becomes hotter than the optimal temperature range of these algae, they are expelled from the clam's tissue. This phenomenon called bleaching is commonly seen in corals but can occur in any animal that hosts zooxanthellae (Fig. 5) (see Fromont and Garson 1999; Leggat et al. 2003; Perez et al. 2001; Venn et al. 2008; McGill and Pomory 2008; Ziegler et al. 2014). Once the major food source is gone, the clam may be able to feed itself by filter feeding, but will not be able to fully sustain itself this way (Klumpp et al. 1992; Klumpp and Lucas 1994). If sea surface temperatures remain high, the clam may not

Fig. 5 Photographs of bleached anemone (a), zooanthids (b), and giant clam (c)

recover from bleaching and will starve (see Norton et al. 1995; Addessi 2001; Leggat et al. 2003; Pappas unpublished data). Although the Red Sea has not experienced many devastating bleaching events (Osman et al. 2018), temperatures are continuing to rise in this region and will have major impacts on the giant clam populations of the Red Sea in the near future (Chaidez et al. 2017; Pappas unpublished data).

Clade A, the genus *Symbiodinium* found in Red Sea clams has been described as a heat tolerant and opportunistic clade in studies focusing on corals and sea anemones (Rowan et al. 1997; Toller et al. 2001; Venn et al. 2008). The extreme temperatures of the Red Sea may have influenced the abundance of this genus in symbiotic organisms in this region. Symbiodiniaceae genera and species may be the key to understanding the ability of photosymbiotic organisms to tolerate or recover from bleaching events, but more research is needed to understand the benefits of the genus *Symbiodinium* in giant clams of the Red Sea.

Although this chapter has focused on the species diversity of both the giant clam and its associated Symbiodiniaceae in the Red Sea, due to the Red Sea being an understudied region in the field of marine biodiversity as compared to other regions, this chapter may not be complete. As species evolve and go extinct, the diversity of these organisms will change in the future and further research may provide missing links in our understanding of the diversity of these bivalves in this region. However, the conspicuousness of the giant clam and the drive for Symbiodiniaceae research has produced many thorough studies of these animals in this region (see Pappas et al. 2017). Further, as the new classification system for Symbiodiniaceae continues to be used, a more accurate description of the species present in the tridacnids of the Red Sea may allow for a better understanding in their ability to tolerate such an extreme environment.

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