THE ECOLOGICAL SIGNIFICANCE AND LARVAL ECOLOGY OF GIANT CLAMS (CARDIIDAE: TRIDACNINAE)

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DECLARATION

I hereby declare that this thesis is original work and it has been written by myself and my co-authors in its entirety. I have duly acknowledged all the sources of information which have been used in the thesis.

This thesis has not been submitted for any degree in any university previously.

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7 AUGUST 2014

SUMMARY

Giant clams (family Cardiidae, subfamily Tridacninae), the largest living bivalves, live in warm, shallow waters in the Indian and Pacific Oceans. They play important ecological roles in coral reef environments, but many of these roles have not previously been elaborated or quantified.

Using data from the literature and original research, Part I of this thesis describes the ecological functions of giant clams. Their tissues, gametes, faeces, and discharges of live zooxanthellae are food for a wide array of predators, scavengers, and opportunistic feeders. Epibionts colonize the shells of giant clams, while commensal organisms live within their mantle cavities. Giant clams increase the topographic heterogeneity of the reef, act as reservoirs of zooxanthellae, and counteract eutrophication via water filtering. Giant clams produce large quantities of calcium carbonate shell material, some of which is eventually incorporated into the structure of coral reefs. As giant clams are under pressure from overfishing and habitat degradation, a better understanding of their ecological contributions will encourage their conservation.

As the larvae of marine invertebrates have greater sensitivity to environmental disturbances than adults, it is important to study all stages of an organisms’ life cycle. Part II of this thesis investigates survival of the fluted giant clam (*Tridacna squamosa*; Lamarck, 1819) pediveligers exposed to elevated temperature and reduced light levels, and examines *T. squamosa* trochophores, veligers, and juveniles under lowered salinities.

In a light reduction experiment, 104,000 *T. squamosa* pediveligers were exposed to four different levels of shading for approximately one month. The most heavily shaded treatment, at 0.4% of ambient light, had significantly lower survival than the other groups, which all received 1% or more of ambient light. In a second experiment, 13,000 *T. squamosa* pediveligers were divided among three treatments averaging 29.5˚ C (ambient), 32.2 ˚ C, and 34.8˚ C. The elevated temperature treatments resulted in near total mortality for pediveligers. The highest temperature survived by any pediveliger in the experiment was 32.8˚ C. Giant clam conservation and restoration programs should consider the impact of anthropogenic sedimentation, as associated turbidity may cause giant clam larvae and juveniles to establish in shallower water, where they will be exposed to higher temperatures.

As salinity is considered one of the most significant ecological stressors for marine bivalves, several larval stages of *T. squamosa* were observed after being exposed to hyposaline water. Late stage pediveligers/early stage juveniles survived in distilled water for 10 min to 5 h, and showed no sign of injury during a 48 h follow-up period. Trochophores were able to survive for 10 min to 3 h in 9 ppt salinity water, and veligers were able to survive for 1 h to 42 h in 12 ppt salinity water. Results suggest that giant clam larvae are able to survive exposure to hyposaline water such as that associated with high rainfall or river outflows in Singapore’s waters.

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CHAPTER 1. INTRODUCTION

1.1. Giant clams (Mollusca: Cardiidae: Tridacninae)

Giant clams, the largest living bivalves (Yonge, 1975), live in warm, shallow waters in the Indian and Pacific Oceans (Lucas 1988). They have provided food and shell material to humans for millennia (Hviding 1993). More recently, commercial harvesting (Lucas 1994), harvesting for local consumption (Hester and Jones 1974), collection for the aquarium trade (Mingoa-Licuanan and Gomez 2002; Wabnitz et al. 2003; Soo et al. 2011), and habitat degradation (Newman and Gomez 2000) have led to population declines (Alcala 1986; Braley 1987; Tan and Yasin 2003) and extirpations (Alcala et al. 1986; Tan and Yasin 2001; Guest et al. 2008; Neo and Todd 2012a; Neo and Todd 2012b). Giant clams are 'charismatic megafauna' whose conservation can draw attention to the destruction of coral reefs and loss of biodiversity. A brief overview of giant clam species is presented in Table 1.1.

Table 1.1. A brief overview of named giant clam species, and their IUCN Red List status as of 1996, the year when that status was last reviewed.

Species	Overview	IUCN Red List Status
Tridacna gigas	This is the largest and fastest growing species. Its shell can be 137 cm long and, like all giant clams, its mantle extends beyond its shell.	Vulnerable
Tridacna derasa	This is the second largest, and second deepest-dwelling, species of giant clam.	Vulnerable
Tridacna tevoroa	This species is found only in Tonga and Fiji, where it is known as the “devil clam”, possibly due to a “warty” tissue appearance. It is the deepest-dwelling species of giant clam.	Vulnerable
Tridacna squamosa	This species has prominent “scutes” on its shell, which help to defend the clam against predators.	Lower Risk / Conservation Dependent
Tridacna maxima	This is the most widespread and populous species. It can partially burrow its shell into coral or limestone substrate.	Lower Risk / Conservation Dependent
Tridacna costata / Tridacna squamosina	This is a newly “discovered” species from the Red Sea. It was previously thought to have been a morph of *T. maxima*.	Not Assessed
Tridacna noae	Another species previously considered a morph of *T. maxima.* It is found off Taiwan and Japan.	Not Assessed
Tridacna rosewateri	No live specimen has been found since the shells were discovered in 1965; it is probably extinct. The shells are found only near Mauritius.	Vulnerable

Tridacna crocea	This species is called the "boring" giant clam because it fully burrows its shell into coral or limestone substrate. It is the smallest giant clam species, with a maximum shell length of 15 cm.	Lower Risk / Least Concern
Hippopus hippopus	This species is called the "horse's hoof clam" due to the shape of its shell.	Lower Risk / Conservation Dependent
Hippopus porcellanus	This species is called the "porcelain clam" due to the appearance of its shell (after it is cleaned of epizoans).	Lower Risk / Conservation Dependent

Giant clams utilize two feeding mechanisms (Purchon 1977). Like most bivalves, they are filter feeders, collecting plankton using their gills (Hardy and Hardy 1969), but in order to survive they also need nutrition supplied by symbiotic photosynthetic dinoflagellates of the genus *Symbiodinium (*Fitt and Trench 1981), referred to as zooxanthellae, that live in a tube system throughout the clams' mantle tissues (Norton et al. 1992; Hirose et al. 2006). Zooxanthellae do not pass from parent clams to offspring, they must be acquired from the marine environment by larvae (LaBarbera 1975; Jameson 1976; Mies et al. 2012). Although giant clams are the most well-known examples, there are other bivalves which have symbiotic relationships with zooxanthellae (Morton 2000) or with chemoautotrophic bacteria (Dufour and Felbeck 2003).

Giant clams are protandrous hermaphrodites (Wada 1952), meaning that they mature first as males, then later as females. They release their gametes into the water column where fertilisation takes place. Within a day, fertilized eggs develop into swimming but non-feeding trochophore larvae, and within another day, the trochophores develop into veligers, which both swim and feed (Jameson, 1976; Alcazar et al., 1987; Mies et al., 2012). Over an additional time period of a few days to a month, the veligers gradually lose their ability to swim and become pediveligers, which crawl on the substrate (Jameson, 1976; Alcazar et al., 1987; Mies et al., 2012). Contrary to popular belief, giant clams retain their ability to crawl as juveniles and adults (Crawford et al., 1986; Huang et al., 2007).

Taxonomy of Tridacnidae dates to 1758, but over 70% of giant clam-related papers were published after 1970 (Munro and Nash 1985). This increase in research was probably due to development of larval culture methods (e.g. LaBarbera 1975; Jameson 1976), which required an understanding of spawning behaviour, larval dietary requirements, and how to handle small juveniles (Yamaguchi 1977). There is now a substantial amount of literature on giant clam symbiosis and nutrition (e.g. Fitt and Trench 1981; Trench et al. 1981), reproduction (e.g. Gwyther and Munro 1981; Neo et al. 2011), shell morphology (e.g. Chan et al. 2009; Neo and Todd 2011), and growth (e.g. Munro and Gwyther 1981; Guest et al. 2008). Field research has concentrated on *T. gigas*, the largest and fastest-growing species, and *T. maxima*, which has the most widespread distribution (Adams et al. 1988). The anatomy and physiology, exploitation, and mariculture of giant clams have been studied far more intensively (Munro 1983; Lucas 1994; Hart et al. 1998) than their ecology, behaviour, and larval biology.

Giant clams are rare in Singapore (Guest et al. 2008; Neo & Todd 2012b), but there are significant areas of habitat they could occupy, provided they could be protected from harvesting, land reclamation, and anthropogenic sedimentation. According to Hilton and Chou (1999), there are 53 fringing reefs and 73 patch reefs around

Singapore’s southern islands. Most of these reefs are 15 m or shallower in depth (Chou, 1985), and because they are sheltered, they are similar to leeward reefs in other parts of the world (Chuang, 1977). They tend to have wide reef flats, but lagoons and true reef crests are absent and there is no distinct coral zonation (Chuang, 1977). Singapore’s reefs, which were considered pristine 50 years ago, but are now degraded (Chou, 1997), would probably see improvements in biodiversity and water quality if repopulated with giant clams.

1.2. Aims and objectives of this research

1. To investigate the ecological benefits which giant clams provide to coral reef ecosystems.
2. To add to the body of knowledge concerning the biology and ecology of giant clams, particularly that of their larvae, which have been studied far less than adults.
3. To produce information which will assist people and organizations involved in giant clam restocking and restoration efforts.

1.3. Thesis structure and overview

This thesis is divided into two parts: I) the ecological roles giant clams play on coral reef, and II) the stress thresholds of giant clam larvae. Chapters 2, 3, 4 and 5 are being either published or submitted for publication with co-authors, hence “we/our” is used. Those chapters are presented verbatim as they are published or submitted. In chapters 2 and 3, I contributed to all parts of the papers, and was the primary author of the components on biomass, clearance rates and carbonate production. I am the lead author on the papers represented by chapters 4 and 5, where I conceived, conducted, analysed and wrote up the experiments.

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PART I – THE ECOLOGICAL SIGNIFICANCE OF GIANT CLAMS ON CORAL REEFS

CHAPTER 2. THE ECOLOGICAL SIGNIFICANCE OF GIANT CLAMS (CARDIIDAE: TRIDACNINAE) AND WHY THEIR CONSERVATION IS IMPORTANT FOR CORAL REEFS[1]

Abstract

Giant clams (*Hippopus* and *Tridacna* species) are thought to play various ecological roles in coral reef environments, but many of these have not previously been quantified. Using data from the literature and our own studies we elucidate the ecological functions of giant clams. We show how their tissues are food for a wide array of predators and scavengers, while their discharges of live zooxanthellae, faeces, and gametes are eaten by opportunistic feeders. The shells of giant clams provide substrate for colonization by epibionts, while commensal and ectoparasitic organisms live within their mantle cavities. Giant clams increase the topographic heterogeneity of the reef, act as reservoirs of *Symbionidium* zooxanthellae, and also potentially counteract eutrophication via water filtering. Finally, dense populations of giant clams produce large quantities of calcium carbonate shell material that are eventually incorporated into the reef framework. Unfortunately, giant clams are under great pressure from overfishing and extirpations are likely to be detrimental to coral reefs. A greater understanding of the numerous contributions giant clams provide will reinforce the case for their conservation.

Keywords: Biomass; carbonate budgets; epibiota; eutrophication; zooxanthellae

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2.1. Introduction

As recently summarized by Bridge et al. (2013, p.528) coral reefs globally are "*suffering death by a thousand cuts*". Some of these, including global warming and ocean acidification, are notorious and possibly fatal. Others, such as the loss of particular species or genera, are generally less pernicious and do not garner the same attention. Of course, all reef organisms have a role to play but, due to their sheer size (Rosewater, 1965), incredible fecundity (Lucas, 1994), and capacity to form dense populations (Andréfouët et al., 2005), giant clams (and their disappearance) deserve greater mention than most. Based on fossil tridacnine taxa, these iconic invertebrates have been associated with corals since the late Eocene (Harzhauser et al., 2008) and facies of more recent *Tridacna* species are common in the upper strata of fossilized reefs (Accordi et al., 2010; Ono and Clark, 2012). Modern giant clams are only found in the Indo-West Pacific (Harzhauser et al., 2008) in the area bounded by southern Africa, the Red Sea, Japan, Polynesia, and Australia (bin Othman et al., 2010). There are currently 12 extant species of giant clams (see Table 2.1 for species descriptions), with two recently rediscovered: *Tridacna noae* (now separated from *T. maxima*) and *T. squamosina* (previously known as *T. costata*), and an undescribed cryptic *Tridacna* sp. (Huelsken et al., 2013). *Tridacna maxima* is the most widespread while *Hippopus porcellanus*, *T. noae*, *T. mbalavuana* (previously known as *T. tevoroa*), *T. rosewateri*, and *T. squamosina* have much more restricted distributions (Rosewater, 1965; bin Othman et al., 2010; Su et al., 2014). *Tridacna gigas* is by far the largest species, reaching shell lengths of over 120 cm and weights in excess of 200 kg (Rosewater, 1965). Since pre-history, giant clams' high biomass and heavy calcified shells have made them useful to humans as a source of food and material (Miller, 1979; Hviding, 1993). However, as a result of habitat degradation, technological advances in exploitation, expanding trade networks and demand by aquarists, their numbers are declining throughout their range (Mingoa-Licuanan and Gomez, 2002; Kinch and Teitelbaum, 2010; bin Othman et al., 2010).

Table 2.1. Giant clam species list (Rosewater, 1965; bin Othman et al., 2010; Huelsken et al., 2013; Su et al., 2014) and their conservation status categories listed by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Molluscs Specialist Group, 1996; Wells, 1996).

Species name	**Description**	**Global conservation status**
Hippopus hippopus (Linnaeus, 1758)	Species has strong radial ribbing and reddish blotches in irregular bands on shells, growing to about 40 cm. Unlike *Tridacna* species, *Hippopus* mantle does not extend over shell margins and has a narrow byssal orifice.	Lower Risk/conservation dependent
Hippopus porcellanus Rosewater, 1982	Species is distinguished from *H. hippopus* by its smoother and thinner shells, and presence of fringing tentacles at incurrent siphon, growing to approximately 40 cm.	Lower Risk/conservation dependent
Tridacna crocea Lamarck, 1819	Smallest of all clam species, reaching lengths of about 15 cm. Burrows and completely embeds into reef substrates.	Lower Risk/least concern
Tridacna derasa (Röding, 1798)	Second largest species, growing up to 60 cm. Has heavy and plain shells, with no strong ribbing.	Vulnerable A2cd
Tridacna gigas (Linnaeus, 1758)	Largest of all clam species, growing to over 1 m long. Easily identified by their size and elongate, triangular projections of upper shell margins.	Vulnerable A2cd
Tridacna maxima (Röding, 1798)	Species is identified by its close-set scutes. Grows up to 35 cm. Tends to bore partially into reef substrates.	Lower Risk/conservation dependent
Tridacna mbalavuana Ladd, 1934 (formerly *T. tevoroa* Lucas, Ledua, Braley, 1990)	Species is most like *T. derasa* in appearance, but distinguished by its rugose mantle, prominent guard tentacles present on the incurrent siphon, thinner valves, and colored patches on shell ribbing. Can grow over 50 cm long. Restricted to Fiji and Tonga.	Vulnerable B1+2c
Tridacna rosewateri Sirenko and Scarlato, 1991	Species is most like *T. squamosa* in appearance, but distinguished by its thinner shell, large byssal orifice and dense scutes on primary radial folds. Only found in Mauritius, with largest specimen measured at 19.1 cm.	Vulnerable A2cd

Tridacna squamosa Lamarck, 1819	Species is identified by its large, well-spaced scutes, with shell lengths up to 40 cm.	Lower Risk/conservation dependent
Tridacna noae (Röding, 1798)	Species is most like *T. maxima* in appearance, but distinguished by its sparsely distributed hyaline organs and oval patches with different colors bounded by white margins along mantle edge. Shell lengths between 6 to 20 cm. Distributed in Taiwan, Okinawa and Ishigaki Islands of Japan.	No status
Tridacna squamosina Sturany, 1899 (formerly *T. costata* Roa-Quiaoit, Kochzius, Jantzen, Zibdah, Richter, 2008)	Species is most like *T. squamosa* in appearance, but distinguished by its crowded, well-spaced scutes, asymmetrical shell, and grows up to 32 cm. Only found in the Red Sea.	No status
Cryptic *Tridacna* sp. (undescribed in Huelsken et al., 2013)	Recently determined as a widely distributed cryptic species; forms an evolutionarily distinct monophyletic group.	No status

Giant clams are especially vulnerable to stock depletion because of their late sexual maturity, sessile adult phase, and broadcast spawning reproductive strategy (Munro, 1989; Lucas, 1994). Fertilization success requires a sufficient number of spawning individuals, and low densities result in reduced (or zero) recruitment and eventual population collapse (Neo et al., 2013). Presently, all giant clam species, other than the recently rediscovered *T. noae* and *T. squamosina*, and the cryptic *Tridacna* spp., are protected under Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and listed in the IUCN Red List of Threatened Species (Table 2.1). Conservation efforts are ongoing (Heslinga, 2013) including essential basic research (Guest et al., 2008; Adams et al., 2013; Dumas et al., 2014) and the development of new restocking techniques (Waters, 2013). There are also several giant clam sanctuaries under legal protection, for example in Australia (Rees et al., 2003) and French Polynesia (Andréfouët et al., 2005, 2013), however, stocks are declining rapidly in many countries (bin Othman et al., 2010; Andréfouët et al., 2013) and extirpations are occurring (Kinch and Teitelbaum, 2010; Neo and Todd, 2012, 2013).

There exists a substantial body of work on the biology and mariculture of giant clams, but their significance in the coral reef ecosystem is not well understood. Some previous researchers have provided anecdotal insights into their likely roles, i.e. as food, as shelter, and as reef-builders and shapers. For example, Mercier and Hamel (1996, p.113) remarked: *"Tridacna face many dangers. They are most vulnerable early in their life cycle, when they are prey to crabs, lobsters, wrasses, pufferfish, and eagle rays."* In a popular science article, Mingoa-Licuanan and Gomez (2002, p.24) commented: *"clam populations add topographic detail to the seabed and serve as nurseries to various organisms… Their calcified shells are excellent substrata for sedentary organisms."* Finally, Hutchings (1986, p.245) stated: *"giant clams are recognisable in early Holocene reefs and if similar densities occurred to those on recent reefs, giant clams have had a considerable ongoing impact on reef morphology."* Even though there is evidence that giant clams contribute to the functioning of coral reefs, this has never been quantified. Here, based on existing literature and our own observations, we examine giant clams as contributors to reef productivity, as providers of biomass to predators and scavengers, and as nurseries and hosts for other organisms. We also examine their reef-scale roles as calcium carbonate producers, zooxanthellae reservoirs, and counteractors of eutrophication. Our findings lead to the conclusion that healthy populations of giant clams benefit coral reefs in ways previously underappreciated, and that this knowledge should help prioritize their conservation.

2.2. Giant clams as food

2.2.1. Productivity and biomass

Giant clams are mixotrophic (Jantzen et al., 2008), being capable of generating biomass through both primary and secondary production. Primary production is controlled by the photosynthetic efficiency of their symbiotic photoautotrophic zooxanthellae (Jantzen et al., 2008; Yau and Fan, 2012). Secondary production, on the other hand, is strongly influenced by the uptake rate of ambient dissolved inorganic carbon (DIC) via filter feeding (Jones et al., 1986; Watanabe et al., 2004). The acquisition of DIC is related to clearance rates (i.e. the volume of water each clam pumps per unit time), and therefore clam body size (Klumpp et al., 1992). To help make between-taxa comparisons, the net primary productivity (NPP) from an array of reef organisms, including giant clams, is presented in Fig. 2.1. We acknowledge that different productivity measures were used across studies; however, our aim is to provide estimate figures for relative rates among reef organisms. The NPP of the giant clams, *T. maxima* (28.16 g O_2 m^{-2} d^{-1}) and *T. squamosa* (18.14 g O_2 m^{-2} d^{-1}) are higher than most of the other coral reef primary producers. From the examples in Fig. 2.1, the NPP of *T. maxima* and *T. squamosa* are respectively ~74.1× and ~47.7× higher than the lowest NPP presented—that of the hard coral (*Manicina* sp.) (0.38 g O_2 m^{-2} d^{-1}), and approximately double that of the relatively fast growing branching coral *Acropora palmata*. The contribution of giant clams to overall reef productivity is hence potentially very substantial, especially when populations are dense (Rees et al., 2003; Andréfouët et al., 2005; Gilbert et al., 2006).

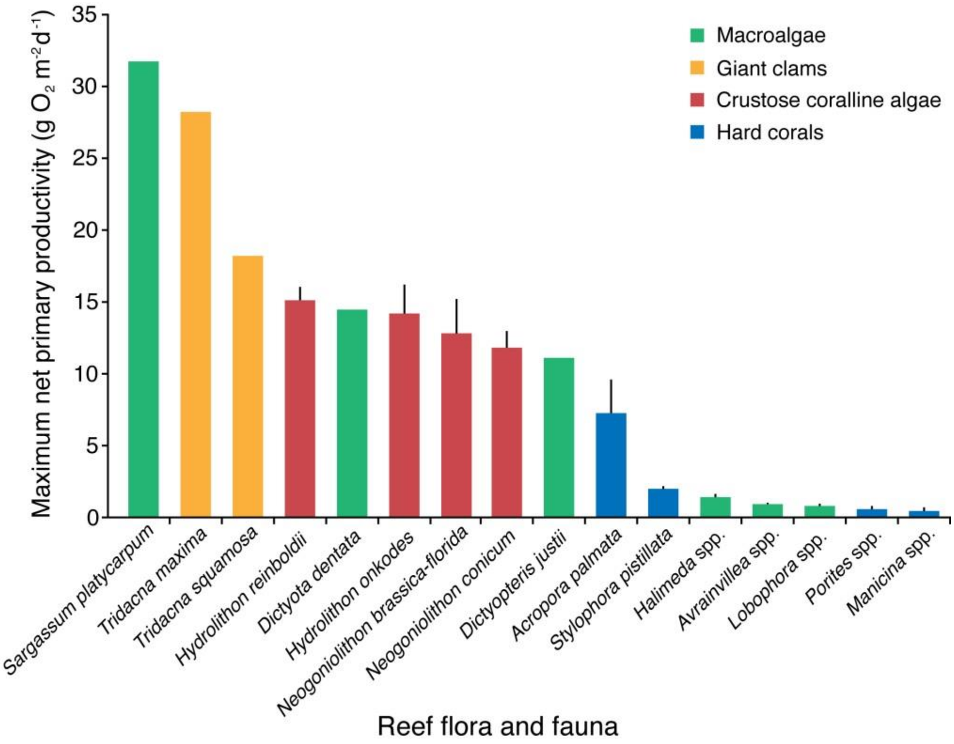

Fig. 2.1. Maximum net primary productivity (NPP) of the different reef flora and fauna, measured in terms of net oxygen production (units = g O_2 m^{-2} d^{-1}). NPP values are arranged from the highest to lowest producers. Standard deviation provided when available. Information extracted from: Wanders (1976); Rogers and Salesky (1981); Porter et al. (1984); Chisholm (2003); Jantzen et al. (2008); Naumann et al. (2013).

To determine how much biomass (i.e. NPP plus assimilated filter fed material) giant clams can contribute to a coral reef, we combined data and equations from surveys that provided clam densities and size distributions (see Table 2.2) with additional clam biomass equations elicited from Klumpp and Griffiths (1994), Hawkins and Klumpp (1995) and Ricciardi and Bourget (1998). Estimates of the standing stock of giant clams per hectare of coral reef for three species are provided in Table 2.2. We also estimated annual biomass production which, if the giant clam populations were in equilibrium, would equal the amount of food provided to predators and scavengers per year. Giant clams will contribute more to productivity on reefs where there is recruitment of juvenile clams, as these are faster-growing. In French Polynesia, the Tatakoto atoll population of *T. maxima*, a medium-sized species, has a high standing crop (1041 kg dry weight ha^{-1}) and very high productivity, being capable of producing 238 kg dry weight ha^{-1} yr^{-1} of biomass. This population is maintained by especially rapid recruitment, probably due to thermal variations caused by the geography of the atoll (Gilbert et al., 2006). The example *T. gigas* population from the Great Barrier Reef (Table 2.2) has a standing crop of 718 kg dry weight ha^{-1}, but is essentially a relict population, consisting primarily of large adult clams. The lack of younger, faster-growing *T. gigas* clams explains why the annual production of new biomass is so low (14 kg dry weight ha^{-1} yr^{-1}). *Tridacna crocea* appears to contribute minimally on a per hectare basis (due to its smaller size and low population density) in the examples provided in Table 2.2, but in patches of favourable habitat, *T. crocea* can have densities exceeding 100 clams m^{-2} (Hamner and Jones, 1976) and hence may be important at very local scales. While we have only presented data for single species, it is possible for up to six to co-exist on the same reef (e.g. Hardy & Hardy, 1969; Rees et al., 2003), occupying different niches based on depth and substrate type. We predict that a mixed assemblage would have a combined biomass exceeding that produced by only one species.

Table 2.2. Estimates of ecologically relevant parameters of giant clam populations found per hectare of reef area (based on data extracted from the references cited in the table). DD = data deficient.

Location	Population density (ind. ha^{-1})	Standing biomass (kg dry weight)	Annual biomass production (kg dry weight)	Shell weight (kg)	Annual shell production (kg)	Water filtration (l h^{-1})	Source of population data
Tridacna crocea							
Lee-Pae Island, Andaman Sea, Thailand	2441	17	DD	391	DD	8144	Chantrapornsyl et al., 1996
Tioman Island, Malaysia	955	4	DD	98	DD	2115	Todd et al., 2009
Tridacna maxima							
Fangatau atoll, French Polynesia	381919	878	217	89023	23372	DD	Gilbert et al., 2006
Tatakoto atoll, French Polynesia	909466	1041	238	102833	37040	DD	Gilbert et al., 2006
Ningaloo Marine Park, Western Australia	8600	36	7	3898	562	DD	Black et al., 2011
Tridacna gigas							
Great Barrier Reef, Australia	432	718	14	18839	356	28121	Pearson and Munro, 1991

2.2.2. Food for predators and scavengers

Predation on juvenile giant clams has been studied extensively (e.g. Alcazar, 1986; Perio and Belda, 1989; Govan et al., 1993), particularly during the ocean nursery phase of mariculture (Govan, 1992a). Heslinga and Fitt (1987) assumed larger tridacnines were immune to predation, but there have been reported attacks on mature adults (Alcazar, 1986). It is apparent that giant clams are widely utilized food sources on coral reefs, with 75 known predators (Table 2.3). Jawed fishes—wrasse, triggerfish, and pufferfish—prey on both juvenile and adult giant clams (Alcazar, 1986; Richardson, 1991; Govan, 1992b) and bite marks on the mantle edges of wild clams are common (Fig. 2.2). In mariculture, ectoparasitic pyramidellids and ranellids are often abundant and their attacks devastate juvenile cohorts (Perron et al., 1985; Boglio and Lucas, 1997), but they have less impact on clams on reefs, where natural predators of these ectoparasites are present (Cumming and Alford, 1994; Govan, 1995).

Table 2.3. Predators of giant clams, including those listed by Govan (1992a, 1992b), plus new observations and additional findings from grey literature.

Predator species	Method of predation	Literature source(s)
PORIFERA: Family Clionaidae (Boring sponges)		
Unknown	Bore into shells, weakening shells	Govan, 1992b
FLATWORM: Family Turbellaria		
Stylochus (*Imogene*) *matatasi*	Enter the clam through either the byssal orifice or inhalant siphon	Newman et al., 1991, 1993
Stylochus (*Imogene*) sp.		Govan, 1992a, 1992b
Polyclad sp. 1		Govan, 1992a
MOLLUSCS: Family Buccinidae (Whelks)		
Cantharus fumosus	-	Perio and Belda, 1989
Family Costellariidae (Mitres)		
Vexillum cruentatum	-	Govan, 1992b
V. plicarium	-	Richardson, 1991
Family Fasciolariidae (Tulip snails)		
Pleuroploca trapezium	Immobilize clam by clasping mantle with foot preventing valve closure, insert proboscis into soft tissues	Govan, 1992b
Pleuroploca sp.		Alcazar, 1986
Family Muricidae (Murexes)		
Chicoreus brunneus	Drill holes into shells of juvenile clams	Abdon-Naguit and Alcazar, 1989; Govan, 1992a, 1992b
C. microphyllum	Drill holes into shells	Govan, 1992a, 1992b
C. palmarosae	Often drill through valves; may attack via valve gape or byssal orifice	Govan et al., 1993
C. ramosus	Insert proboscis into byssal gape to reach soft tissues, inject paralytic substance	Heslinga et al., 1984; Alcazar, 1986; Govan, 1992b
Cronia fiscella	Drill holes into shells of juvenile clams	Govan, 1992b
C. margariticola	Through valve gape	Govan, 1992a, 1992b
C. ochrostoma	Drill holes into shells	Govan, 1992b
Morula granulata	Drill holes into shells	Govan, 1992a, 1992b
Muricodrupa fiscella	Drill holes into shells	Govan, 1992a
Thais aculeata	Attack through valve gape	Govan, 1992a, 1992b
Family Octopodidae (Octopus)		
Octopus sp.	Chip shells; pry valves apart to feed	Heslinga et al., 1984; Barker et al., 1988; Govan, 1992b; Mercier and Hamel, 1996
Family Pyramidellidae		
Turbonilla sp.	Use their long, flexible proboscis to suck clams' body fluids, either from mantle edge or through byssal orifice	Govan, 1992a, 1992b
Tathrella iredalei		Heslinga et al., 1990; Govan, 1992b
Family Ranellidae (Tritons)		
Bursa granularis	Insert proboscis between valves of prey	Govan et al., 1993
Cymatium aquatile	Injection of an immobilizing fluid through mantle or byssal orifice, then feed on soft tissues	Abdon-Naguit and Alcazar, 1989; Govan, 1992a, 1992b, 1995
C. muricinum		Perron et al., 1985; Govan, 1992a, 1992b, 1995
C. nicobaricum		Govan, 1992a, 1992b, 1995
C. pileare		Govan, 1992a, 1992b, 1995
C. vespaceum		Perio and Belda, 1989; Govan, 1992b

Family Volutidae (Volutes)		
Melo amphora	-	Loch, 1991
Melo sp.	-	Govan, 1992b
ECHINODERM		
Seastar	Exert powerful suction and tire adductor muscles (pry open clam)	Weingarten, 1991
CRUSTACEANS: Family Diogenidae (Hermit crabs)		
Dardanus deformis	Crushed 26 juvenile *T. gigas* in 3 days	Heslinga et al., 1984
D. lagopodes	Chip valve ends	Govan, 1992a
D. pedunculatus	Crush or chip valves of prey	Govan, 1992a; Govan et al., 1993
Family Gonodactylidae (Mantis shrimps)		
Gonodactylus chiragra	Smash shells	Govan, 1992a
Gonodactylus sp.	-	Govan, 1992b
Family Portunidae (Swimming crabs)		
Thalamita admete	Chip shells; attack via byssal orifice	Govan, 1992a
T. coerulipes		Govan, 1992a
T. crenata	Crush shells; may pry clam open via ventral margin	Ling, 2007
T. danae	Crush or chip valves; attack via byssal orifice of clams	Govan et al., 1993
T. spinimana	-	Richardson, 1991
T. stephensoni	Chip shells; attack via byssal orifice	Govan, 1992a
T. cf. *tenuipes*		Govan, 1992a
Thalamita sp.	Penetrate soft tissues of adults through either byssal orifice or the inhalant siphon	Alcazar, 1986; Govan, 1992b
Family Xanthidae (Stone crabs)		
Atergatis floridus	Crush or chip valves	Richardson, 1991; Govan et al., 1993
A. integerrimus		Richardson, 1991
Atergatis spp.		Govan, 1992b
Carpilius convexus	Crush or chip valves of juvenile clams	Alcazar, 1986; Govan, 1992a, 1992b; Govan et al., 1993
C. maculatus	Crush shells	Govan, 1992a, 1992b
Demania cultripes	Crush shells of juvenile clams	Alcazar, 1986; Govan, 1992b
Leptodius sanguineus	Crush shells	Govan, 1992a, 1992b
Lophozozymus pictor	Crush or chip shells	Richardson, 1991; Govan, 1992b
Myomenippe hardwickii	Crush shells; may attack via byssal orifice	Ling, 2007
Zosimus aeneus	Crush shells	Govan, 1992a, 1992b
FISH: Family Balistidae (Triggerfish)		
Balistapus undulatus	Feed on mantle and the exposed byssus and foot of adult clams	Alcazar, 1986; Perio and Belda, 1989
Balistoides viridescens	Crush or chip shells	Heslinga et al., 1990
Balistoides sp.		Govan, 1992b
Pseudobalistes flavimarginatus		Heslinga et al., 1990; Chambers, 2007
Pseudobalistes sp.		Govan, 1992b
Rhinecanthus sp.		Govan, 1992b
Family Lethrinidae (Emperors)		
Monotaxis grandoculis	Directly consumed 50 juvenile *T. squamosa* in <2 h	Heslinga et al., 1984; Govan, 1992b
Family Labridae (Wrasses)		
Cheilinus fasciatus	-	Richardson, 1991
Cheilinus sp.	Crush or chip shells	Govan, 1992b
Choerodon anchorago	-	Richardson, 1991
C. schoenleinii	-	Richardson, 1991
Choerodon sp.	Crush or chip shells	Govan, 1992b
Halichoeres sp.	Feed only on the byssus and foot of	Alcazar, 1986; Govan, 1992b

	unanchored clams	
Thalassoma hardwicke	-	Richardson, 1991
T. lunare	-	Richardson, 1991
<u>Family Myliobatidae (Eagle rays)</u>		
Aetobatis narinari	Crush shells	Heslinga et al., 1990; Govan, 1992b; Chambers, 2007
<u>Family Tetraodontidae (Pufferfish)</u>		
Canthigaster solandri	-	Richardson, 1991
C. valentini	Crush or chip shells	Perio and Belda, 1989; Govan, 1992b
Tetraodon stellatus		Heslinga et al., 1990; Govan, 1992b; Chambers, 2007
TURTLES: <u>Family Cheloniidae</u>		
Caretta caretta	-	Bustard, 1972
Chelonia mydas	Break off shell flukes and ingest as calcium carbonate dietary supplement	Weingarten, 1991

The wide array of defences exhibited by giant clams is also indicative of their importance as a food source. Giant clams and their predators are likely to have been in an evolutionary arms race for millions of years. To resist attack, tridacnines have evolved large body sizes (Carter, 1968), reduced byssal orifices, and heavy strong shells (Perron et al., 1985; Alcazar, 1986; Govan et al., 1993). Neo and Todd (2011a) found that shell strength is a phenotypically plastic trait in juvenile *T. squamosa*, with specimens exposed to predator effluents being harder to crush. The shell projections (called scutes) in some *Tridacna* species probably offer protection from crushing predators such as crabs and jawed fishes (Ling et al., 2008). Other defence mechanisms include aggregation of conspecifics (Huang et al., 2007), camouflage (Todd et al., 2009), rapid mantle withdrawal (McMichael, 1974), and squirting of water from siphons (Neo and Todd, 2011b).

The scavenging guild is critical to nutrient recycling on coral reefs (Keable, 1995; Rassweiler and Rassweiler, 2011) and dead or dying giant clams will attract a variety of small invertebrate scavengers including isopods, ostracods, amphipods, leptostracans, mysids, polychaetes, and small decapods and snails (Keable, 1995).

Many of these have not been reported to prey on healthy clams; for example, the muricid gastropod (*Drupella rugosa*) only acts as a scavenger and not a predator on giant clam juveniles (Perron et al., 1985).

2.2.3. Expelled materials

Opportunistic feeders may feed upon the materials (gametes, faeces, and pseudofaeces) expelled by giant clams (Ricard and Salvat, 1977; Lucas, 1994). For example, at the Silaqui ocean nursery, Bolinao, Philippines, a large school of blue sprat (*Spratelloides delicatulus*) fed for at least three hours on the gametes released by *T. gigas* (Maboloc and Mingoa-Licuanan, 2011). Routine releases of undigested, photosynthetically functional zooxanthellae in the faeces (Ricard and Salvat, 1977; Trench et al., 1981) can be important sources of organic matter in closed or semi-closed systems, such as the atoll lagoons in French Polynesia (Ricard and Salvat, 1977; Richard, 1977). Finally, giant clams faeces contain substantial amounts of nutritious mucus and protein (Ricard and Salvat, 1977) that can make a significant dietary contribution to reef fish (Chan, 2007).

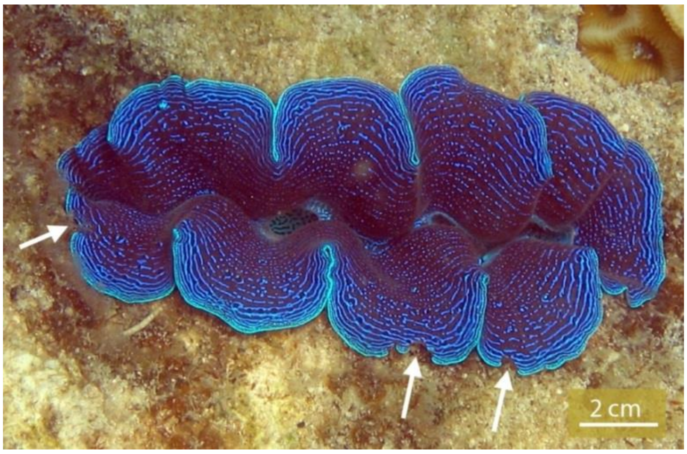

Fig. 2.2. Fish bite marks on the mantle edge of a *Tridacna crocea* (Shell length ~140 mm).

2.3. Giant clams as shelter

2.3.1. Shelters for coral reef fish

Coral reef fish diversity is related to coral cover (Bell and Galzin, 1984; Ault and Johnson, 1998) and substrate complexity (Gratwicke and Speight, 2005; Lingo and Szedlmayer, 2006). Dense aggregations of giant clams can increase topographic heterogeneity of the seabed and serve as nurseries and shelters for fishes. A restoration study in the Philippines demonstrated that *T. gigas* introduced onto degraded reefs significantly improved fish diversity and abundance compared to control plots (Cabaitan et al., 2008). An increase in habitat relief usually facilitates recruitment and settlement of juvenile fish and helps reduce predation by providing refuges (Beukers and Jones, 1997; Lecchini et al., 2007) while the shell ridges of giant clams represent suitable obscure surfaces for the deposition of fishes' egg masses (Weingarten, 1991). The large mantle cavities of tridacnines also afford shelter to smaller fishes, such as the pearlfish (*Encheliophis homei*) (Trott and Chan, 1972) and anemone fishes in the absence of host anemones (Arvedlund and Takemura, 2005).

2.3.2. Shell surfaces for epibionts

On coral reefs, where settlement surfaces are limiting, epibiosis is an alternative colonization strategy for sessile organisms (Wahl and Mark, 1999; Harder, 2008). Nevertheless, while epibiosis may be common in marine ecosystems (Harder, 2008), only a handful of studies have discussed its ecological importance (e.g. Abellö et al., 1990; Creed, 2000; Botton, 2009). Giant clam shells have been reported to harbor a variety of burrowing (Yonge, 1955; Turner and Boss, 1962) and encrusting (Roscoe, 1962; Rosewater, 1965) reef inhabitants (Fig. 2.3), although the authors of these studies did not list specific taxa. Our own observations of clam-associated epibionts include macroalgae, sponges, ascidians, nudibranchs, bryozoans, tubeworms, hard and soft corals, as well as small mobile invertebrates. Some, such as macroalgae (Fatherree, 2006), boring sponges (Norton et al., 1993), the boring worm (*Oenone fulgida*) (Delbeek and Sprung, 1994), and pest anemones (*Aiptasia* spp.) (Fatherree, 2006) can harm their tridacnine hosts. In addition, uncontrolled algae growth on juvenile clams can reduce growth and lead to death by interfering with valve movement (personal observations, 2014). Conversely, other epibionts may protect their hosts by contributing anti-predator defenses (Feiferak, 1987) and/or camouflage (Harder, 2008).

Fig. 2.3. Epibiota diversity amongst giant clam species. (a) *Tridacna gigas* with a burrowing giant clam (*Tridacna crocea*) in its shell; Mecherchar Island, Republic of Palau, March 2011. (b) *Tridacna derasa* with hard coral (*Favites* sp.) growing on it; Ouvea island of the Loyalty Islands, New Caledonia, August 2010. (c) *Hippopus* sp. with encrusting crustose coralline algae; Bali, Indonesia, May 2011. (d) *Tridacna maxima* hosting a range of encrusting epibionts; Kumejima, Okinawa, Japan; November 2009.

Vicentuan-Cabaitan et al. (2014) identified the community living on the valves of *T. squamosa* in Singapore. They found at least 49 species belonging to a minimum of 36 families living on the shells of eight *T. squamosa* individuals (shell lengths 236–400 mm). Vicentuan-Cabaitan et al. (2014) also highlighted that giant clam shells provide much more surface area for colonization compared to the patch of substrate they occupy (a 26:1 ratio based on three adult *T. squamosa* specimens). A complete taxa checklist was not provided in their short paper, but it is now included here (Table 2.4). As this list is for just one tridacnine species at a single locality, we expect that it represents only a small percentage of the taxa that live on the shells of all giant clam species (that vary in size, shell morphology, habitat preference, and global distribution).

Table 2.4. List of epibiont families found on *Tridacna squamosa* in Singapore (*n* = 8). Crustose coralline algae (CCA) was also very common, but not identified to species level.

Taxa group	Family	No. of species
Algae	Bryopsidaceae	1
	Cladophoraceae	1
	Corallinacea	1
	Dictyotaceae	2
	Galaxauraceae	1
	Gracilariaceae	2
	Hypneaceae	1
	Rhodomelaceae	1
	Sargassaceae	1
Sponges	Ancorindae	1
	Chalinidae	2
	Dysideidae	1
	Petrosiidae	1
	Spongiidae	1
	Tedaniidae	1
	Tetillidae	1
Polychaetes	Eunicidae	1
	Hesionidae	1
	Terebellidae	1
Brittlestars	Ophiotrichidae	1
Crustaceans	Alpheidae	1
	Galatheidae	1
	Melitidae	1
	Paramelitidae	1
	Portunidae	1
	Sphaeromatidae	1
	Tychidae	1
	Xanthidae	2
Chitons	Chitonidae	1
Gastropods	Cypraeidae	2
	Trochidae	1
Bivalves	Arcidae	6
	Malleidae	2
	Mytilidae	1
	Pteriidae	2
Ascidians	Styelidae	2

2.3.3. Hosts for ectoparasites

Various cyclopoid copepods live within giant clams (Table 2.5). Even though they are capable of influencing the growth, fecundity, and survival of their hosts (Finley and Forrester, 2003; Johnson et al., 2004), the biology of these cyclopoids is poorly understood. *Anthessius* and *Lichomolgus* are usually found inside the mantle cavity (Humes, 1972, 1976), while *Paclabius* inhabits the pericardium, i.e. the membrane enclosing the heart (Kossmann, 1877). Multiple cyclopoid species have also been found within the same clam host (Humes, 1972, 1976). Ectoparasitic gastropods are also known to plague giant clams (also see 2.2.), and are especially severe in cultured juveniles (Cumming and Alford, 1994).

2.3.4. Hosts for commensals

Bivalves host a wide diversity of commensal fauna (Blanco and Ablan, 1939; De Grave, 1999), providing refuge (Rosewater, 1965) and/or food (Fankboner, 1972). The recorded commensals for tridacnines include pinnotherid pea crabs (Fig. 2.3; Table 2.6) and pontoniinid shrimps (Fig. 2.4; Table 2.7). Pea crabs are common within the mantle cavities of bivalves (Stauber, 1945; Schmitt et al., 1973), positioning themselves on the ctenidial surface (gills) with their strong grip and gaining access to food aggregated by the host (Stauber, 1945). *Xanthasia murigera* (Fig. 2.3) is probably the most widespread, being found in five clam species (Table 2.6). Pontoniinid shrimps can also inhabit the mantle cavities of giant clams. With hooked walking-leg dactyls (Fujino, 1975), they anchor themselves against the currents generated by the gills, avoiding expulsion (Fankboner, 1972). While some species are commensal to multiple tridacnine species (Table 2.7), *Anchistus gravieri* appears to be obligate to *H. hippopus* (McNeill, 1953; Bruce, 1977, 1983) whilst *Paranchistus armatus* is restricted to *T. gigas* (Bruce, 1983, 2000). Due to their long lifespans, giant clams can host many generations of commensals and the absence of any trauma to collected examples suggests that life within tridacnines is secure (Bruce, 2000).

Table 2.5. Cyclopoid copepods known to occur in specific host tridacnines. Information extracted from: Humes and Stock (1965); Humes (1972, 1973, 1976, 1993); Kossmann (1877).

Cyclopoid copepods species	Host giant clam species	Recorded localities
Anthessius alatus Humes and Stock, 1965	*Tridacna gigas*	Marshall Islands
	Tridacna maxima	Marshall Islands; New Caledonia; Red Sea
	Tridacna squamosa	Madagascar; Marshall Islands; Moluccas; New Caledonia
Anthessius amicalis Humes and Stock, 1965	*Hippopus hippopus*	Marshall Islands
	Tridacna maxima	New Caledonia; Red Sea
	Tridacna squamosa	Madagascar; Marshall Islands; New Caledonia
Anthessius discipedatus Humes, 1976	*Hippopus hippopus*	Moluccas
Anthessius solidus Humes and Stock, 1965	*Tridacna squamosa*	Madagascar; Marshall Islands
Lichomolgus hippopi Humes, 1976	*Hippopus hippopus*	Moluccas
Lichomolgus tridacnae Humes, 1972	*Hippopus hippopus*	Moluccas
	Tridacna gigas	Marshall Islands
	Tridacna squamosa	Marshall Islands
Paclabius tumidus Kossmann, 1877	*Tridacna* sp.	Philippines
	Tridacna squamosa	New Caledonia

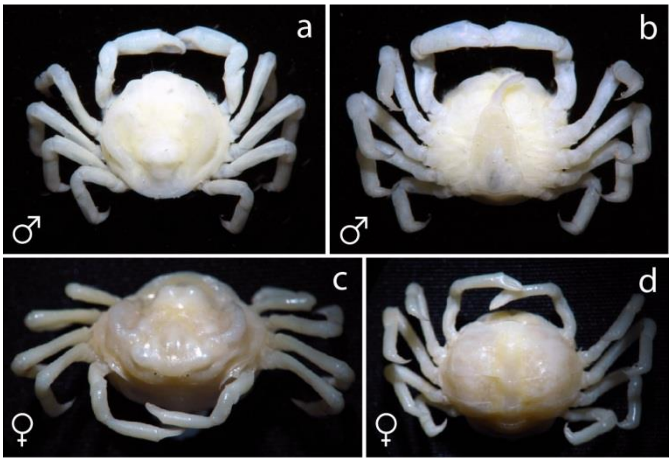

Fig. 2.4. Commensal pinnotherids (*Xanthasia murigera*; ZRC2013.0790) found within the mantle cavity of a fluted giant clam (*Tridacna squamosa*; shell length = 150 mm). (a, b) Carapace length (CL) = 5 mm. (c, d) CL = 11.5 mm.

Table 2.6. Pinnotherid pea crabs known to occur in specific host tridacnines. Information extracted from: Ahyong and Brown (2003); Ahyong and Ng (2005); Blanco and Ablan (1939); Garth et al. (1987); Grant and McCulloch (1906); McNeill (1968); Rosewater (1965); Schmitt et al. (1973); Takeda and Shimazaki (1974).

Pinnotherid pea crab species	Host giant clam species	Recorded localities
Ostracotheres tridacnae (Rüppell, 1830)	Giant clams	Red Sea; South Africa
Synonymised taxa: *Pinnotheres tridacnae* Rüppell, 1830	*Tridacna maxima*	Unknown
Tridacnatheres whitei (De Man, 1888)	Giant clams *Tridacna* sp. *Tridacna gigas*	Malayan Peninsula; Mergui Archipelago Singapore Unknown
Synonymised taxa: *Xanthasia whitei* De Man, 1888	*Tridacna squamosa*	Malaysia; Vietnam
Xanthasia murigera White, 1846	Giant clams	Andaman Islands; Australia; Fiji; India; Indonesia; Marshall Islands; Mergui Archipelago; Mozambique; New Caledonia; Palau; Philippines; Papua New Guinea (PNG)
	Hippopus sp.	Australia
	Hippopus hippopus	Great Barrier Reef (GBR), Australia
	Tridacna crocea	Australia; Santa Cruz Islands; Thailand
	Tridacna gigas	Marshall Islands
	Tridacna maxima	GBR, Australia
	Tridacna squamosa	GBR, Australia; Philippines; Thailand

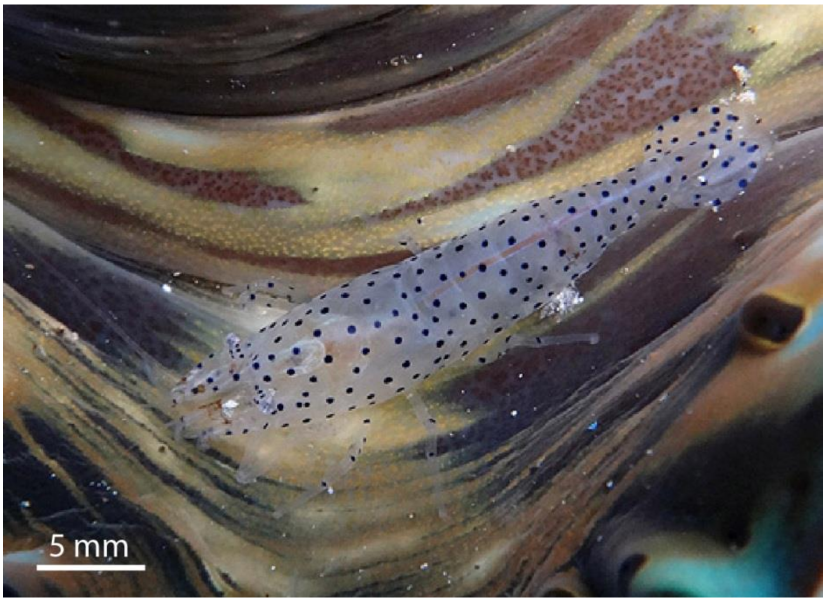

Fig. 2.5. A commensal pontoniinid (*Anchistus* sp.; body length = 34 mm) found resting on the mantle of a fluted giant clam (*Tridacna squamosa*; shell length = 243 mm).

Table 2.7. Pontoniinid shrimps known to occur in specific host tridacnines. Information extracted from: Borradaile (1917); Bruce (1973, 1974a, 1974b, 1975, 1976, 1977, 1978, 1979, 1980, 1991, 1993); Bruce and Coombes (1995); Dana (1852); De Grave (1999, 2001); Devaney and Bruce (1987); Fankboner (1972); Fransen (1994); Fransen and Reijnen (2012); Holthuis (1952, 1953); Johnson (1961); Kemp (1922); Kubo (1940, 1949); Li (1997, 2004); McNeill (1953, 1968); Miyake and Fujino (1968); Pesta (1911).

Pontoniinid shrimp species	Host giant clam species	Recorded localities
Anchistus australis Bruce, 1977	*Hippopus hippopus*	Papua New Guinea (PNG)
	Tridacna sp.	Australia; Fiji; Indonesia; Marshall Islands; New Caledonia
Synonymised taxa:		
Anchistus australis sp. nov., forma ***typica***	*Tridacna derasa*	Great Barrier Reef (GBR), Australia
	Tridacna gigas	PNG
Anchistus australis sp. nov., forma ***dendricauda***	*Tridacna squamosa*	GBR, Australia; Indonesia; Malaysia; PNG
Anchistus demani Kemp, 1922	*Tridacna* sp.	Andaman Islands; Kenya; Madagascar; Marshall Islands; PNG; Seychelles; Thailand; Zanzibar
	Tridacna crocea	Malaysia
	Tridacna gigas	GBR, Australia
	Tridacna maxima	GBR, Australia; Central East Africa; Mayotte, Comoro Islands; PNG; Seychelles; Thailand; Vietnam
	Tridacna squamosa	Central East Africa; PNG
Anchistus gravieri Kemp, 1922	*Hippopus hippopus*	GBR, Australia; New Caledonia; Santa Cruz Islands
Anchistus miersi (De Man, 1888)	*Hippopus hippopus*	Australia; China, South China Sea (SCS); Malaysia; Marshall Islands; Palau
	Tridacna sp.	Anambas Islands, Indonesia; China, SCS; Malaysia; Maldives; PNG; Seychelles; Singapore; Spratly Islands, Vietnam

	Tridacna crocea	Palau
	Tridacna gigas	GBR, Australia
	Tridacna maxima	Central East Africa; Mayotte, Comoro Islands; PNG; Seychelles; Vietnam
	Tridacna squamosa	Central East Africa; Indonesia; Malaysia; Palau; Seychelles; Vietnam
Conchodytes tridacnae Peters, 1852	*Tridacna* sp.	Andaman Islands; Australia; China, SCS; Japan; Laccadive Islands; Maldives; Marshall Islands; Palau; Samoa; Seychelles; Spratly Islands, SCS
	Tridacna crocea	Palau
	Tridacna derasa	GBR, Australia
	Tridacna gigas	Unknown
	Tridacna maxima	GBR, Australia; Central East Africa; Seychelles; Thailand
	Tridacna squamosa	GBR, Australia
Marygrande mirabilis Pesta, 1911 Currently accepted as partim *Anchistus miersi*, partim *Anchistus custos* (Forskål, 1775)	*Tridacna gigas*	Samoa
Paranchistus armatus (H. Milne-Edwards, 1837) Synonymised taxa: *Anchistus ohshimai* Kubo, 1949 *Paranchistus biunguiculatus* Holthuis, 1952 *Pontonia armata* H. Milne-Edwards, 1837	*Tridacna* sp.	GBR, Australia; Indonesia; Gilbert Islands; Marshall Islands; Palau Islands; PNG
	Tridacna gigas	GBR, Australia; Japan; Palau Islands; PNG

2.4 Reef-scale contributions of giant clams

2.4.1. Contributors of carbonate

The calcium carbonate framework of coral reefs is maintained by opposing processes of carbonate production and removal (Le Campion-Alsumard et al., 1993; Mallela and Perry, 2007). Scleractinian corals are the primary carbonate producers on most tropical reefs (Hubbard et al., 1990; Vecsei, 2004), followed by calcareous algae, gastropods, bivalves, and foraminiferans (Mallela and Perry, 2007; Perry et al., 2012). Giant clams are rarely mentioned as carbonate contributors to reef frameworks, even though they have large shells, mostly made up of aragonite—a calcium carbonate polymorph (Moir, 1990). Shell carbonates are generally derived from ambient dissolved inorganic carbon (Romanek and Grossman, 1989), but also include carbon from metabolic respiration and zooxanthellae photosynthesis within the mantle tissues (Jones et al., 1986; Watanabe et al., 2004). Based on studies by Klumpp and Griffiths (1994) and Gilbert et al. (2006), we estimated shell production by *T. gigas* and *T. maxima* (Table 2.2). The relict population of *T. gigas* from the Great Barrier Reef may only produce 356 kg ha^{-1} yr^{-1} of new shell material but the *T. maxima* atoll populations in French Polynesia are capable of producing 23 to 37 t ha^{-1} yr^{-1} (Table 2.2) and are so dense that they create small islands called *mapiko* (Gilbert et al., 2006).

2.4.2. Bioeroders

Bioeroders such as grazers, etchers, and borers can increase the removal rate of the reef's carbonate framework (Clapp and Kenk, 1963; Hutchings, 1986). The boring giant clam species, *T. crocea* (Hamner and Jones, 1976) and, to a lesser extent, *T. maxima* (Yonge, 1980; Hutchings, 1986), are usually found embedded in either dead coral heads or dead patches of live colonies (Morton, 1990). Burrowing by *T. crocea* has been described as both a mechanical process and chemical etching. Mechanically, *T. crocea* enlarge their burrows by grinding back and forth within them, and fine shell corrugations on their valves wear away at the burrow walls (Yonge, 1953; Hamner and Jones, 1976). Chemical etching (Hedley, 1921; Yonge, 1980) is performed by an extension of the pedal mantle tissue out of the byssal opening, dissolving the substrate under and around the clam via excreted solvents (Yonge, 1980; Fatherree, 2006). Given sufficient time and enough settling and growing individuals, *T. crocea* will eventually flatten a dead coral head (Hamner and Jones, 1976; Glynn, 1997), but this erosive effect is limited to these particular *T. crocea* habitats, and does not lead to wide scale attrition of the reef (Paulay and Kerr, 2001; Aline, 2008). Even though little is known about the effects of *T. maxima*'s burrowing, McMichael (1974) and Hutchings (1986) both remarked that, due to their higher densities, they could contribute significantly to biological erosion on coral reefs.

2.4.3. Topographic enhancement

Mollusc shells are known to influence their environments, either by creating or modifying habitats for other organisms (Gutiérrez et al., 2003). Giant clams can modulate water flow and fluid transport as they add topographical relief to the seabed (Weingarten, 1991; Cabaitan et al., 2008). Depending on their density, their influence on water flow can be significant. Giant clam shells are expected to agitate flow boundary layers much more than the shells of smaller bivalves (Grant et al., 1992; Pilditch et al., 1998), since flow perturbation is correlated to the heights and diameters of protruding objects (Eckman and Nowell, 1984). Aggregations of giant clams are likely to further increase flow perturbation and cause turbulence eddies (Lenihan, 1999). These hydrodynamic disturbances in turn affect the rates at which transport of particles and solutes can occur (Gutiérrez et al., 2003). For instance, aggregations of bivalves have been shown to alter sediment transport patterns and rates (Grant et al., 1992; Lenihan, 1999) and enhance phytoplankton down-flux (Pilditch et al., 1998). Even after a clam's death, their heavy valves remain and continue to affect water flow.

2.4.4. Source of zooxanthellae (Symbiodinium spp.)

Nutrient cycling between zooxanthellae and their coral hosts is the key to both organisms' success in oligotrophic coral reef environments (Muscatine and Porter, 1977) and similar cycling occurs between zooxanthellae and other organisms, such as zooxanthellate jellyfish (Pitt et al., 2009). Zooxanthellae within giant clams utilize the hosts' nitrogenous waste with virtually no loss from the system (Hawkins and Klumpp, 1995), meaning that they have far greater access to nitrogen than they would if living in the surrounding seawater. Giant clams also protect their symbiotic zooxanthellae from predation (Fankboner, 1971) and excessive ultraviolet irradiation (Ishikura et al., 1997).

Giant clams release large numbers of zooxanthellae in their faecal pellets. To regulate symbiont density a *T. derasa* can discharge 4.9×10^5 cells clam^{-1} d^{-1} of intact zooxanthellae (Maruyama and Heslinga, 1997) and *T. gigas* can discharge 4.7×10^5 cells clam^{-1} d^{-1} (Buck et al., 2002). These are both several orders of magnitude higher than the release rates of corals (Yamashita et al., 2011). As noted by Maruyama and Heslinga (1997, p.475), "*most of the discharged zooxanthellae were indistinguishable from intact algal cells freshly isolated from the mantle.*" Trench et al. (1981) also found that zooxanthellae in faecal pellets were intact, photosynthetically active, and culturable. The branched tubular system extending from a giant clam's stomach into its mantle (Fankboner and Reid, 1990; Norton et al., 1992) provides numerous microhabitats for zooxanthellae (Norton et al., 1992) allowing multiple clades or multiple types from a single clade of symbionts to co-exist in a single host (Baillie et al., 2000; DeBoer et al., 2012). The substantial quantities of zooxanthellae released from giant clams become available for other zooxanthellate species to ‘take up’, hence contributing to the wider coral reef ecosystem.

2.4.5. Counteractors of eutrophication

In coastal marine waters, corals may be competitively excluded by macroalgae or heterotrophic filter feeders as the water becomes more eutrophic (Fabricius, 2005). Shallow water benthic bivalves are known to be natural controllers of eutrophication (Officer et al., 1982) and giant clams can perform this function in two ways: by filtering water and by sequestering nutrients (Klumpp and Griffiths, 1994). Here, we calculated the filtration rates of known populations of *T. crocea* and *T. gigas* using equations from Klumpp and Griffiths (1994). Giant clams filter large quantities of seawater; even a sparse population of mature *T. gigas* (0.04 clams m^{-2}) on the Great Barrier Reef is capable of filtering over 28 000 l ha^{-1} h^{-1} (Table 2.2). Giant clams also clear water of algal cells efficiently, i.e. *Tridacna* species ingest 51-58% while *H. hippopus* ingests 81% (Klumpp and Griffiths, 1994). Whether algal biomass is assimilated by the clams or excreted as faeces, it is removed from the water column in the short term and will therefore not contribute to turbidity. By locking assimilated nutrients away in their biomass (Table 2.2), giant clams sequester them from the water where they could otherwise encourage algae to flourish.

2.5. Conclusions

This review details how giant clams are effective ecosystem engineers that play multiple roles in coral reefs. Their high biomass production, coupled with their wide range of known predators and scavengers, suggests that giant clams are an important food item. In addition, their gametes and faeces are food to opportunistic feeders. Due to their large shell size, giant clams can shelter reef fish as well as support a diverse and abundant array of epibionts, ectoparasites, and commensals. Furthermore, some species, such as the pontoniinid shrimp (*Paranchistus armatus*), are only found in tridacnine hosts. At the reef-scale, dense populations of giant clams can annually contribute 100s to 1000s kg ha^{-1} of shell material to a coral reef, far outweighing localized erosion by *T. crocea* and *T. maxima*. Giant clams provide their symbiotic *Symbionidium* zooxanthellae with nutrients and protection, resulting in tridacnines acting as algal 'reservoirs'. They also filter large volumes of water—which can potentially counteract eutrophication. While we have only evaluated the ecological roles of the more common giant clam species: *H. hippopus*, *T. crocea*, *T. derasa*, *T. gigas*, *T. maxima*, and *T. squamosa*, we expect that the rarer species perform functions similar to those of their close relatives.

Even though there have been numerous giant clam population collapses (e.g. Munro, 1989; Kinch and Teitelbaum, 2010; Neo and Todd, 2012), it is difficult to measure the ecosystem-level effects of these events due to the concomitant impacts of multiple stressors that typify contemporary reefs (Hughes and Connell, 1999). Nevertheless, some negative consequences are predictable, for example, biomass and carbonate production, surface area for epibionts, and water filtering, are all expected to decrease linearly with reduced giant clam abundance. Other effects might require thresholds to be breached, for example, a minimum density of giant clams may be needed before they act as effective fish nurseries. It is unlikely that researchers would experimentally remove clams from a healthy reef to measure the outcome. On the other hand, restocking programmes present an excellent opportunity to monitor the response of the reef to enhanced clam numbers; unfortunately this is rarely done. The one exception is Cabaitan et al. (2008), who specifically set out to test the localized effects of transplanting maricultured giant clams (*T. gigas*, >40 cm shell length) into replicate 5 × 5 m^2 plots of degraded patch reef in the Philippines (25 clams per plot). Within three months, their "other biota" category (i.e. ascidians, anemones, gorgonians, soft corals, sponges, and zoanthids) had increased significantly from 2.0% to 14.8% cover; with no change observed in the control plots. Within the same time period fish species richness and abundance also increased significantly. Cabaitan et al. (2008) represents the only study to experimentally demonstrate the benefits that giant clams can have on coral reefs. Similar research at different locations, and with other species and densities, is needed.

Any significant ecological benefits will likely only accrue where giant clams are present in healthy, i.e. self-sustaining, populations and hence their conservation is paramount. As highlighted by Neo and Todd (2013), the CITES and IUCN data for giant clams are outdated and potentially misleading. Importantly, there are now three species recently rediscovered or undescribed that have no official conservation status (see Table 2.1). Giant clams should feature more prominently when planning marine protected areas and integrated coastal management schemes (van Wynsberge et al., 2014) and national/local assessments must be part of this process. Notably, not only are giant clams useful for the functioning of coral reefs, they can help protect them by acting as surrogate species. Giant clams are already considered an indicator species by Reef Check (Hodgson, 2001) and, being well-known charismatic invertebrate megafauna, they have the potential to play a flagship role (sensu Walpole and Leader-Williams, 2002, but see Favreau et al., 2006) in reef conservation.

We are not proposing that giant clams are essential to the survival of coral reefs; however, there can be no doubt that they make a positive contribution to these critically important tropical ecosystems. Based on the wide range of ecological functions they perform, giant clams are unique among reef organisms and therefore deserve attention. In combination with their status as the world’s largest bivalves and their popularity with SCUBA divers, a greater understanding of giant clams’ contributions will provide managers with ‘ammunition’ to justify their protection. Crucially, both their international and local conservation statuses need to be updated and monitored (Brito et al., 2010; Neo and Todd, 2013) if appropriate management strategies are to be developed. Whatever safeguards can be established will not only boost giant clam populations but, by extension, also benefit coral reefs.

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CHAPTER 3. GIANT CLAMS HOST A MULTITUDE OF EPIBIONTS[2]

3.1. Introduction and Methods

Giant clams (family Cardiidae, subfamily Tridacninae), well known for their large size and colorful mantles, are thought to play various important ecological roles in tropical coral reef ecosystems (e.g., Mingoa-Licuanan and Gomez 2002). These roles, however, have never been quantified. To assess one purported function, i.e., their ability to provide hard substrate on which other organisms can live, we collected and identified the epibionts inhabiting the valves of eight fluted giant clams, *Tridacna squamosa* (23.4 to 40.0 cm shell length, SL), in Singapore. We also measured the shell surface area and the shell 'footprint' of three *T. squamosa* specimens (SL = 25.5, 28.5 and 29.3 cm) using small aluminium foil pieces cut carefully to follow the morphological features of the valves.

3.2. Results and Discussion

We found the *T. squamosa* shells were colonized by a diverse array of epibionts (Fig. 3.1), comprising of at least 49 species belonging to a minimum of 36 families. These included algae (9 families), ascidians (1), bivalves (4), brittlestars (1), crustaceans (8), chitons (1), gastropods (2), polychaetes (3), and sponges (7). Algae were predominant (e.g., *Acanthophora spicifera*, *Chaetomorpha* sp., *Gracilaria salicornia*, *Hydropuntia edulis*, see Fig. 3.1 A), with crustose coralline algae being the most common (see Fig. 3.1 B). However, the soft coral, *Sinularia* sp., was observed to cover an entire valve of one large *T. squamosa* (B). The mean shell surface area of

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the three specimens examined was 2601 cm^2 while the mean footprint was 98 cm^2, hence, one of these mature *T. squamosa* provides approximately 26 times more surface area for colonization compared to the patch of substrate on which it is situated.

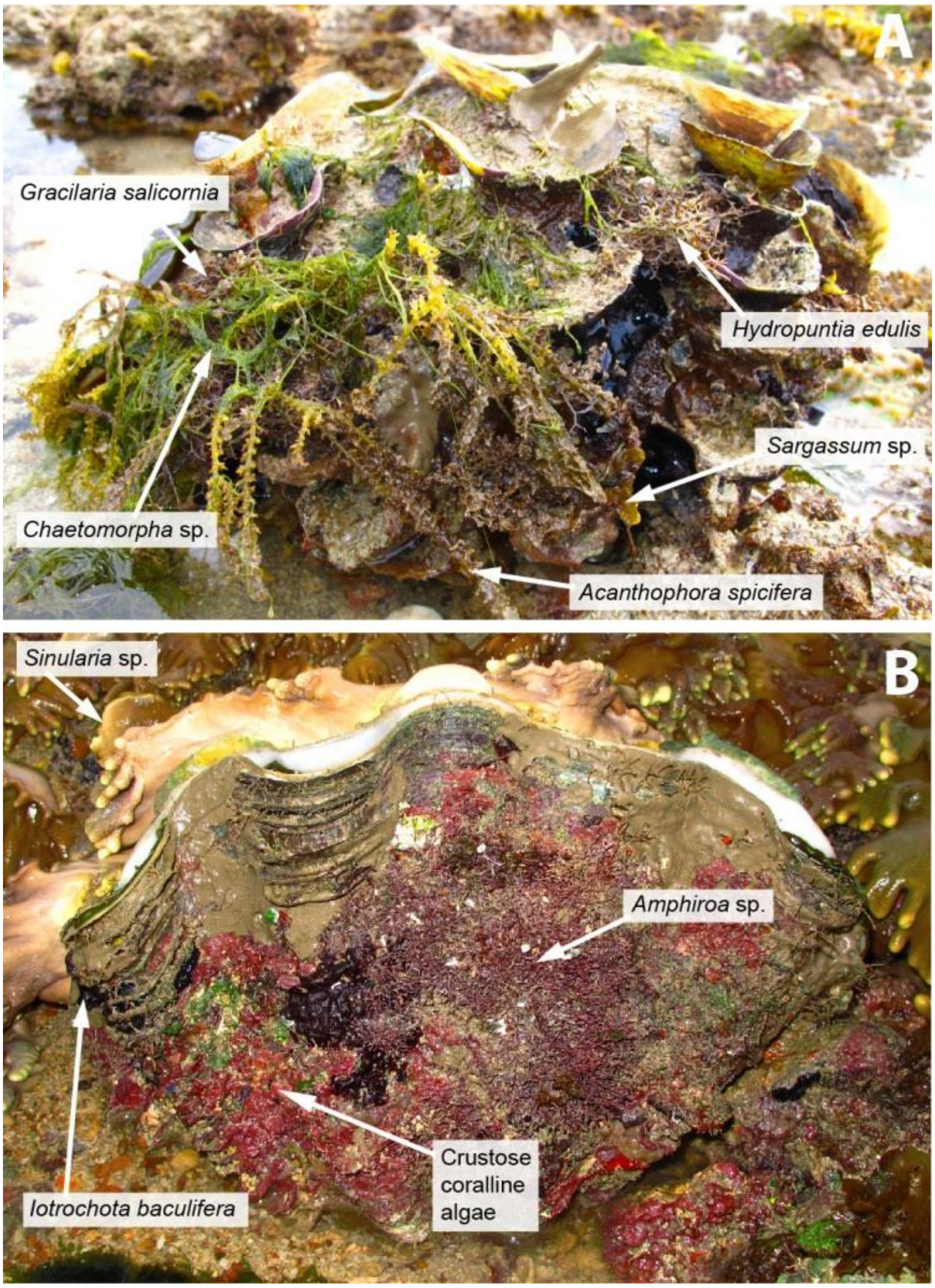

Fig. 3.1. *Tridacna squamosa* in Singapore hosting a wide range of epibionts, e.g. macroalage *Chaetomorpha* (A) and crustose coralline algae (B).

There are presently ten known giant clam species with a combined range that spans from southern Africa to the Red Sea, Japan, Polynesia and Australia (bin Othman et al. 2010). These species vary in their size, shell morphology, and habitat preference (Rosewater 1965). Hence, we predict that the epibionts we found on the valves of the small number of *T. squamosa* individuals examined here represents only a fraction of the taxa that live on giant clams globally. Similarly, the shell surface area to footprint ratio will also vary among species, but we are confident that all giant clams provide more hard substrate than the area they occupy.

Clearly, giant clam shells provide a habitat suitable for a wide range of species. Unfortunately, these iconic marine invertebrates are under tremendous pressure from overfishing (Kinch & Teitelbaum 2010) and coral reef degradation (Neo & Todd 2012). Giant clam restocking efforts can assist in the restoration of coral reefs by providing substantial areas of natural hard substrate suitable for colonization by a diverse fauna and flora. Conversely, harvesting giant clams also results in the reduced abundance of their associated epibionts. Giant clams probably play other important functions on coral reefs, for example as food (Govan 1992) and as contributors of calcium carbonate (Hutchings 1986). Quantifying the ecological roles that giant clams perform is a key step in strengthening the case for their conservation.

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PART II – TOLERANCE TO STRESS IN GIANT CLAM LARVAE

CHAPTER 4. LETHAL LOW LIGHT AND HIGH TEMPERATURE THRESHOLDS FOR LARVAE OF THE FLUTED THE GIANT CLAMS (*TRIDACNA SQUAMOSA*)[3]

Abstract

As the larvae of marine invertebrates may have greater sensitivity to environmental disturbances than the adults, it is important to study all stages of an organisms' life cycle in order to better understand its ability to cope with stressors. This paper examines the responses of *Tridacna squamosa* pediveligers to elevated temperature and reduced light levels. In a light reduction experiment, a total of 104,000 *T. squamosa* pediveligers were exposed to four different levels of shading for approximately one month. The most heavily shaded treatment, at 0.4% of ambient light, had significantly lower survival than the other groups, which all received 1% or more of ambient light. In a second experiment, for approximately two weeks 13,000 *T. squamosa* pediveligers were divided among three treatments: one at ambient temperature averaging 29.5˚ C and two with elevated temperatures averaging 32.2 and 34.8˚ C. The elevated temperature treatments resulted in near total mortality for pediveligers. The highest temperature survived by any pediveliger in the experiment was 32.8˚ C. We recommend that giant clam conservation and restoration programs investigate methods to reduce anthropogenic sedimentation, as associated turbidity may cause giant clam larvae to settle in shallower water, where they will likely be exposed to higher temperatures.

Keywords: Bivalve, climate change, coral reef, stress, Tridacninae

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4.1. Introduction

Giant clams (Cardiidae: Tridacninae) inhabit warm, shallow marine waters in the Pacific and Indian oceans (Yonge, 1975; Knop, 1996; Fatherree, 2006). They are the world's largest bivalves (Yonge, 1975), able to grow to 137 cm long (Lucas, 1994) due to symbiosis with photosynthesizing algae (zooxanthellae) (Yonge, 1975). Even though they are filter feeders, giant clams are unable to survive without the photosynthate contributions of their symbionts (Fitt and Trench, 1981). Many of the waters giant clams inhabit are being affected by increasing sedimentation and/or eutrophication (Fabricius, 2005; Erftemeijer et al., 2012), both of which reduce available light and thus the maximum depth at which they can survive.

To operate effective giant clam conservation programs, especially those that include restocking, it is important to understand the clams' ability to cope with environmental stress. Knowing their tolerances will facilitate the improvement of mariculture protocols, identification of appropriate locations for restocking, and designation of marine protected areas (MPAs). The larval life stages are likely to be especially vulnerable to stressors. When compared to adults, larvae of aquatic invertebrates have been shown to have lower resistance to toxins (Eissa et al., 2011) and pathogens (Gomez-Leon et al., 2008), so it is reasonable to expect their tolerances for other environmental stressors to also be lower. In a location undergoing environmental change, such as increasing temperature, sedimentation, or eutrophication, a healthy adult population may be observed, but if larvae cannot survive, the species will ultimately be extirpated.

Under experimental conditions, fertilized giant clam eggs develop into a non-feeding motile planktonic trochophore stage within 11 to 20 hours, and by the age of 20 to

48 hours they develop into a feeding motile planktonic veliger stage which is capable of ingesting zooxanthellae (Jameson, 1976; Alcazar et al., 1987; Mies et al., 2012). Settlement is not a one-time event; at ages ranging from 4 days to 29 days the veligers develop into pediveligers which alternate between crawling on the substrate and swimming, gradually losing the ability to swim as their shells increase in weight and their swimming structures degenerate (Jameson, 1976; Alcazar et al., 1987; Mies et al., 2012). There is no standard definition of a juvenile giant clam (Fitt and Trench, 1981; Fitt et al., 1984; Alcazar et al., 1987; Hirose et al., 2006), but the final major ontogentic change in morphology is the shell becoming opaque, which Jameson (1976) found to occur from age 47 to 91 days in *T. crocea* and *T. maxima*. Even as juveniles and adults, giant clams maintain some locomotory capabilities (Crawford et al., 1986; Huang et al., 2007) and therefore may be able to move towards more favorable light conditions.

Giant clams differ from corals in that they do not pass zooxanthellae on to their eggs (LaBarbera, 1975; Mies et al., 2012) and that they do not host zooxanthellae intracellularly (Norton et al., 1992; Hirose et al., 2006). Veligers ingest planktonic zooxanthellae, some of which are digested (Fitt and Trench, 1981; Hirose et al., 2006) while others survive long enough to eventually move into their clam's zooxanthellal tube system (Norton et al., 1992; Hirose et al., 2006). Although there have been varying reports as to the relative importance of filter feeding to adult giant clams (Fitt and Trench, 1981; Klumpp et al., 1992; Klumpp and Griffith, 1994; Klumpp and Lucas, 1994; Hawkins and Klumpp, 1995; Griffiths and Klumpp, 1996), there have been no claims that they can survive long term without zooxanthellae.

To our knowledge, the shade tolerances of giant clams—or any other zooxanthellate organisms—have not been studied during their larval stages. Juvenile and adult *T. derasa* (Klumpp and Lucas, 1994)*, T. tevoroa* (Klumpp and Lucas, 1994)*,* and *T. squamosa* (Guest et al., 2008; Jantzen et al., 2008; Adams et al., 2013) have been subjected to controlled shading experiments, as have adult *T. maxima* (Jantzen et al., 2008). The effects of shade on adult *T. gigas* were also studied in an *in situ* experiment (Elfwing et al., 2003), although there were confounding factors such as physical contact with the sediments that were reducing light penetration. Many of these experiments documented reduced growth with decreased light levels, but no significant mortality occurred. Lucas et al. (1989) found mortality in juvenile *T. gigas* placed under "90% synthetic shade cloth", but the total light reduction (due to shading by the tank system and attenuation by the water) was not reported.

Investigations into the effect of elevated temperature on marine bivalves have primarily focused on polar species (Portner et al., 1999; Abele et al., 2001; Peck et al., 2004; Richard et al., 2012) or temperate species that are commercially important (Joyner-Matos et al., 2009; Marshall et al., 2012; Dowd and Somero, 2013; Matoo et al., 2013). Research in this area has focused on adult organisms, with only a few studies on larvae and/or juveniles (Brenko and Calabrese, 1969; Calabrese, 1969; His et al., 1989; Talmage and Gobler, 2011). The effects of elevated temperature on most tropical marine bivalves is not well understood, but pearl oysters have been studied at the egg (Wang et al., 2012), larval (Doroudi et al., 1999; de Albuquerque et al., 2012), juvenile (Mills, 2000), and adult (Saucedo et al., 2004; Mondal, 2006) stages. Research into *T. squamosa* thermal tolerances has been carried out at the egg and first larval (trocophore) stage (Neo et al., 2013), the juvenile stage (Watson et al., 2012), and the adult stage (Elfwing et al., 2001), but not at the veliger or pediveliger stages. Bivalve research has generally focused on finding optimal values of environmental parameters for aquaculture, rather than finding limits beyond which the organisms are unlikely to survive. Similarly, giant clam hatchery manuals provide optimal temperature ranges for larval culture, but do not specify lethal limits (Braley, 1992; Ellis, 1998).

In a light reduction experiment, we exposed pediveligers of the fluted giant clam, *T. squamosa*, to four different shading levels for approximately one month. *Tridacna squamosa* is considered a moderately shade-tolerant species (Fatherree, 2006), but we hypothesized that very low light levels would lead to reduced larval survival. In a temperature increase experiment, we exposed *T. squamosa* pediveligers to three different temperature levels for approximately two weeks. We hypothesized that increased temperature would lead to reduced larval survival. Our ultimate intent with these experiments was to locate the boundaries of reduced light and increased temperature beyond which larval *T. squamosa* are unlikely to survive.

4.2. Materials and methods

The experiments were conducted between March and October of 2012 at the Tropical Marine Science Institute, National University of Singapore, located on St John's island (103.85°E, 1.22°N), off the southern coast of Singapore Island. The aquaria used were supplied with sand-filtered flow-through water pumped in from the sea nearby. A single layer of shade netting was suspended over the entire outdoor aquaria area, including all of the tanks used in our studies.

4.2.1. Light reduction experiment

Thirty six rectangular plastic aquarium tanks were used. The water volume of each tank was 27 L after a drain hole was cut into one side and the substrate materials displaced water. The tanks were placed on nine metal racks arranged in triangles. In order to prevent an influx of freshwater during rainstorms, a white colored PEVA sheeting was secured to create a 'tent' above each rack. A custom made 37 × 23 × 1 cm^3 cement tile, held 5.5 cm off the tank bottom by PVC legs, was inserted into each tank as a substrate for the pediveligers.

Two 100 L elevated reservoirs gravity fed each of the 36 tanks with 5.65 $cm^3 s^{-1}$ of sand-filtered seawater via aquarium tubing. HOBO Pendant® light and temperature loggers were placed in 24 of the tanks, evenly distributed among the treatments. Two loggers of the same model were placed on the roof of a nearby building, outside the shade netted area, to record ambient light levels for comparison.

Adult *T. squamosa* were induced to spawn following Mingoa-Licuanan and Gomez (2007) and the larvae were raised to the pediveliger stage. At the age of 13 days, ~ 2,900 pediveligers were placed into each tank resulting in a density of 3.4 pediveligers cm^{-2} of substrate. The next morning, either one, two, or three layers of garden shade netting were installed across the tops and two longer sides of the 27 non-control tanks. The two shorter sides of all tanks, including the controls, had previously been painted black. Due to the triangular arrangement of the racks, there were three different tank orientations. An equal number of tanks of each treatment type were assigned to each orientation, but within this constraint, individual tanks were assigned randomly to racks. Within-rack placements were also allocated randomly.

The pediveligers were allowed to grow undisturbed in the tanks for 28 to 37 days before sampling. Due to time constraints, it was only possible to sample 4 or 8 tanks each day, so an equal number were randomly selected from each of the three treatment groups and control on each sampling date. Four randomly placed 19.6 cm^2 circular areas (using a 9 cm section Ø 5 cm PVC pipe) of each tile were sampled, equal to 9.2% of the tile's surface area. The sampling locations were siphoned, and the pediveligers collected in a sieve made with 80 µ mesh. The collected pediveligers were then immediately counted using a dissecting microscope. They were considered alive if they exhibited some form of activity within one minute of observation, such as moving their foot, closing their valves, or maintaining an extended excurrent siphon.

4.2.2. Temperature increase experiment

The experiment used the same arrangement as in the light reduction experiment, but with 12 tanks and 1,100 larvae placed into each. This density of 1.3 pediveligers cm^{-2} of substrate was lower than in the previous study due to fewer larvae being available at the time of the experiment. No shade netting was used, and the ends of the tanks were not painted black. An aquarium heater (EHEIM aquatics, model number 3616) was placed underneath the raised cement tile in each tank. In the control group, the aquarium heaters were given a low setting and therefore did not produce heat during the experiment. The heaters in the two treatment groups were given moderate or high settings, and therefore increased the water temperatures in their tanks. Every tank contained a HOBO Pendant® light and temperature logger.

The pediveligers were placed into the tanks at the age of 8 days, and were allowed to grow undisturbed for 13 to 17 days before sampling. Five randomly placed 19.6 cm^2 circular areas of each tile were sampled, equal to 11.5% of the tile's surface area. The sampling locations were siphoned and the pediveligers collected and counted following the same procedure described in the previous study.

4.2.3. Data analysis

The data for both experiments were analyzed using version 2.15.3 of R. For experiments which have bounded results (in this case, the number of larvae cannot go below zero or above their initial number) and random effects (in this case, the multiple larval tanks for each treatment), generalized linear mixed models are the most appropriate statistical technique (Bolker et al., 2009). The glmmPQL() function was used, with a quasibinomial link function due to overdispersion, to determine whether there was any significant difference between treatment means. General linear hypothesis testing was then performed with the glht() function, to compare each treatment group to all of the others and identify the pairs with significant differences.

4.3. Results

4.3.1. Light reduction experiment

The four shading levels of this experiment resulted in an average of 7.12%, 2.23%, 1.04%, and 0.40% of ambient light reaching the interior of the tanks (Table 4.1). The generalized linear mixed model and post-hoc Tukey tests determined that, at the end of the experiment, the ‘three shade net’ group had very highly significantly lower survival (0.5%) than the ‘two shade net’ group (survival = 8.8%), the ‘one shade net’ group (survival =11.9%), and highly significantly lower survival than the control group (survival =5.9%). There were no other statistically significant differences between means (Fig. 4.1, Table 4.2).

Table 4.1 Light reduction experiment: percent ambient light, mean temperature and mean survival at the end of the experiment. Note; the levels of shade netting listed here are in addition to the nets that covered the entire facility.

Shade netting	Ambient light	Mean temp. (˚C) ± S.E.	Mean survival rate (%) ± S.E.
Zero nets	7.12%	29.1 ± 0.08	5.95 ± 1.45
One net	2.23%	29.2 ± 0.03	11.94 ± 2.47
Two nets	1.04%	29.2 ± 0.05	8.78 ± 1.35
Three nets	0.40%	29.2 ± 0.04	0.54 ± 0.22

Table 4.2 Light reduction experiment: linear mixed-effects model fit by maximum likelihood.

Level of shading	Value	S.E.	df	t-value	p-value
One net	0.866	0.472	32	1.834	0.076
Two nets	0.471	0.481	32	0.979	0.335
Three nets	-2.192	0.725	32	-3.022	0.005
Intercept	-3.054	0.350	108	-8.714	<0.001

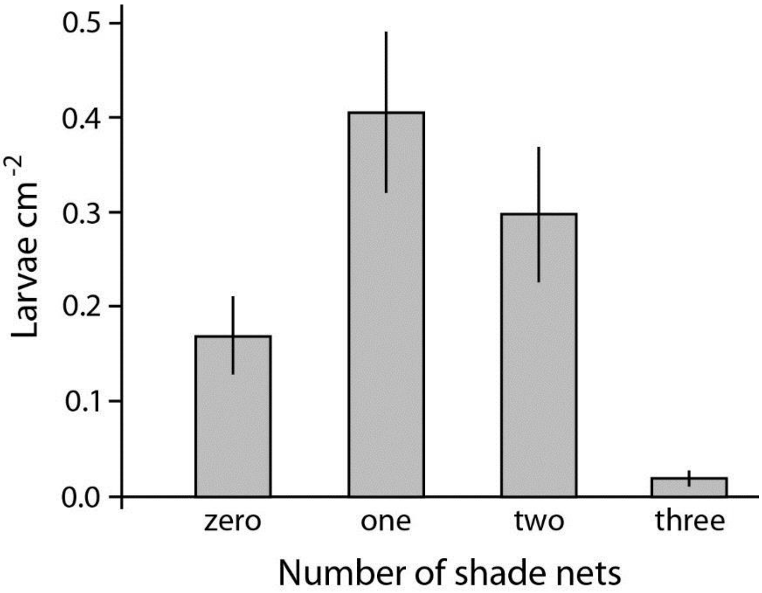

Fig. 4.1. Light reduction experiment: surviving larvae cm^{-2}

4.3.2. Temperature increase experiment

The temperature differences were sucessfully maintained at 2.6 – 2.7 ˚C between treatments (Table 4.3). Based on the continuously logged data, the highest peak temperature survived by any pediveliger in the experiment was 32.8° C (in a moderate treatment tank). The lowest temperature experienced in any tank was 26.5° C, but this did not result in mortality beyond background levels. The generalized linear mixed model and post-hoc Tukey tests determined that the control group had significantly higher survival (10.3%) than the medium (survival = 0.4%) and high (survival = 0.0%) temperature groups (Fig. 4.2, Table 4.4). There was no significant difference in survival between the medium and high groups.

Table 4.3 Temperature increase experiment: mean temperatures and survival rates at the end of the experiment.

Temperature level	Mean temp. (˚C) ± S.E.	Mean survival rate (%) ± S.E.
Control	29.5 ± 0.02	10.26 ± 2.66
Moderate	32.2 ± 0.35	0.39 ± 0.39
High	34.8 ± 0.11	0.00 ± 0.00

Table 4.4 Temperature increase experiment: linear mixed-effects model fit by maximum likelihood.

Temperature level	Value	S.E.	df	t-value	p-value
Moderate	-3.192	1.066	9	-2.993	0.015
High	-3.839	1.347	9	-2.849	0.019
Intercept	-2.395	0.480	48	-4.995	<0.001

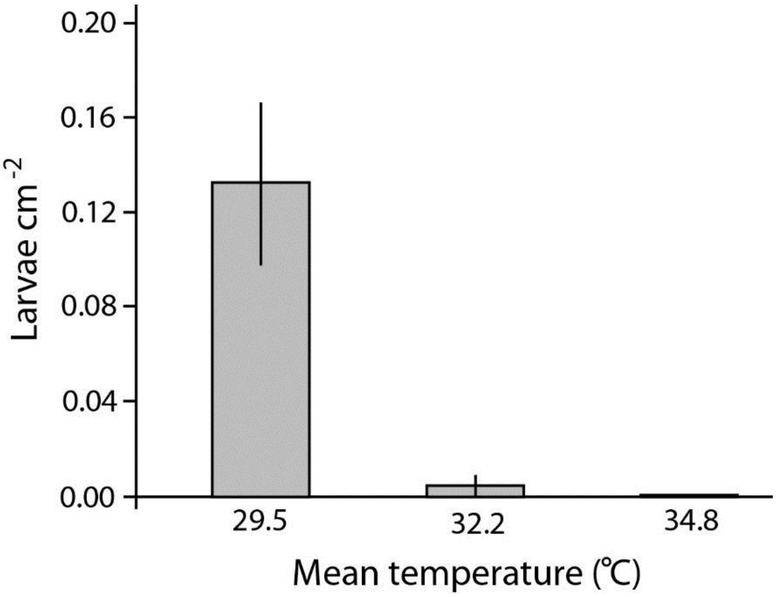

Fig. 4.2. Temperature increase experiment: surviving larvae cm^{-2}

4.4. Discussion

Populations of organisms with larval stages, such as bivalves, depend on larval survival in order to persist. Very few studies, however, investigate the environmental tolerances of marine bivalve larvae, and this is the first paper to do so for giant clam pediveligers. Temperature and turbidity are two environmental factors which potentially limit where giant clam larvae are able to settle and survive. Determining the lethal low light and high temperature thresholds for the *T. squamosa* larvae can help conservation managers understand ongoing population declines in this species as well as assist in restocking efforts. Our results indicate that the upper thermal limit for survival of *T. squamosa* pediveligers is 32.8˚C. Furthermore, *T. squamosa* pediveligers need more than 0.4%, and possibly as much as 1%, of surface light levels in order to survive in significant numbers.

In the light reduction experiment, the least shaded tanks did not experience the lowest mortality, but this is probably not indicitave of mortality caused directly by sunlight as adult giant clams can live in the intertidal zone (Lucas et al., 1989), and are even capable of photosynthetic activity during emersion (Mingoa-Licuanan and Lucas, 1995). However, light-enhanced algal overgrowth can be a major cause of mortality for larval and juvenile giant clams in grazer-free environments such as aquaculture facilities (Crawford ,1986), and we did observe growth of a brown mat algae on the control and single shade net tiles. It is likely that a moderate amount of shade benefited the clams by reducing this algal growth. It is also possible that the larvae in the shaded tanks benefitted from reduced peak water temperatures.

It has been stated that the symbiotic relationship between giant clams and their zooxanthellae does not begin during the clams' larval stages (Fitt and Trench, 1981; Fitt et al., 1984; Hirose et al., 2006) even though they acquire zooxanthellae as larvae—first within their stomachs and then within their zooxanthellal tube system. Fitt and Trench (1981), however, reported higher growth and survival rates of larvae with zooxanthellae and Fitt et al. (1984) recognized the possibility that larvae may absorb photosynthates released by zooxanthellae in their stomachs. Anecdotal evidence of early symbiosis is provided by hatchery manuals, which recommend inoculation of veligers with zooxanthellae on day 3 (Braley, 1992) or day 4 (Ellis, 1998). Mies et al. (2012) provide the best evidence to date for early symbiosis by demonstrating higher growth and survival rates for *T. crocea* larvae with zooxanthellae. The differential survival rates of the treatment groups in the shading experiment here provide additional support for early symbiosis.

The temperature increase experiment confirmed that larval *T. squamosa* have lower thermal tolerances than juveniles. Watson et al. (2012) found that 57% of juveniles survived 60 days at 31.5˚ C, while none of the pediveligers in our two experiments survived a sustained temperature above 31.4˚ C. Analyzing the combined water temperature and survival data from the two experiments, we postulate that the temperature-induced mortalities were due to high-temperature peaks, rather than elevated temperatures over time. There were several tanks which had no surviving larvae, where the maximum temperature spiked above known (from tanks in the same experiment) survivable values, but whose mean temperature was below that of tanks with surviving larvae. The highest peak temperature survived by any of the pediveligers was 32.8˚ C. In large areas of *T. squamosa*'s range (Fatherree, 2006), sea surface temperatures are already approaching 32˚ C (NOAA 2013). Moreover, those areas are maintaining high temperatures throughout the year (University of Wisconsin 2013), meaning there may no longer be a lower-temperature breeding season when giant clam larvae could survive.

Surveys of *T. squamosa* consistently fail to locate juveniles (Hardy and Hardy, 1969; Dolgov, 1992; Roa-Quiaoit, 2005; Guest, 2008). While it is possible that the density of breeding adults has fallen below a reproductive threshold, another possibility is that environmental conditions have changed to the point that larvae are unable to survive. Populations of giant clams may not be able to adapt to changing environmental conditions as quickly as other marine invertebrates, due to the clams' long life cycles. Even the fastest-developing giant clams require at least two years to reach male maturity (Lucas, 1988), while *T. gigas* may take four to five years (Braley, 1998). Reaching female maturity can take five years for *T. derasa* (Adams et al., 1988), and nine or ten years for *T. gigas* (Braley, 1998). In addition, many giant clam populations have a limited genetic base to work from. Surveys of *T. squamosa* have found densities of one clam per 37 m^2 in Vietnam (Dolgov, 1992), 157 m^2 in Palau

(Hardy and Hardy, 1969), 322 m^2 in Jordan (Roa-Quiaoit, 2005), and 650 m^2 in Singapore (Guest, 2008).

Pediveligers should be able to settle and survive in locations where the combination of depth and turbidity results in at least 1% of ambient light reaching the substrate. Increasing turbidity will potentially force newly-recruited clams to establish in shallower waters to meet their light requirements, where they may be exposed to higher water temperatures (as well as being more vulnerable to poaching and storm damage). Hence, the thermal vulnerability of pediveligers places further importance on turbidity reduction for giant clam conservation or restoration programs. If giant clam pediveligers can settle in deeper water and still receive adequate sunlight, they will be exposed to less severe midday temperature peaks and have a greater chance of survival. It is likely, however, that in the rapidly changing sea-surface temperature environments that are characteristic of the contemporary Indo-Pacific, giant clam larvae will more frequently be exposed to lethal temperatures.

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CHAPTER 5. OBSERVATIONS ON THE HYPOSALINITY TOLERANCE OF FLUTED GIANT CLAM (TRIDACNA SQUAMOSA, LAMARCK 1819) LARVAE

Abstract

In conservation management, it is important to understand environmental tolerances at every stage of a species' life cycle. As salinity is considered one of the most significant ecological stressors for marine bivalves, this *ex-situ* study observed several larval stages of the fluted giant clam (*Tridacna squamosa* Lamark, 1819) exposed to hyposaline water. Late stage pediveligers/early stage juveniles survived in distilled fresh water for 10 min to 5 h, and showed no sign of injury during a 48 h follow-up period. Trochophores were able to survive for 10 min to 3 h in 9 ppt salinity water, and veligers were able to survive for 1 h to 42 h in 12 ppt salinity water. Results suggest that giant clam larvae in Singapore's waters are able to survive exposure to hyposaline water such as that associated with high rainfall or river outflows.

Keywords: **M**arine bivalve larvae, pediveliger, salinity, Singapore, *Tridacna squamosa,* trochophore, veliger

5.1. Introduction

Giant clams are now extremely rare in Singapore (Guest et al. 2008; Neo & Todd 2012). They face threats from harvesting, land reclamation, industrial pollutants, and anthropogenic turbidity, but conservation efforts, including a restocking programme, are underway (Neo et al. 2012). In order to determine appropriate locations for protecting and/or restocking giant clams, and to further understand their ecology, it is important to understand their environmental tolerances at every stage of their life cycle.

Salinity is considered one of the most consequential environmental stressors for marine bivalves (Tettelbach & Rhodes 1981; Miller et al. 2007; de Albuquerque et al. 2012). When experiencing water with elevated temperatures and low salinity, many bivalve species have the ability to settle in, or migrate to, deeper water which is cooler and more saline. This is not an option for giant clams in turbid waters such as those around Singapore, as their algal symbionts require light for photosynthesis. Marine larvae in Singapore's waters are likely to encounter hyposaline water, either in tidepools or other shallow water during periods of heavy rain, or in the vicinity of river or reservoir outflows. Fresh water may also be used in giant clam mariculture facilities as a method of killing parasites or to remove algal mats.

There has been very little research into the salinity tolerances of giant clams at the larval or other life stages. Neo et al. (2013) exposed *Tridacna squamosa* larvae to water with reduced salinity, but only as low as 27 ppt, while Blidberg (2004) exposed *Tridacna gigas* larvae to salinities as low as 20 ppt. Although the older life stages are easier to study experimentally, we are aware of only one hyposalinity study on *Tridacna gigas* juveniles (Rachman & Anshary 1997), and one on *Tridacna squamosa* adults (Blidberg 1998).

There have been attempts to infer the salinity tolerances of bivalve larvae empirically by recording environmental variables at locations where larvae are present or absent (Thompson et al. 2012; Soria et al. 2013; Borges et al. 2014), but this approach carries the risk of unidentified confounding factors, and is unlikely to be successful with giant clams, the timing of whose reproductive cycle is not fully understood. Studies on gill tissues have been used to determine a theoretical maximum salinity tolerance for some species (Yaroslavtseva et al. 1990; Yaroslavtseva & Sergeeva 2009), but there is no guarantee that larvae can survive up to this theoretical point. There are also reports of within-species differences in tolerance based on genetic variation (Innes & Haley 1977; Newkirk 1978; Deng et al. 2009; Eierman & Hare 2013), and evidence that the timing of salinity changes can impact mortality (Davenport et al. 1975).

Much of the marine bivalve research into larval hyposalinity tolerance has little applicability to *Tridacna squamosa*'s ability to survive such conditions. Rather than directly record mortality, many marine bivalve studies instead investigate fertilization success (Wang et al. 2012), trochophore motility (Suquet et al. 2013), larval growth rate (Thiyagarajan & Ko 2012), vertical migration (Hidu & Haskin 1978; Mann et al. 1991; Dekshenieks et al. 1996; Ishida et al. 2005), or settlement (Devakie & Ali 2000; Tezuka et al. 2013). Studies that do examine salinity-induced mortality are often conducted on brackish-water species (Cain 1973; Verween et al. 2007) or species which are euryhaline. Euryhaline oysters in the genus *Crassostrea* are the most frequently studied marine bivalves in larval salinity tolerance research (Lemos et al. 1994; Tan & Wong 1996; Xu et al. 2011), although larvae of many other euryhaline species are also used, including pearl oysters (*Pinctada)* (Doroudi et al. 1999; O'Connor & Lawler 2004), other oysters (*Crassostrea*, *Ostrea* and *Placuna*) (Davis 1958; Davis & Ansell 1962; Madrones-Ladja 2002), mussels (*Mytilus*) (Brenko & Calabrese 1969; Qiu et al. 2002; Yaroslavtseva & Sergeeva 2009; Vekhova et al. 2012), shipworms (*Teredo*) (Hoagland 1986) and sediment-dwelling clams (*Cyrtopleura*, *Donax*, *Mercenaria*, *Mulinia*, *Mya*,and *Ruditapes*) (Davis 1958; Stickney

1964; Calabrese 1969; Gustafson et al. 1991; Numaguchi 1998; Carstensen et al. 2010). Low salinity responses of the larvae of more stenohaline marine bivalve species such as scallops (*Argopecten, Mimachlamys,* and *Pecten*) (Tettelbach & Rhodes 1981; O'Connor & Heasman 1998; Christophersen & Strand 2003) may be more comparable to those of giant clams, which are fully marine. There are also studies into the effects of hypersaline water on marine bivalve larvae (Iso et al. 1994; Arellano & Young 2011; Voorhees et al. 2013), but hypersaline conditions only occur in Singapore in the immediate vicinity of desalination plant effluent, or in tidal pools during the dry season. Some previous experiments have produced limited results as only a narrow range of salinities was tested (Nell & Holliday 1988; Robert et al. 1988; His et al. 1989), whereas others have used a broad range of salinities and established lethal limits for their target species (Davis 1958; Davis & Ansell 1962; Calabrese 1969).

We conducted several *ex-situ* observational studies, exposing *Tridacna squamosa* larvae to extremely low salinities to observe changes in behavior and determine whether survival was possible under these conditions. If exposure to low salinities (such as those associated with high rainfall or river outflows) were to cause mortality during the larval dispersal phase it would have implications for the conservation management of *Tridacna squamosa*. Such information is also useful to determine whether it is safe to use fresh water as a parasite/algal control method in giant clam aquaculture.

5.2. Materials and methods

All three observational studies used larvae of *Tridacna squamosa* which were spawned and reared at the Tropical Marine Science Institute, on St. John's Island, Singapore.

Study 1. In November of 2012, six late stage *T. squamosa* pediveligers/early stage juveniles of shell length from 2.3 to 3.0 mm were placed in zero-salinity distilled water for time periods ranging from ten minutes to five hours. The studies were carried out indoors in an air-conditioned room. Each clam was removed from the flow-through seawater aquaculture system, and placed directly into a well plate (one clam per well) which contained approximately 15 ml of distilled water. Each clam was left for a different time period (10 min, 20 min, 30 min, 1 h, 2 h, and 5 h) after which it was placed in a petri dish of seawater for immediate observation under a dissecting microscope and then moved outdoors to its own 1 L glass container which received flow-through seawater. The clams were then monitored for 48 h for any mortality; behavior was also observed.

Study 2. In May of 2014, 4 ml samples of seawater (salinity 32 ppt) containing *Tridacna squamosa* trochophores were added to five wells in a well plate containing 10 ml of distilled water, and one well containing seawater as a control. The salinity of the non-control wells (10 ml distilled water + 4 ml seawater) was verified to be 9 ppt using a hand-held refractometer. The study was carried out in a large outdoor shed which provided some shade, but was not air-conditioned. After varying periods of time (10 min, 30 min, 1 h, 2 h, and 3 h), the water was removed from the well plate and placed into a petri dish full of seawater. The petri dish was then observed under a dissecting microscope for actively swimming trochophores.

Study 3. Also in May of 2014, 6 ml samples of seawater (salinity 32 ppt) containing *T. squamosa* veligers were added to ten wells each containing 10 ml of distilled water, and two wells containing seawater as controls. The salinity of the non-control wells (10 ml distilled water + 6 ml seawater) was verified to be 12 ppt using a hand-held refractometer. The studies were carried out in the same shed as the trochophore experiment. After varying periods of time (1 h, 2.5 h, 4 h, 6 h, two at 18 h, two at 24 h, and two at 42 h), the water was removed from the well plate and placed into a petri dish full of seawater. The petri dish was then observed under a dissecting microscope for actively swimming veligers, and observed a second time one hour later to determine if swimming patterns had changed.

5.3. Results and Discussion

Upon being placed in distilled water (Study 1), the six late stage pediveligers/early stage juveniles withdrew their mantle tissue and siphons and closed their valves tightly. This is a short-term survival strategy, as if employed for extended time periods, it will induce hypoxia (Kim et al. 2001). When returned to seawater, the clams opened their valves and extended their mantle and siphon tissues within 30 minutes. The clams which had been kept in distilled water longer appeared to take longer to return to their normal state, however, this was possibly an effect of longer exposure to low water temperatures (due to the room’s air conditioning). All of the clams survived during the 48 h follow-up observation period, and were able to climb up the sides of their glass containers to the air-water interface (a common behavior among *Tridacna squamosa* of this size when kept in smooth-surfaced containers).

Upon being placed in water of 9 ppt salinity (Study 2), all trochophores ceased swimming and sank to the bottom of the well plates. This sinking behavior may benefit the organisms in the wild: when larvae near the ocean's surface are exposed to hyposaline water during rainstorms, they may sink into deeper, more saline water where it is safe to resume their normal activities. When the trochophores in this experiment were placed back into seawater, some in each group resumed swimming, although those in the 2 h and 3 h groups swam with a weak tumbling motion, rather than the distinctive vigorous circling pattern of healthy trochophores. The subsequent veliger experiment raises the possibility that this weaker swimming pattern may have been temporary.

Upon being placed in water of 12 ppt salinity (Study 3), the veligers also ceased all swimming activity and sank to the bottom of the well plates. When placed back into seawater, some veligers in each group resumed swimming, although they appeared to be pivoting around a point rather than swimming in large circles (their usual behavior). However, after remaining in seawater for one hour, the veligers had resumed their normal swimming activity. Shortly before the 42 h observation, veligers were seen actively swimming in one of the hyposaline (12 ppt) wells. As they were not under continuous observation, it is possible that they periodically engaged in short periods of swimming in order to obtain oxygen. It is also possible that evaporation from the well raised the salinity above a threshold where the veligers could conduct normal activities safely.

As *Tridacna spp.* have a short pelagic larval cycle, the long-term exposure of trochophores and veligers to hyposalinity cannot be studied. However, settlement rates of *Tridacna* larvae under hyposaline conditions could be measured, as has been done for other species (Devakie & Ali 2000; Tezuka et al. 2013). Pediveligers and juveniles could be exposed to sublethal hyposalinity for longer time periods, which in other marine bivalves affects immune response (Gagnaire et al. 2006; Matozzo et al. 2007) and growth rate (Nell & Holliday 1988; Navarro & Gonzalez 1998). Chronic hyposalinity may even lead to a 'dwarf' bivalve population (Westerbom et al. 2002; Riisgard et al. 2013). A longer growth period or smaller ultimate size will impact survival, as smaller bivalves are less likely to survive adverse environmental conditions (Nell & Paterson 1997), and may not reach an 'escape size' from some forms of predation. Bivalves living in hyposaline water may also be more vulnerable due to weaker shells, adductor muscles, and/or byssal threads (Wang et al. 2012).

Giant clams in Singapore which are exposed to hyposaline water are likely to be simulataneously exposed to additional stressors, particularly elevated water temperatures and turbidity-induced shading. Being exposed to these additional stressors is likely to reduce the clams' tolerance for hyposalinity (Chanley 1958; Castagna & Chanley, 1973; La Peyre et al. 2013), therefore multi-stressor studies will be necessary to determine *Tridacna squamosa*'s tolerance to the hyposaline waters under natural conditions.

5.4. References

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CHAPTER 6. CONCLUSIONS AND RESEARCH LIMITATIONS

6.1. Conclusions and research limitations

Chapter 2 of this thesis represents the first attempt to catalogue and, where possible, quantify the ecological roles of giant clams in coral reef ecosystems. Many of these roles have been mentioned anecdotally, but there are no previous efforts to produce a comprehensive list. This chapter has been accepted (with revisions) for publication in the journal Biological Conservation. As the biomass of giant clams will eventually become food for predators and scavengers, I estimated both the standing stock and annual production for several giant clam populations of several species. Giant clam shell material serves as substrate in a space-limited ecosystem, and some percentage of it will also eventually be incorporated into the calcium carbonate structure of its coral reef. Therefore, I estimated both standing stock and annual production of shell material. Eutrophication is an increasing problem for coral reefs in coastal waters (Fabricius, 2005), and giant clams filter algae and other matter from the water column. I estimated the volume of water cleared of particulate matter by several populations of giant clams, including two different species. This type of quantitative analysis of giant clam data has never been performed before, and it may serve as an important resource for those who promote giant clam restocking efforts or those who advocate protecting giant clams from fishing activity.

Chapter 3 represents another attempt to assess an ecological role of giant clams: their provision of hard substrate for colonization by epibiota. Although the presence of epibionts is obvious to any observer of giant clams in the wild, no one has previously attempted to identify the taxonomic groups those organisms fall into, or to calculate the surface area of inhabitable substrate giant clams shells provide.

Chapters 4 and 5 investigate the environmental tolerances of *Tridacna squamosa* larvae. It is important to understand larval tolerances, as larvae are less likely to survive stress than adult organisms. If environmental conditions change to the point that larvae cannot survive, an apparently healthy population of adult giant clams will eventually face extirpation. There are instances of adult giant clam populations where size classes are largely absent due to multiple years of recruitment failure (Pearson and Munro 1991) and most, if not all, field surveys are unable to locate juvenile giant clams. Further investigation will be necessary to determine whether these findings are the result of giant clams failing to reproduce, or the failure of the resulting larvae to survive.

Despite the importance of understanding larval survival and behaviour, most giant clam research focuses on juveniles or adults rather than larvae. The most likely reason is that numerous obstacles must be overcome when attempting larval research. The first difficulty is the acquisition of larvae to use in experiments. While there has been one instance of successful collection of post-settlement larvae in the wild (Remoissenet et al. 2009), this was in an unusual environment where a dense population of *T. maxima* was located within an enclosed atoll. In most other locations, the timing of giant clam reproduction is unknown, and any wild harvesting would likely also collect numerous larvae of other bivalve species (which are difficult to distinguish from giant clam larvae). The alternative to collecting larvae in the wild is to maintain a breeding population of mature adults, artificially induce them to spawn, and raise the larvae as well as the algal species needed to feed the larvae.

Larvae in their pelagic or semi-pelagic stages cannot be housed in a flow-through system. They would be washed away unless a filter were placed over the tank's outflow, and if a filter were in place, water pressure would crush the larvae against it. Without flow-through, frequent (labor-intensive) water changes are necessary.

Once larvae have been spawned and reared to the age appropriate for an experiment, there are additional difficulties in conducting research. There is no visual feedback as to how an experiment is progressing unless samples are taken and examined under the microscope, and sampling an experiment before its conclusion is likely to interfere with it. Pelagic larvae do appear as small white specks in the water, but it is impossible to determine their metamorphic state or even whether they are alive or dead.

A different set of difficulties occur after sampling. Pelagic larvae move rapidly, and even benthic pediveligers may crawl actively, making accurate counts difficult. Samples could be fixed, but it would be impossible to determine which larvae were alive at the time the fixing solution was added, and which had died previously. While some pediveligers appear to crawl continuously, others may show no signs of movement for 30 seconds or more, meaning that many empty valve sets must be viewed for at least a minute before they can be discounted. Researchers may be tempted to count live versus dead pediveligers by the density and colour of algae within the valves (using this method, clear valves and valves with dark concentrations of algae would be counted as dead, while medium concentrations of typically brownish zooxanthellae colour would be counted as alive), but numerous times during these experiments, pediveligers with no visually apparent zooxanthellae extended a foot or a siphon, and other pediveligers with what appeared to be healthy zooxanthellae populations were verified as being dead when a ciliate swam between the valves. Even locating the pediveligers within a sample can be difficult, as they may cling to pieces of mat algae, or be mistaken for sand grains which abrade from the substrate tiles.

The larval research in chapters 4 and 5 investigate larval tolerances of *T. squamosa* to elevated temperatures, reduced light levels, and lowered salinity. Temperature and salinity are generally recognized as the two most lethal stressors for marine bivalve larvae (Tettelbach and Rhodes 1981), and lack of light can be a severe problem for giant clams, which unlike most marine bivalves, rely on the photosynthetic activities of their zooxanthellae. Chapter 4 establishes lethal thresholds of high temperature and low light for *T. squamosa* larvae, and is the first research to do so for any giant clam species. It has been submitted for publication to the Journal of Experimental Marine Biology and Ecology. Chapter 5 provides a baseline for future research into the salinity tolerances of giant clam larvae, indicating potential starting points for salinity levels and durations. It has been accepted for publication in the journal Nature in Singapore.

In appendix A, I describe an additional research project which did not produce enough data to be publishable, presenting a brief description and anecdotal results. In appendix B, I display photographs of several additional experiments which had to be terminated prematurely. The experiments in the appendices were not completed due to mass die-offs in cohorts of larval or juvenile *T. squamosa*. The difficulty of raising giant clams to adulthood may indicate that restoration/restocking efforts should be subordinate to other forms of giant clam conservation, such as protection of mature giant clams in the wild and preserving habitat suitable for settlement by giant clam larvae. The limited success of past giant clam restocking efforts (Teitelbaum and Friedman 2008), and mixed results of other restoration efforts for marine and coastal organisms such as mangroves and corals, further supports the conclusion that preserving wild organisms and their habitat should take priority (Ellison 2000; Spurgeon and Lindahl 2000; Kojis and Quinn 2001; Spurgeon 2001; Precht et al. 2005).

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APPENDIX A. ABILITY OF JUVENILE TRIDACNA SQUAMOSA TO WITHSTAND HIGH-SPEED CURRENTS

This experiment placed juvenile giant clams in cylindrical water chambers containing motorized paddles which generated a constant high-speed current. Between 48 and 72 *T. squamosa* ranging in size from 2.6 to 4.3 cm in shell length were used in multiple iterations of the experiment. All clams were given several days (in a separate tank) to firmly attach byssal threads to cement substrates, and were manually checked for firm attachment before being placed into the cylinders.

After one or more days in a current speed of approximately 0.37 ms^{-1}, many of the juveniles detached from the substrates and were then toppled over by the current. They were unable to right themselves while the current continued. The juveniles did not appear to suffer any immediate harm from lying on their sides, however this is an inefficient position for making use of the zooxanthellae in their mantles, and it also exposes their byssal opening to predators and parasites, so it would not be an expected position for juvenile clams in the wild.

At a current speed of 0.22 ms^{-1}, the juveniles were able to withstand the current for several days. However, the experiment had to be cancelled when they began to die in significant numbers. The deaths occurred in both the experimental and control chambers, and were therefore not due to the current. They are believed to have died due to water quality issues, as several unrelated experiments in the same building (using the same water supply) had to be cancelled due to near total mortality in their Asian green mussels (*Perna viridis).*

Fig. A.1. Juvenile *Tridacna squamosa* in current-generating water chambers.

APPENDIX B. PHOTOGRAPHS OF ADDITIONAL UNPUBLISHED PROJECTS

Fig. B.1. Rigid multi-level settlement structure for giant clam larvae.

Fig. B.2. Flexible multi-level settlement structure for giant clam larvae.

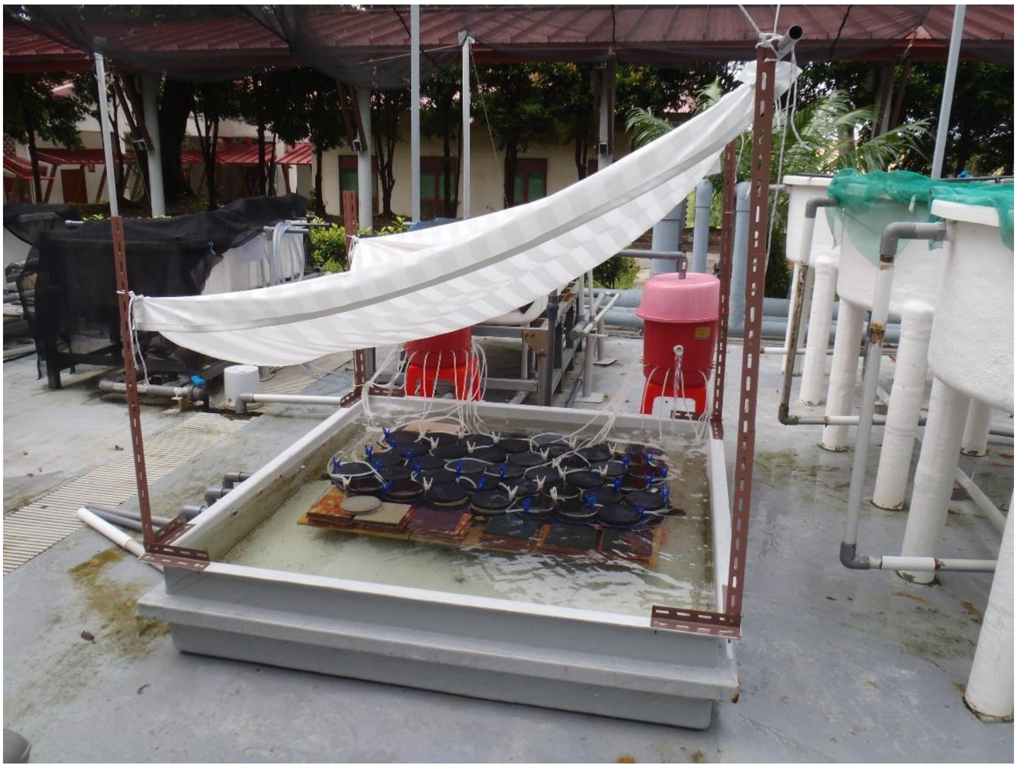

Fig. B.3. Smaller shade experiment using a water bath to moderate high temperatures.

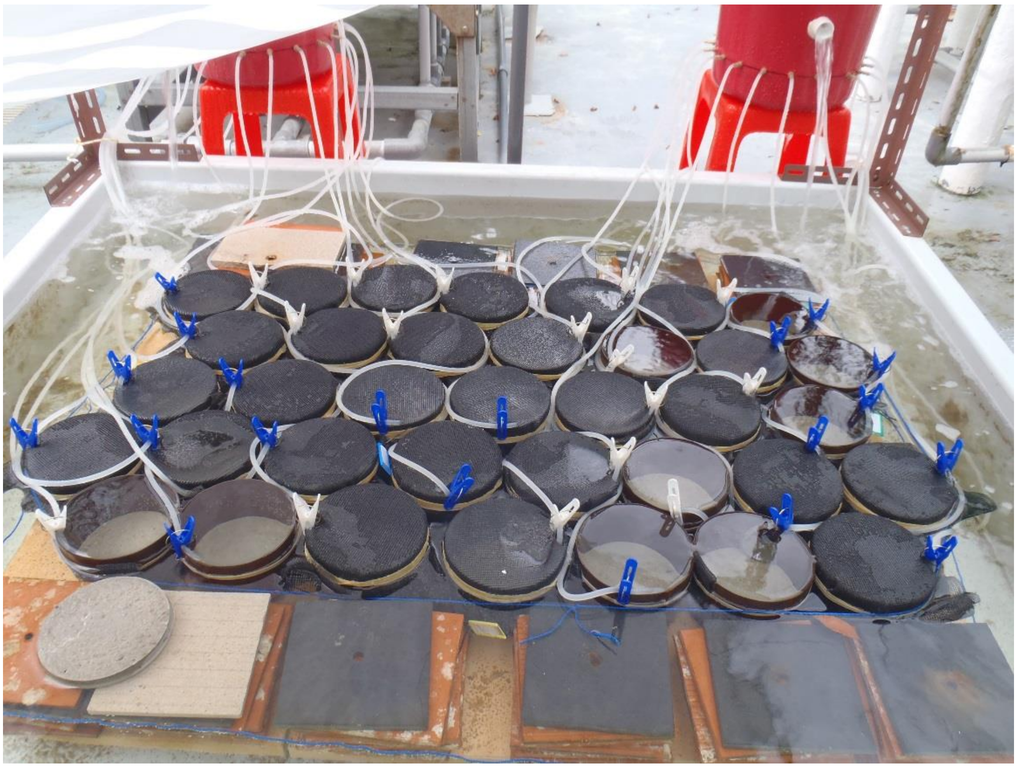

Fig. B.4. Close-up of smaller shade experiment.

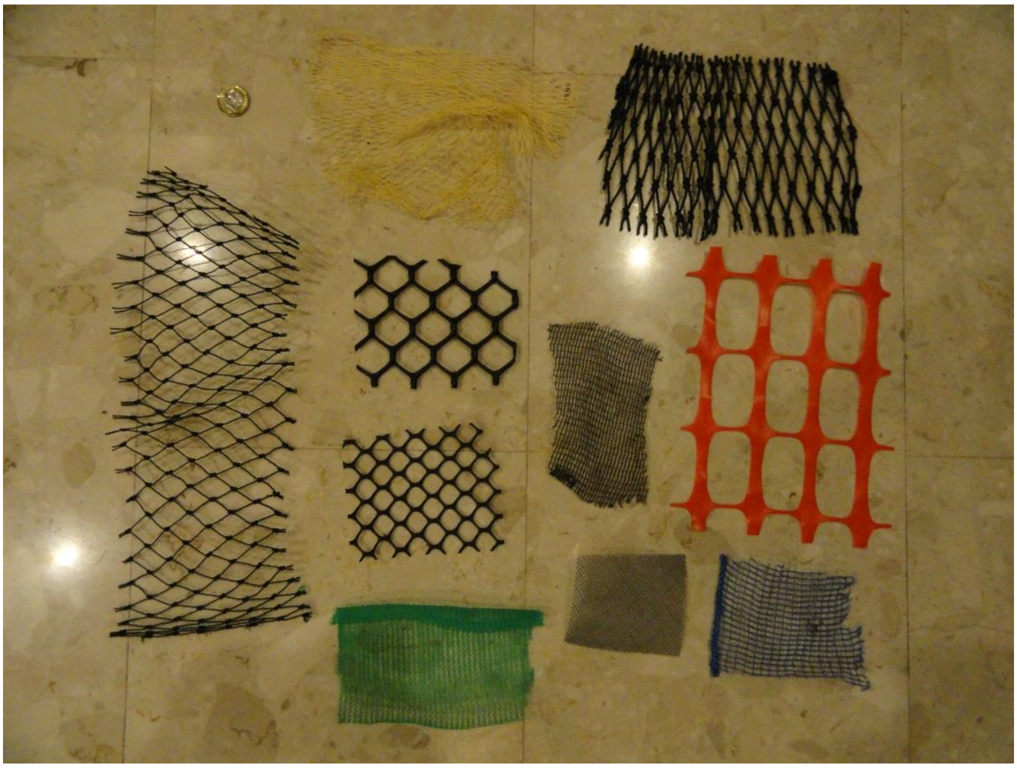

Fig. B.5. Proposed mesh materials for anti-predator cages. In situ biofouling tests were performed.