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GIANT CLAMS (MOLLUSCA: BIVALVIA: TRIDACNINAE) IN SINGAPORE: HISTORY, RESEARCH AND CONSERVATION

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ABSTRACT. — This review presents the history of giant clams (S.F. Tridacninae) in Singapore as derived from artifacts, primary and grey literature, museum collections, and anecdotal evidence. Archaeological finds from the 14th century include giant clam valves of at least two species: *Tridacna crocea* (Lamarck, 1819) and *T. squamosa* (Lamarck, 1819). An 1847 publication lists *T. gigas* (Linnaeus, 1758) in Singapore, a species that is absent from later inventories. *Hippopus hippopus* (Linnaeus, 1758) and *T. maxima* (Röding, 1798) also used to be found on the reefs surrounding Singapore's Southern Islands, bringing the total number of recorded species to five. Early literature describes how inhabitants of 19th century Singapore relied heavily on fishing and collection of shells for food and trade and that this activity was already impacting clam stocks. Exploitation was probably the main cause of giant clam decline until the 1960s when intense coastal development became an additional contributor. Contemporary surveys of 29 reef sites show very low densities of *T. crocea* and *T. squamosa* and a complete absence of *H. hippopus*, *T. gigas*, and *T. maxima*. Very little research was conducted on giant clams in Singapore until 1998 when a mariculture project was initiated. This was succeeded by a programme of basic research that produced papers on mariculture, behaviour, shell morphology, reproduction, and conservation; here we present an outline of some of the more important findings. Finally, we discuss conservation strategies designed to ensure that giant clams will not disappear from Singapore's reefs altogether.

KEY WORDS. — giant clams, distribution, applied ecology, behaviour

INTRODUCTION

Globally, there are ten living giant clam (Tridacninae) species. These are distributed among the shallow coral reefs of the Indian and South Pacific Oceans (Rosewater, 1965; Richter et al., 2008; Othman et al., 2010). Population numbers are in decline in various counties, including Australia, Indonesia, Malaysia, and Philippines (Alcala, 1986; Braley, 1987; Copland & Lucas, 1988; Pringgenies et al., 1995; Tan & Yasin, 2003). This can generally be attributed to environmental degradation (Newman & Gomez, 2000), exploitation for food (Hester & Jones, 1974), plus the sale and export of wild specimens (Wells, 1997). Data from the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) indicate that the international trade in non-captive bred giant clams increased from ~40,000 individuals in 1993 to ~100,000 in 2001 (Wabnitz et al., 2003). To alleviate fishing pressure on wild stocks, there has been a concerted effort to sell cultured clams (e.g., O'Callaghan, 1995; Heslinga, 1996; Bell et al., 1997). The deterioration of coral reef habitats has potentially the greatest negative impact on giant clam populations throughout the Indo-Pacific. For example, development occurring around Singapore's coastline has caused extensive loss of coral reefs and their associated fauna and diversity (Chou, 1999; Todd et al., 2010).

Even though giant clams are prominent reef fauna (Mingoa-Licuanan & Gomez, 2002), their ecological roles are not well understood. When common, they can be major contributors to a reef's overall productivity (Hardy & Hardy, 1969; Jantzen et al., 2008). Giant clams can provide three sources of food:

tissue, faeces, and gametes (which are broadcast spawned) to a wide range of predators and opportunistic feeders (Ricard & Salvat, 1977; Govan, 1992; Maboloc & Mingoa-Licuanan, 2011). They also add topography and, in high densities, serve as nurseries to various organisms (Mingoa-Licuanan & Gomez, 2002; Cabaitan et al., 2008). For example, the presence of *T. gigas* on degraded patch reefs has been shown to increase both abundance and species richness of fish and other biota (Cabaitan et al., 2008). Their calcified shells provide a stable substrate for sedentary taxa such as corals (Dizon et al., 2008). The burrowing and semi-burrowing giant clam species, *T. crocea* and *T. maxima* respectively (Rosewater, 1965; Hamner & Jones, 1976) contribute calcium carbonate sediments (Aline, 2008), e.g., a single *T. crocea* can produce up to 200g per m^2 per year (Hamner & Jones, 1976). Finally, the shells of all giant clam species represent a substantial quantity of dense calcium carbonate that eventually becomes incorporated into the three-dimensional reef structure (Weingarten, 1991).

Giant clams have been important to people as food and for materials in many countries and historical periods (Miller, 1979; Hviding, 1993); they are also steeped in folklore. Pacific islanders previously misunderstood them as 'killer clams' due to their large size and strong shell valves (Rosewater, 1965) and believed they were able to drown divers by holding onto them. Early accounts in Cobb (1939) reported casualties caused by *T. gigas* that resulted in a diver's death and another who lost his legs (Rosewater, 1965). *Tridacna gigas* was also strongly associated with religious beliefs throughout the Solomon Islands (Hviding, 1993) and considered taboo food (e.g., they could not be eaten by women). The heavily calcified shells of giant clams have frequently been used as household items such as soap dishes, door stops, and food troughs for domesticated animals (Hocart, 1931; Charatsee & Hylleberg, 1992; Heslinga, 1996). In the past, Solomon locals bartered with 'disc money' made from tridacnid valves (Weingarten, 1991). Giant clam shells continue to be crafted into ornaments (Heslinga, 1996) and exported to various countries including Japan, Australia, Europe, and the USA (Dawson & Philipson, 1989; Charatsee, 1994; Mingoa-Licuanan & Gomez, 2002). As a construction material, fossilised valves from *T. derasa* and *T. gigas* buried in reef flats off Java have been used to make terrazzo tiles (Brown & Muskanofola, 1985). Collection, however, has been reported to cause extensive damage to coral reefs of the Thousand Islands (Pulau Seribu), West Java (Salm, 1981), by breaking up reef flats and producing sediment clouds. Unfortunately, this tile trade has also led to the exploitation of living clams.

Tridacnids are still highly prized for their adductor muscle, mantle flesh, and shells (Hester & Jones, 1974; Mingoa-Licuanan & Gomez, 2002). On the Pacific Islands, clam meat is an important source of protein nutrition (Tisdell, 1986) and it is believed by islanders that consumption prevents night blindness; indeed, this may be the case as high amounts of vitamin A can be found in the zooxanthellae (Hviding, 1993). While the islanders heavily harvested *T. crocea* as a staple food, other clam species were only taken during special occasions (Hviding, 1993). From the early 1990s, Taiwan and Okinawa have been the most established markets for clam meat, particularly the adductor muscle (Dawson & Philipson, 1989; Shang et al., 1991). Pearson (1977) estimated that since 1960, Taiwanese vessels alone have harvested up to a million clams per year along the northern regions of the Great Barrier Reef. Captured Taiwanese clam vessels yielded >80 tons of clam muscle taken from over 500,000 clams (Pearson, 1977; Hirschberger, 1980). All giant clams are protected by the CITES (Appendix II) and, in Singapore, *T. squamosa* is listed as 'Endangered' on the Singapore Red Data Book (Davison et al., 2008).

Naturalists visiting Singapore in the early 19th century described the intense exploitation of marine flora and fauna by local fishermen (Traill, 1847; Belcher, 1848; Denny, 1894). These accounts include the first mention of giant clams in Singapore, where two *Hippopus* species: one unnamed and the other *H. maculatus* (synonymised to *H. hippopus*), and three *Tridacna* species: *T. crocea*, *T. gigas* and *T. squamosa* were found (Traill, 1847). Subsequent literature (e.g., Chuang, 1961, 1973; Johnson, 1964; Rosewater, 1965; Purchon, 1977; Purchon & Purchon, 1981; Henrey, 1982; Wells, 1988, 1989; Lim et al., 1994; Ng et al., 1995; Wells, 1997; Chua et al., 2003) notes the presence of *H. hippopus, T. crocea* and *T. squamosa*, as well as a previously unmentioned species: *T. maxima*. The Raffles Museum of Biodiversity Research (RMBR) had its first two giant clams specimens deposited in 1933. The mention of *T. gigas* by Traill (1847) is noteworthy since this species is absent in the 20th century literature and is not listed as native to Singapore by the International Union for Conservation of Nature (IUCN) (Wells, 1996). Surveys of 29 Southern Island reefs conducted in 2009/2010 found *T. crocea* and *T. squamosa* in extremely low numbers and no specimens of *H. hippopus*, *T. gigas*, or *T. maxima* (Neo & Todd, 2012). Here we review three aspects of giant clams in Singapore: history (evidence of presence and exploitation), research (mariculture, behaviour, and autecology), and conservation (present status of local clams and future restoration strategies).

HISTORY

The earliest evidence for giant clams in Singapore comes from an aggregation of old tridacnid shells (shell lengths 49.8–190.0 mm) discovered during archaeological excavations at four sites along Singapore River and the former coastline (Fig. 1): Pulau Saigon (PS), Empress Place (EMP), Parliament House Complex (PHC), and St Andrew's Cathedral (STA). However, the stratum layers of the PS, PHC, and EMP sites were disturbed, mostly due to anthropogenic activities (Miksic, 2004), thus the shells could not be dated with confidence. STA was built on what was an indigenous settlement from at least the mid-14th to early 17th century. The Temenggong of Johore later reoccupied it until the British arrived in the early 19th century. An Anglican church was first built on these grounds in 1834 (Miksic & Lim, 2004) and construction of the present cathedral commenced in 1856. STA was the least disturbed of the four excavation sites and based on the black sand (stained by charcoal; Miksic, 2004) found on shell surfaces, it is likely that the giant clams specimens found there are ~500 years old (pers. comms. Miksic, J.N.).

Various literature indicates that early inhabitants of modern Singapore relied heavily on fishing and collection of shells to provide sustenance (Traill, 1847; Denny, 1894; Chua & Chou, 1992). Traill (1847) mentioned that the poorer Malays and Chinese heavily exploited shellfish as food and searched the shores for them with such diligence that they were already scarce along some parts of the coast. This shell collection continued until the early 1990s when a few of Singapore's Southern Islands still supported fishing villages (Tan, 1966; Manap, 1983). Giant clams were known to the Malay fishers as '*Siput kima*' (*T. squamosa*) and '*Siput lupat*' (*H. hippopus*) (Chuang, 1961; Purchon & Purchon, 1981) and were regularly harvested as food (Harrison & Tham, 1973; Chou, 1984). The clams were not usually eaten immediately, but stored under the fishers' stilted houses to maintain freshness (pers. comms. Bin Duriat, M.R.), a practice also observed among Pacific Islanders (MacLean, 1978; Larrue, 2006). Most of the evidence on harvesting in Singapore points to domestic consumption (Dawson, 1986), with a limited market for clam meat (Dawson & Philipson, 1989; Khoo, 1991). Giant clam shells could also have been used for the production of lime (Denny, 1894), which was a major activity in early Singapore. Many Chinese immigrants worked as lime and brick burners and the native Malays used corals when preparing lime for domestic use (Denny, 1894). Lime production persisted until the 1950s, and villagers located along Tanjong Gul, Tanjong Teritip, and Mata Ikan (between Bedok and Ayer Gemuroh) actively collected coral rocks and seashells in huge amounts for the manufacture of whitewash (Chua et al., 2003). Even though not mentioned explicitly, due to their heavy shells, it is likely that giant clams would also have been sought for the lime industry.

Since its foundation, Singapore has attracted thousands of European and Chinese merchants because of its strategic trade and shipping position (Buckley, 1902). In 1836, Briton John Cameron lauded Singapore's reefs' riches and noted an early market of rare seashells and corals in local harbours (Chua et al., 2003). Denny (1894) also indicated that Singapore was a well recognised "shell collecting centre", where huge quantities of corals, shells, sea fans, and Neptune's cup sponges were harvested by fishers (Belcher, 1848). The extent of this exploitation apparently decimated entire populations of sea fans to satisfy the demand by Europeans (Denny, 1894). Giant clams continued to fascinate foreign visitors with an array of reported uses. 'Breeding pearls' were well known to the residents of Singapore (Denny, 1878), having been alleged to possess the ability to reproduce fresh pearl specimens under certain conditions. Denny (1894) supposedly found one such breeding pearl at Tanah Merah Kechil beach (east Singapore) and stated that very large pearls could be extricated from *T. gigas*. He also noted that one specimen used to be found at the foot of the stairs leading to Raffles Library. Rosewater (1965) mentioned the export of live *T. maxima* from Singapore to the United States of America, but no information was provided on the origins of these clams.

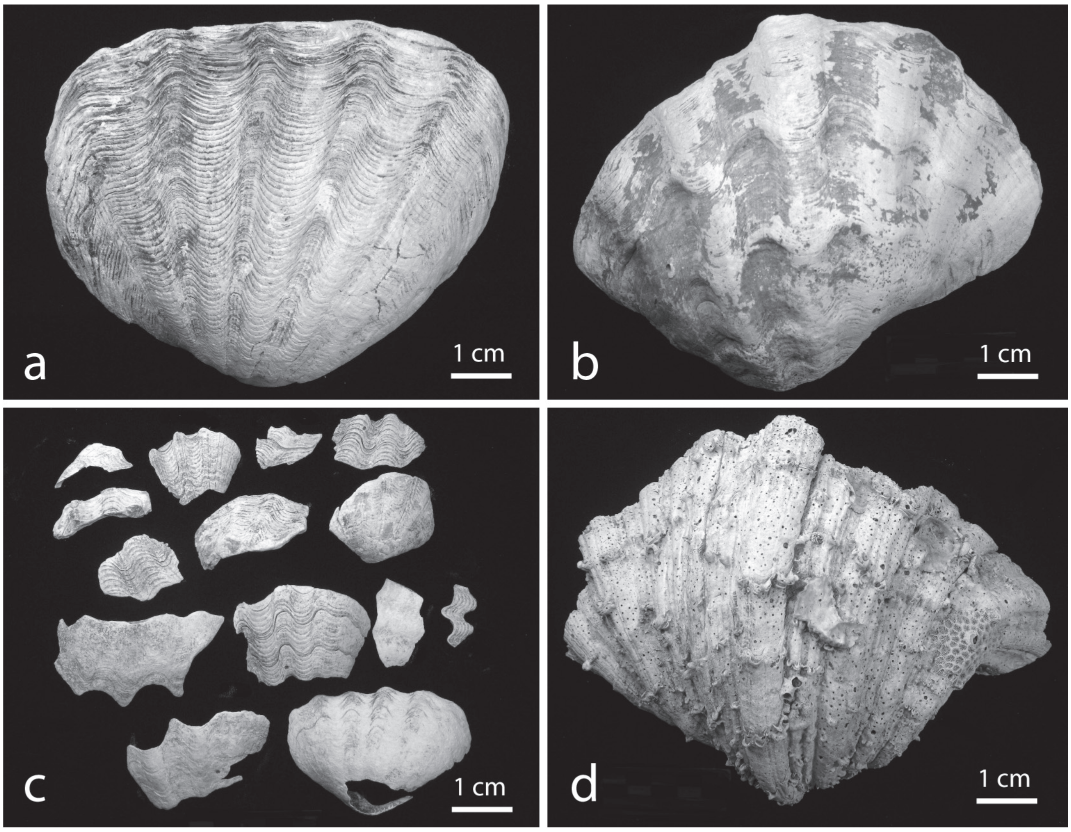

Fig. 1. Shell remains and fragments from the pre-colonial settlement sites near Singapore River. a) *Tridacna crocea* (St Andrew's Cathedral); b) *T. squamosa* (St Andrew's Cathedral); c) fragments from Parliament House Complex; and d) *Hippopus hippopus* (Pulau Saigon).

Table 1. Number of dead (year of death unknown) giant clam shells collected during surveys conducted between Sep.2009 – Aug.2010.

Species	*Hippopus hippopus*	*Tridacna crocea*	*Tridacna maxima*	*Tridacna squamosa*
Number of valves collected	10	17	7	4
Shell length range (mm)	146–321	29–128	53–100	123–362

Interest in *T. gigas*, the largest of the giant clams, was sparked when a 2007 excavation of a site near Tyrwhitt Road (presently People's Association Headquarters) uncovered some large *T. gigas* shells, of which ten single valves were donated to RMBR in Sep.2009. These shells had to pre-date 1932, as Victoria School was located there from 1932–1984. The site was a previously a Malay village located beside the Kallang River (Buckley, 1902) and hence the shells could have been harvested from Singapore reefs for food and local trade, although the possibility that they originated from outside Singapore cannot be ruled out. Other accounts regarding *T. gigas* are anecdotal, such as the "The Great Oyster from Singapore (*Tridacna gigas*)" placed on display at the fisheries exhibition in London (Whymper, 1883) and the *T. gigas* shell at Mr. Rule's London Oyster House on Maiden Lane, which supposedly fed fourteen people in Singapore for six weeks (Daily Telegraph, 1914)! The strongest support for *T. gigas*'s presence in Singapore is from the list of molluscs provided by William Traill in his chapter "A Few Remarks on Conchology and Malacology" in The Journal of the Indian Archipelago and Eastern Asia (Volume 1, Number 5) published in 1847. Here, *T. gigas* is clearly named (and is unlikely to be misidentified), the only caveat is that the full title of Traill's list is "Catalogue of the shells of Singapore and its vicinity" (although on subsequent pages "and its vicinity" is omitted)—leaving a small doubt that he may have included islands beyond Singapore's waters. Singapore is certainly within *T. gigas*'s range (Othman et al., 2010) and, together, the evidence suggests that they once inhabited local reefs.

It is apparent that giant clams were important food sources and trade items in 19th century Singapore, and these factors were early drivers of the decline in clam numbers (Traill, 1847). Due to its value and conspicuousness, it is not surprising that *T. gigas* would be the first species to disappear. *Hippopus hippopus* was last recorded by Lee (1966), and *T. maxima* by Guest et al. (2008). Recent surveys have confirmed the absence of *T. gigas*, *H. hippopus*, and *T. maxima*, while *T. crocea* and *T. squamosa* are only present in low numbers (Neo & Todd, 2012). The likelihood that Singapore has only recently lost some of these species is highlighted by the number of dead shells that were discovered during contemporary surveys (i.e., Neo & Todd, 2012). For instance, between Sep.2009 and Aug.2010, ten *H. hippopus* and seven *T. maxima* valves were found (Table 1). Unfortunately, such shells are very difficult to age. Less than 60 years ago, tridacnids could be readily observed from the shore at low tide (Purchon & Enoch, 1954), something that is not possible now. Even though giant clams are no longer exploited commercially, coastal developments since the 1960s (Chia & Khan, 1987; Yong et al., 1991) have resulted in the degradation of coral reefs and their associated fauna (Low & Chou, 1994; Chou, 1999;). Fringing and patch reefs once surrounded Singapore's coastline (Chuang, 1973, 1977), but many were buried to provide new land. For example, giant clams were previously found on Tanjong Teritip (Lee, 1966), Pulau Seringat and Terumbu Bayan (Guest et al., 2008) but these reefs have been reclaimed (covered over) in their entirety. Very little is known regarding the status of giant clams in Singapore during the 1970s to early 1990s, however, interest was rekindled in the late 1990s with the initiation of a giant clam mariculture project and subsequent research programmes.

RESEARCH

Giant clam research in Singapore started at the Tropical Marine Science Institute (TMSI) in 1998 (pers. comms. Lam, T. J.). Fifteen *T. squamosa* broodstock were imported from Riau Indonesia (east Indonesia); these were later augmented with Filipino and local *T. squamosa*, including some donated and salvaged individuals. The first studies examined the effects of elevated nutrients and sediments on reproduction and larval survival (Courtois de Vicose & Chou, 1999) as well as demonstrating that crustose coralline algae (CCA) acts as a settlement cue (Courtois de Vicose, 2000), as it does for various other invertebrate larvae (Roberts et al., 2004). Prompted by this finding, Neo et al. (2009) tested whether concrete substrates made with CCA covered coral rubble (CCACR) would attract *T. squamosa* larvae. They thought that encouraging colonisation of near shore concrete structures by using ground CCACR as an aggregate may be a useful ecological restoration tool. When given a choice of small tablets made with 0%, 30%, or 60% CCACR, larvae preferred the substrate containing the most. However, in another experiment using the same three concentrations but in larger tiles, no significant differences among the CCACR treatments were found after six weeks. Neo et al. (2009) concluded that concrete made with CCACR can promote early larval settlement but that this technique does not enhance overall, longer-term, recruitment of juvenile *T. squamosa*.

Mariculture studies have continued from 1998 to the present. For instance, Neo et al. (2011) spawned *T. squamosa* and, out of the four treatments tested, they found that the most optimal egg-sperm ratio was 1:50. Fertilised eggs showed cell division after three to four hours, and developed into trochophores after one day. Acquisition of zooxanthellae occurred on day five while settlement occurred eight days after fertilisation (Neo et al., 2011). Neo (2007) examined the combined effects of temperature (~22.5°C and ~29.5°C) and salinity (27‰ and 30‰) on fertilisation success and development of embryos. While salinity had no effect, embryo development was approximately two times greater at the higher temperature (but higher temperatures had a negative effect on the development of trochophores). They also found that a mixed-algal diet of *Tetraselmis suecica* + *Chaetoceros mulleri* + yeast resulted in increased larval survival in the first 24 h of development. This information contributes to larval rearing knowledge for *T. squamosa*, and is currently referred to during all spawning efforts conducted in Singapore.

Coral reefs in Singapore regularly experience heavy sedimentation loads and poor light penetration (Chou, 2008). To examine potential impacts on giant clam growth and survivorship, Guest et al. (2008) conducted shade and out-plant experiments using 200 *T. squamosa* imported from the Philippines. They found that the mean growth rate for clams raised in aquaria under 50% ambient PAR (photosynthetically active radiation) was 7.4 mm month^{-1}, at 25% ambient PAR it was 5.9 mm month^{-1}, and at 12% ambient PAR it was 3.0 mm month^{-1}, indicating that even at low light levels this species can still grow. Of the 144 clams out-planted onto Southern Island reefs, 116 (80.6%) were recovered after seven months and the specimens exhibited growth rates similar to those described elsewhere (e.g., Morton, 1983; Foyle et al., 1997). It is surprising, but encouraging, that these clams can survive and grow despite the high levels of sedimentation and turbidity on Singapore's reefs. Moreover, these key experiments have been important for developing local restocking strategies.

In 2005, a new research programme focusing on giant clam autecology and behaviour was established. In particular, anti-predatory mechanisms were studied. The most obvious defense adult giant clams possess is their large, heavy and robust shell that provides excellent protection from crushing predators. Juveniles, however, remain vulnerable to crabs and fish with powerful chela or jaws (Govan et al., 1992). *Tridacna squamosa* valves are ornamented with rows of scutes (Fig. 2): finger-nail like projections (Lucas, 1988; Chan et al., 2008) that are a key taxonomic feature (Rosewater, 1965). In other mollusc species, external sculptures such as corrugations and spines are thought to be economical defensive adaptations (Vermeij, 1974, 1993). To test whether the scutes of juvenile *T. squamosa* provide protection against crushing predators such as crabs, Ling et al. (2008) measured the forces required to crush scutes and valves of shells from clams that had died naturally at the TMSI aquarium on St John's Island. The chela strength of a predator, the stone crab, *Myomenippe hardwickii*, was also quantified and the results used to create two models of how scutes can help protect juvenile *T. squamosa*. In the first, scutes increase the overall size of the clam, reducing the number of predators large enough to hold and crush the prey. In the second model, the additional chela gape required to grasp the clam leads to enough decrease in power to prevent the crab from breaking the scutes, and thus the shell.

Huang (2006) also tested the role of scutes as a defense tool in juvenile *T. squamosa* by experimentally removing them. Four treatments: (i) uncaged with scutes; (ii) uncaged without scutes; (iii) caged with scutes; and (iv) caged without scutes, were deployed on the reef flat off St John's Island for 24 h. Uncaged clams experienced significantly greater mortality when scuteless than when their scutes were still intact, suggesting strongly that lack of scutes lowered the clams' defences against predators (Fig. 3). After Ling et al. (2008) and Huang (2006) demonstrated that scutes can provide protection, Neo & Todd (2011a) hypothesized that giant clams exposed to crab (*M. hardwickii*) effluent would develop longer and stronger scutes and/or heavier and tougher shells. Predator-induced defenses have been produced in other marine molluscs (e.g., Leonard et al., 1999; Smee & Weissburg, 2006). Specimens were exposed to three different treatments: water-borne cues from 'fed crabs', 'starved crabs', and 'no crabs'. After 182 days, significant differences in various shell parameters relating to shape and strength (but not scute length) were found. The effluent from 'starved crabs' had less effect than effluent from 'fed crabs', possibly because the starved crabs were perceived as weaker (and hence less risk). Beadman et al. (2003) discuss how it is possible to "toughen up" bivalves by exposing them to predators and suggest using this as a management tool to increase shell strength before transplantation and outgrowing in the field.

In addition to the protection provided by their shells, giant clams defend themselves via rapid mantle withdrawal, polymorphism and camouflage, aggregation, and squirting jets of water at potential predators. Todd et al. (2009) showed

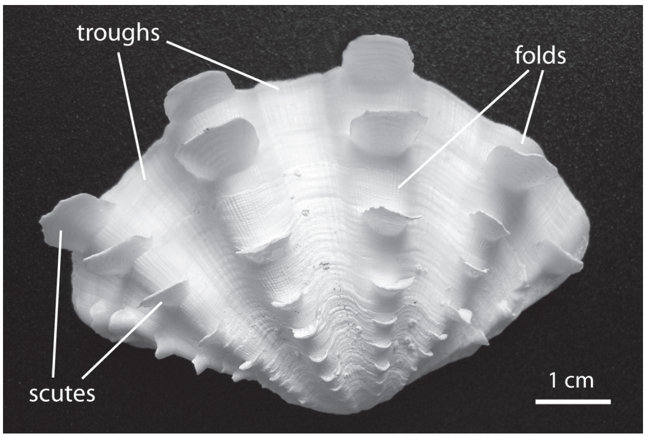

Fig. 2. A typical *Tridacna squamosa* valve.

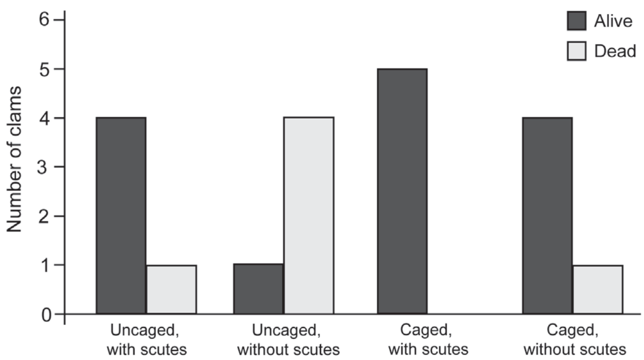

Fig. 3. Frequency distribution of juvenile *Tridacna squamosa* that survived and died during the predator-exclusion experiment (n = 5). There was a significant association between survivorship and treatment (Fisher Exact Probability Test; $p<0.05$).

that the boring giant clam, *T. crocea*, is colour/pattern polymorphic and that relative morph frequency changes with clam size. Furthermore, mantle colours (red/blue/green values) extracted from digital images correlated positively with substrate colours, indicating background matching (crypsis). Huang et al. (2007) tested aggregation in juvenile *T. squamosa* by placing specimens in regular patterns on grids in tanks and then measuring their position after three days. Based on a statistical parameter for 'clumpiness' (McGarigal et al., 2002), they showed that the clams aggregated more than could be explained by random walk or random distribution alternatives. Similar results were found for live runs conducted in natural (reef) conditions. Huang et al. (2007) discussed how aggregation could provide defense against predation, as being in clumps reduces the risk each animal would experience (Krause & Ruxton, 2002). Squirting behaviour (ejecting a stream of water, usually from the exhalant siphon) was known to occur in at least five species of giant clam, but this had never been quantified. Neo & Todd (2011b) analysed stills from video recordings of juvenile *T. squamosa* aerial squirts to calculate the pressure exerted by each squirt. They concluded that larger clams produce more powerful jets and, if they are able to orientate their squirts (as suggested by others, e.g., Fankboner 1981), squirting could scare or disorientate predators.

Giant clams are excellent model organisms with fascinating behaviours and life histories. They are also relatively easy to maintain in aquaria and hence amenable to experimentation. Future 'pure' research could examine the effects of water flow on growth and morphology, the presence of predators on aggregation, and determine exactly how effective are the proposed defenses such as background matching and water squirting. A greater understanding of clam biology and ecology not only adds to basic knowledge, but can help managers tailor better strategies for their protection. Applied research also can contribute to conservation efforts by providing information useful for coastal managers, such as the degree of population connectivity; and new mariculture techniques will help any future restocking.

CONSERVATION

The first giant clam distribution and abundance study in Singapore was conducted in 2003 at seven coral reef sites around the Southern Islands (Guest et al., 2008). The surveys encompassed almost 10,000 m^2 but only 23 individual clams from three species (*T. squamosa* = 14, *T. crocea* = 7, and *T. maxima* = 1) were found (equal to a mean density of 0.24 per 100 m^2). In a much more extensive and detailed survey (29 reefs; total area = 87,515 m^2) conducted in 2009 and 2010, Neo & Todd (2012) recorded a much reduced density of just 0.067 per 100 m^2. Only two species, *T. crocea* and *T. squamosa*, were encountered. They also examined the genetic relatedness within these two species populations using cytochrome *c* oxidase subunit I and determined that *T. crocea* exhibited higher levels of polymorphism and genetic diversity compared to *T. squamosa*; possibly due to *T. crocea* being less harvested and hence retaining more diversity. In both the Guest et al. (2008) and Neo & Todd (2012) surveys no juvenile clams were observed, pointing to a lack of natural recruitment. An overall summary of the sites where clams have been found, both past and present, is presented in Table 2 and Fig. 4.

It is clear that giant clams in Singapore have been impacted by overexploitation for food (Traill, 1847; Denny, 1878), sediment pollution, and habitat loss through land reclamation (Dawson & Philipson, 1989; Chou, 1999). Existing reefs continue to be deleteriously affected by coastal developments, resulting in their slow deterioration. The absence of *T. maxima* and low abundance of *T. crocea*, for instance, may be due to the lack of large substratum surfaces suitable for these burrowing species (Hamner & Jones, 1976). Sediment pollution continues to be one of the major causes of coral reef loss in Singapore (Chou, 2008). Associated turbidity reduces photosynthesis by zooxanthellae critical to the clams' nutritional needs (Hirose et al., 2006; Jantzen et al., 2008) and probably explains the local absence of giant clams below 6 m. Settling sediments may physically interfere with giant clams' feeding (Rogers, 1990; Bell, 2004) and can result in damage to the gills (Purchon, 1955). Sediment layers on substrates are known to impede larval settlement (e.g., Rogers, 1990; Te, 1992). The overall effect of these stressors is to reduce clam density to a point where it is unlikely that the gametes from these broadcast spawners can meet and fertilise (the Allee effect), making the present populations unviable (Neo & Todd, 2012). As Guest et al. (2008, pg 577) concluded "if measures are not implemented to boost dwindling giant clam populations it is highly likely that this iconic invertebrate species will disappear from Singapore's coral reefs".

As it is doubtful whether the few remaining *T. crocea* and *T. squamosa* are capable of regenerating substantial healthy populations, some intervention is necessary. Mariculture of giant clams can produce large numbers of juveniles suitable for restocking corals reefs where natural recruitment is absent. Reintroduction of giant clams has been well studied (e.g., Copland & Lucas, 1988; Munro, 1993; Gomez et al., 2000)

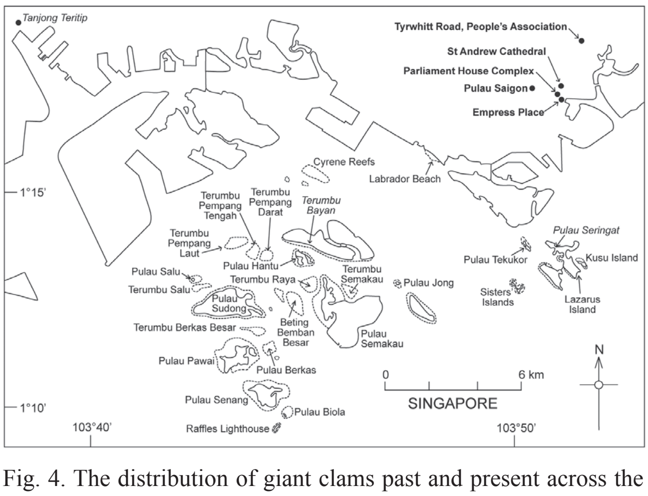

Fig. 4. The distribution of giant clams past and present across the Southern Islands and mainland Singapore. Past: five archaeological sites (in **Bold**) and three reclaimed reefs (in *italics*). Present: 24 extant reefs (in regular text). Dotted lines represent the boundaries of fringing and patch reefs.

Table 2. Chronological list of giant clams records in Singapore. HH = *Hippopus hippopus* (Linnaeus, 1758); TC = *Tridacna crocea* (Lamarck, 1819); TG = *Tridacna gigas* (Linnaeus, 1758); TM = *Tridacna maxima* (Röding, 1798); TS = *Tridacna squamosa* (Lamarck, 1819). Legend: Pulau = island, abbreviated to P.; Terumbu = patch reef, abbreviated to T.

Timeline	Source	Site	HH	TC	TG	TM	TS
14th century	Miksic & Lim, 2004	St. Andrew's Cathedral (2003)	X	X		X	X
Before 1847	Traill, 1847	Singapore	X	X	X		X
1866	Daily Telegraph, 1914	Singapore			X		
19th century	Miksic & Lim, 2004	P. Saigon (1987–1988), Empress Place (1998), Parliament House Complex (1994)	X	X		X	
1933	ZRC1975.8.1.1 (*H. hippopus*), ZRC1975.8.1.2 (*T. crocea*), Raffles Museum of Biodiversity Research (RMBR)	P. Pawai	X	X			
1950–1960	Purchon & Purchon, 1981	Raffles Lighthouse (P. Satumu)					
	Morris & Purchon, 1981		X	X			X
1952	Purchon & Enoch, 1954		X	X			X
1952–1953	Purchon, 1955		X	X			X
1963	Rosewater, 1965	P. Tekukor					X
	Lee, 1966	Tanjong Teritip		X	X		
1968–1973	Trigg Collection, 1997 Natural History Museum UK (NHMUK)	Singapore				X	X
1975–1976	Chuang, 1977	P. Salu, P. Sudong		X			
1982	Chou & Wong, 1985	P. Salu					X
	Wong, 1983			X			
1994	Lim et al., 1994	Labrador beach		X			X
1997	pers. comms. Courtois de Vicose, G.	Raffles Lighthouse (P. Satumu)		X			X
	ZRC1997.71, RMBR	P. Seringat				X	
1998	ZRC.MOL.2898, RMBR	Southern Islands		X			
1999	pers. comms. Courtois de Vicose, G.	P. Hantu		X			
	Courtois de Vicose & Chou, 1999	Raffles Lighthouse (P. Satumu)		X			X
	ZRC.MOL.2899, RMBR						X
2003	Guest et al., 2008	Raffles Lighthouse (P. Satumu)		X		X	X
		P. Hantu		X			X
		P. Semakau		X			
		T. Bayan, Sisters' Islands (P. Subar Laut, P. Subar Darat), Kusu Island (P. Tembakul)					X
2003–2008	pers. comms. Tan, R.	Raffles Lighthouse (P. Satumu), P. Semakau		X			X
		P. Hantu		X			
		Cyrene Reefs (T. Pandan), P. Jong, Sisters' Islands (P. Subar Laut, P. Subar Darat)					X
2006	pers. comms. Lin, J.	Lazarus Island (P. Sakijiang Pelepah)					X
2009–2010	Neo & Todd, 2012	Raffles Lighthouse (P. Satumu), P. Biola, P. Senang, P. Salu, P. Semakau, T. Raya, T. Semakau, P. Hantu		X			X
		T. Berkas Besar, T. Salu, T. Pempang Darat, T. Pempang Laut		X			
		P. Pawai, P. Sudong, P. Berkas, Beting Bemban Besar, P. Jong, Sisters' Islands (P. Subar Laut, P. Subar Darat), Kusu Island (P. Tembakul), T. Pempang Tengah, Cyrene (T. Pandan)					X

and, as long as harvesting does not resume, research to date suggests that restoring clam populations in Singapore is a feasible option (Guest et al., 2008). A giant clam restocking programme for Singapore commenced in mid 2011, using existing broodstock plus new specimens imported for the project. The first cohort of new clams was produced in early 2012 and was accompanied by new research into egg viability and larval settlement behaviour.

It is generally acknowledged that active management is necessary for the survival of Singapore's reefs. Coral reef rehabilitation efforts are already being explored (e.g., Loh et al., 2006) and the addition of giant clam restocking will contribute significantly to the general push to improve Singapore's marine environment. Giant clams can also play an important "flagship" role for coral reefs due to their conspicuous and charismatic nature, and their potential to highlight that intervention can produce effective results in relatively short time scales. The discovery that *T. gigas* was once present in Singapore (Traill, 1847) opens up the intriguing possibility of reintroducing this species. It is a popular choice for mariculture and restocking elsewhere in the region (e.g., Bolinao, Philippines) and there should be few technical barriers to raising stocks in Singapore. Apart from helping to recreate Singapore's former reef community, due to their spectacular size, *T. gigas* should help stimulate public interest in the marine life found around Singapore's coastline.

There now exists a substantial giant clam research base in Singapore. Work done to date covers both basic and applied research; aquaria and field-based studies. We know that, at least for *T. squamosa*, giant clams can survive on local reefs, even under their present, heavily sedimented conditions (Guest et al., 2008). The survey results of Guest et al. (2008) and Neo & Todd (2012) provide a baseline that will help future studies monitor ecosystem health. As discussed in Todd & Chou (2009), the research on giant clam defenses described in the previous section has implications for restocking. For instance, to increase protection, and to mimic their natural behaviour, clams should be placed in groups when they are transplanted to a reef. The work on scutes shows that young clams are vulnerable and measures should be taken to protect them, for example via caging or delayed release into the wild. When transplanting giant clams, matching mantle colouration with substrate should help increase camouflage and thus help reduce predation. However, for restocking to be successful, additional studies are required. In particular, the source-sink dynamics of giant clam larval dispersal within the Singapore Straits should be modelled to help answer questions such as: "What are the best potential sites for clam nurseries", and "At what density of clams are required to make a population self-sustainable"?

CONCLUSIONS

The evidence suggests that giant clams in Singapore were once abundant and diverse, with five recorded species: *H. hippopus*, *T. crocea*, *T. gigas*, *T. maxima*, and *T. squamosa*. Since the 1960s, *T. gigas*, *H. hippopus*, and *T. maxima* have been extirpated and the numbers of remaining *T. crocea* and *T. squamosa* severely depleted due to exploitation, loss of habitat, and reduced water quality. The substantial research conducted on giant clams in Singapore has provided the baseline knowledge and strategic framework for the current restocking plans. If these are a success, hundreds of mature clams will become established on numerous reefs, returning them to a state they have not experienced for the last two centuries. The ultimate goal is that the out-planted clams will breed naturally and recruitment will follow, obviating the need for any more restocking. These charismatic organisms not only aesthetically enhance coral reefs; they also serve important ecological roles. A fully-fledged conservation programme will raise awareness of the plight of Singapore's giant clams and, with commitment (and some luck), they might yet have a chance to thrive again.

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