



## Review

## The ecological significance of giant clams in coral reef ecosystems

Mei Lin Neo<sup>a,b</sup>, William Eckman<sup>a</sup>, Karen Vicentuan<sup>a,b</sup>, Serena L.-M. Teo<sup>b</sup>, Peter A. Todd<sup>a,\*</sup><sup>a</sup> Experimental Marine Ecology Laboratory, Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543, Singapore<sup>b</sup> Tropical Marine Science Institute, National University of Singapore, 18 Kent Ridge Road, Singapore 119227, Singapore

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## ABSTRACT

Giant clams (*Hippopus* and *Tridacna* species) are thought to play various ecological roles in coral reef ecosystems, but most 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 zooxanthellae (*Symbiodinium spp.*), 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.

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\* Corresponding author. Tel.: +65 65161034.

E-mail addresses: [tmsnml@nus.edu.sg](mailto:tmsnml@nus.edu.sg) (M.L. Neo), [dbspat@nus.edu.sg](mailto:dbspat@nus.edu.sg) (P.A. Todd).

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## 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 giant clams (Cardiidae: Tridacninae), by virtue of their sheer size (Yonge, 1975), well developed symbiosis with zooxanthellae (Yonge, 1980), and highly threatened status throughout much of their geographic range (Lucas, 1994), perhaps deserve special consideration. 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 (excluding New Zealand and Hawaii), and Australia (bin Othman et al., 2010). There are currently 13 extant species of giant clams (see Table 1), including two recently rediscovered: *Tridacna noae* (Su et al., 2014; Borsa et al., 2014) and *Tridacna squamosina* (previously known as *T. costata*) (Richter et al., 2008), one new species: *Tridacna ningaloo* (Penny and Willan, 2014), and an undescribed cryptic *Tridacna* sp. (Huelsenken et al., 2013). *Tridacna maxima* is the most widespread, while *Hippopus porcellanus*, *Tridacna mbalavuana* (previously known as *T. tevoroa*), *T. ningaloo*, *T. noae*, *Tridacna rosewateri*, and *T. squamosina* have much more restricted distributions (Rosewater, 1965; bin Othman et al., 2010; Penny and Willan, 2014; 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, giant clam numbers are declining throughout their range (Mingoa-Licuanan and Gomez, 2002; Kinch and Teitelbaum, 2010; bin Othman et al., 2010).

Giant clams are especially vulnerable to stock depletion because of their late sexual maturity, sessile adult phase, and broadcast spawning strategy (Munro, 1989; Lucas, 1994). Fertilization success requires sufficient numbers of spawning individuals, and low densities result in reduced (or zero) recruitment and eventual population collapse (Braley, 1984, 1987; Neo et al., 2013). Presently, all giant clam species, other than the new species, *T. ningaloo*, the recently rediscovered *T. noae* and *T. squamosina*, and the cryptic *Tridacna* sp., 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 1). Conservation efforts are ongoing (Heslinga, 2013) including essential basic research (e.g. restocking of clams in heavily impacted coral reefs, Guest et al., 2008; effects of shade on survival and growth of juvenile clams, Adams et al., 2013; early chemotaxis contributing to active habitat selection, Dumas et al., 2014) and the development of new restocking techniques (Waters et al., 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 very rarely been quantified. Cabaitan et al. (2008) represents the only study to experimentally demonstrate the benefits that giant clams can have on coral reefs. They showed that, compared to control plots, the presence of clams had significantly positive effects on the richness and abundance of fish species and various invertebrates. 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. Methods

### 2.1. Literature survey

In this review, we first drew upon our own archives of publications, proceedings, dissertations, books, manuals, technical reports, popular science magazines, and grey literature that have been collected during more than 10 years of giant clam research. These archives ( $n = 481$  publications) were supplemented with key-word searches in five major literature databases, i.e. Google Scholar, JSTOR, PubMed, ScienceDirect, and Web-of-Science. We also used “snowball” sampling (see Lescureux and Linnell, 2014), that is, we manually searched through the reference lists of the most relevant giant clam papers to identify (and subsequently retrieve) some of the more obscure literature.

### 2.2. Population estimates of ecologically relevant parameters

For all the estimates described below, we first identified surveys of natural giant clams that included both population density and size distribution (i.e. Pearson and Munro, 1991; Chantrapornsy et al., 1996; Black et al., 2011; Gilbert et al., 2006; Todd et al., 2009). All densities were converted to per hectare values prior to the calculations. The reported size distributions did not provide individual measurements for each clam; rather they stated the

**Table 1**

Giant clam species list (Rosewater, 1965; Richter et al., 2008; bin Othman et al., 2010; Borsa et al., 2014; Huelsken et al., 2013; Penny and Willan, 2014; 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
<i>Hippopus hippopus</i> (Linnaeus, 1758)	Species has strong radial ribbing and reddish blotches in irregular bands on shells, growing to about 40 cm. Unlike <i>Tridacna</i> species, <i>Hippopus</i> mantle does not extend over shell margins and has a narrow byssal orifice	Lower risk/conservation dependent
<i>Hippopus porcellanus</i> Rosewater, 1982	Species is distinguished from <i>H. hippopus</i> by its smoother and thinner shells, and presence of fringing tentacles at incurrent siphon, growing to approximately 40 cm	Lower risk/conservation dependent
<i>Tridacna crocea</i> Lamarck, 1819	Smallest of all clam species, reaching lengths of about 15 cm. Burrows and completely embeds into reef substrates	Lower risk/least concern
<i>Tridacna derasa</i> (Röding, 1798)	Second largest species, growing up to 60 cm. Has heavy and plain shells, with no strong ribbing	Vulnerable A2cd
<i>Tridacna gigas</i> (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
<i>Tridacna maxima</i> (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
<i>Tridacna mbalavuana</i> Ladd, 1934 (formerly <i>T. tevoroa</i> Lucas, Ledua, Braley, 1990)	Species is most like <i>T. derasa</i> in appearance, but distinguished by its rugose mantle, prominent guard tentacles present on the incurrent siphon, thinner valves, and coloured patches on shell ribbing. Can grow over 50 cm long. Restricted to Fiji and Tonga	Vulnerable B1 + 2c
<i>Tridacna rosewateri</i> Sirenko and Scarlato, 1991	Species is most like <i>T. squamosa</i> 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
<i>Tridacna squamosa</i> Lamarck, 1819	Species is identified by its large, well-spaced scutes, with shell lengths up to 40 cm	Lower risk/conservation dependent
<i>Tridacna ningaloo</i> Penny and Willan, 2014 n. sp.	Species is most like <i>T. maxima</i> in appearance; weakly differentiated morphologically but strongly defined genetically. Holotype specimen measures 17.9 cm. Current known distribution in Western Australia, but possibly extends to Solomon Islands	Not assessed
<i>Tridacna noae</i> (Röding, 1798)	Species is most like <i>T. maxima</i> 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 and 20 cm. Overlapping distributions with <i>T. maxima</i> but generally in lower abundances	Not assessed
<i>Tridacna squamosina</i> Sturany, 1899 (formerly <i>T. costata</i> Roa-Quiaoit, Kochzius, Jantzen, Zibdah, Richter, 2008)	Species is most like <i>T. squamosa</i> in appearance, but distinguished by its crowded, well-spaced scutes, asymmetrical shell, and grows up to 32 cm. Only found in the Red Sea	Not assessed
Cryptic <i>Tridacna</i> sp. (undescribed in Huelsken et al., 2013)	Recently determined as a widely distributed cryptic species; forms an evolutionarily distinct monophyletic group	Not assessed

number of clams in a series of size brackets or 'bins'. For the purpose of our analysis, we assumed the size of each clam in a bin was equal to (minimum bin size + maximum bin size)/2. For the following equations, mass and weight are in grams, and shell length is abbreviated to SL.

Standing tissue biomass calculations: for each size *T. maxima*, wet biomass was first determined using the formulae biomass =  $10^{[(3.0434 \times \text{LOG}(\text{SL}_{\text{cm}})) - 1.6026]}$  (Gilbert et al., 2006) for clams at Tatakoto atoll and biomass =  $10^{[(2.9367 \times \text{LOG}(\text{SL}_{\text{cm}})) - 1.5318]}$  for clams at Fangatau atoll and Ningaloo reefs (Gilbert et al., 2006) and then assumed that 5.8% of wet biomass would convert to dry biomass (Ricciardi and Bourget, 1998). For each size *T. crocea*, dry biomass was determined using the formula biomass =  $(3.23 \times 10^{-6}) \times (\text{SL}_{\text{mm}}^{3.24})$  (Klumpp and Griffiths, 1994), while for *T. gigas*, the formula biomass =  $(0.34 \times 10^{-6}) \times (\text{SL}_{\text{mm}}^{3.36})$  was used (Klumpp and Griffiths, 1994). The biomass for each size class of clams was then multiplied by the number of clams of that size, and the multiplied values were totalled.

Standing shell weight calculations: for each size *T. maxima*, total clam weight was determined using the formulae weight =  $10^{[(3.1335 \times \text{LOG}(\text{SL}_{\text{cm}})) - 0.9173]}$  for clams at Tatakoto atoll (Gilbert et al., 2006) and weight =  $10^{[(3.1634 \times \text{LOG}(\text{SL}_{\text{cm}})) - 0.9495]}$  for clams at Fangatau atoll and Ningaloo reefs (Gilbert et al., 2006) and then subtracting wet tissue weight (calculated above) to give the weight of the shell alone. For each size *T. crocea*, shell weight was determined using the formula weight =  $(2.05 \times 10^{-5}) \times (\text{SL}_{\text{mm}}^{3.51})$  (Klumpp and Griffiths, 1994), while for *T. gigas*, the formula weight =  $(4.76 \times 10^{-5}) \times (\text{SL}_{\text{mm}}^{3.11})$  was used (Klumpp and Griffiths, 1994). The shell weight for each size class of clams was then multiplied by the number of clams of that size, and the multiplied values were totalled.

Annual biomass and shell production calculations: to determine annual biomass and shell production, von Bertalanffy equations (available for *T. gigas* and *T. maxima*, but not *T. crocea*) were used to estimate the age of each size clam from four locations (Pearson and Munro, 1991; Black et al., 2011; Gilbert et al., 2006). For *T. gigas*, growth parameter estimates: asymptotic length ( $L_{\infty}$ ) of 80, growth ( $K$ ) of 0.105, and its theoretical date of 'birth' ( $t_0$ )

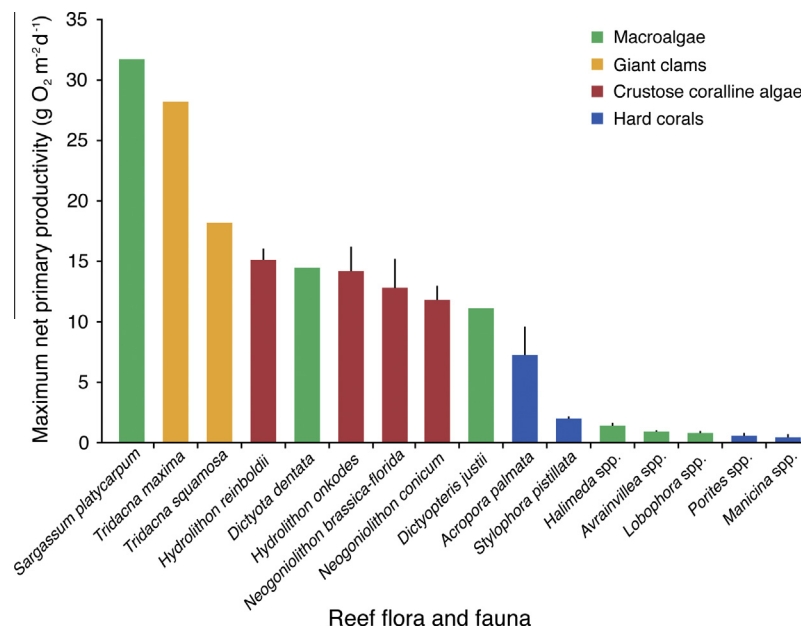
of 0.145 were used (Pearson and Munro, 1991). For *T. maxima*,  $L_{\infty}$  of 27.8,  $K$  of 0.068, and  $t_0$  of 0 were used (Black et al., 2011). Once the ages of the clams were estimated, one year was added, and the von Bertalanffy equation was used to predict a new shell length. The previous calculations were then used to predict biomass and shell weight of the clams at these increased sizes, and annual biomass and shell production were assumed to be the differences between the estimated values on the survey date and the predicted values one year in the future.

Clearance rate (CR) calculations: for *T. gigas*, clearance rate for a single clam ( $\text{l h}^{-1}$ ) was calculated using the formula  $\text{CR} = 3.68 \times (\text{dry weight}^{0.397})$ , while for *T. crocea* the formula used was  $\text{CR} = 0.585 \times (\text{dry weight}^{0.905})$  (Klumpp and Griffiths, 1994). No formula was available for *T. maxima*. The clearance rate for each size class of clams was then multiplied by the number of clams of that size, and the multiplied values were totalled.

### 3. Giant clams as food

#### 3.1. 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 facilitate between-taxa comparisons, the net primary productivity (NPP) from an array of reef organisms, including giant clams, is presented in Fig. 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* ( $28.16 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ) and *T. squamosa*



**Fig. 1.** Maximum net primary productivity (NPP) of different reef flora and fauna, measured in terms of net oxygen production (units =  $\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ). 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).

**Table 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 (individuals)	Standing biomass (kg dry weight)	Annual biomass production (kg dry weight)	Shell weight (kg)	Annual shell production (kg)	Water filtration (Lh <sup>-1</sup> )	Source of population data
<i>Tridacna crocea</i>							
Lee-Pae Island, Andaman Sea, Thailand	2,441	17	DD	391	DD	8,144	Chantrapornsyl et al. (1996)
Tioman Island, Malaysia	955	4	DD	98	DD	2,115	Todd et al. (2009)
<i>Tridacna maxima</i>							
Fangatau atoll, French Polynesia	381,919	878	217	89,023	23,372	DD	Gilbert et al. (2006)
Tatakoto atoll, French Polynesia	909,466	1,041	238	102,833	37,040	DD	Gilbert et al. (2006)
Ningaloo Marine Park, Western Australia	8,600	36	7	3,898	562	DD	Black et al. (2011)
<i>Tridacna gigas</i>							
Great Barrier Reef, Australia	432	718	14	18,839	356	28,121	Pearson and Munro (1991)

(18.14 g O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) is greater than most of the other coral reef primary producers. From the examples in Fig. 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<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>)—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).

It is known that cultured stocks can produce substantial biomass, e.g. 29 t ha<sup>-1</sup> yr<sup>-1</sup> of wet tissue biomass for *T. gigas* (Barker et al., 1988) (estimated 1,682 kg dry weight ha<sup>-1</sup> yr<sup>-1</sup>) and 16 t ha<sup>-1</sup> yr<sup>-1</sup> of wet tissue biomass for *T. derasa* (Heslinga et al., 1984) (estimated 928 kg dry weight ha<sup>-1</sup> yr<sup>-1</sup>). Here, we provide estimates of tissue biomass for natural populations of three giant clam species (Table 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 (1,041 kg dry weight ha<sup>-1</sup>) and high productivity, being capable of producing 238 kg dry weight ha<sup>-1</sup> yr<sup>-1</sup> 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) has a standing crop of 718 kg dry weight ha<sup>-1</sup>, 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<sup>-1</sup> yr<sup>-1</sup>). *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, but in patches of favourable habitat, *T. crocea* can have densities exceeding 100 clams m<sup>-2</sup> (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 and Hardy, 1969; Rees et al., 2003), occupying different niches based on depth and substrate type.

### 3.2. 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) noted that adult tridacnines appeared to be, more-or-less, 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 3). 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). In mariculture, ectoparasitic pyramidellids and ranellids are often abundant and their attacks can 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).

The wide array of morphological and behavioural defences exhibited by giant clams (Soo and Todd, 2014) 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 on giant clam juveniles (Perron et al., 1985).

### 3.3. Expelled materials

Opportunistic feeders may consume 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,



**Table 3**

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

Predator species	Method of predation	Literature source(s)
<b>PORIFERA: Family Clionaidae (Boring sponges)</b>		
Unknown	Bore into shells, weakening shells	Govan (1992b)
<b>FLATWORM: Family Turbellaria</b>		
<i>Stylochus (Imogene) matatasi</i>	Enter the clam through either the byssal orifice or inhalant siphon	Newman et al. (1991,1993)
<i>Stylochus (Imogene) sp.</i>		Govan (1992a,b)
<i>Polyclad sp. 1</i>		Govan (1992a)
<b>MOLLUSCS: Family Buccinidae (Whelks)</b>		
<i>Cantharus fumosus</i>	–	Perio and Belda (1989)
<b>Family Costellariidae (Mitres)</b>		
<i>Vexillum cruentatum</i>	–	Govan (1992b)
<i>V. plicarium</i>	–	Richardson (1991)
<b>Family Fascioliariidae (Tulip snails)</b>		
<i>Pleuroploca trapezium</i>	Immobilize clam by clasping mantle with foot preventing valve closure, insert proboscis into soft tissues	Govan (1992b)
<i>Pleuroploca sp.</i>		Alcazar (1986)
<b>Family Muricidae (Murexes)</b>		
<i>Chicoreus brunneus</i>	Drill holes into shells of juvenile clams	Abdon-Naguig and Alcazar (1989), Govan (1992a,b)
<i>C. microphyllum</i>	Drill holes into shells	Govan (1992a,b)
<i>C. palmarosae</i>	Often drill through valves; may attack via valve gape or byssal orifice	Govan et al. (1993)
<i>C. ramosus</i>	Insert proboscis into byssal gape to reach soft tissues, inject paralytic substance	Heslinga et al. (1984), Alcazar (1986), Govan (1992b)
<i>Cronia fiscella</i>	Drill holes into shells of juvenile clams	Govan (1992b)
<i>C. margariticola</i>	Through valve gape	Govan (1992a,b)
<i>C. ochrostoma</i>	Drill holes into shells	Govan (1992b)
<i>Morula granulata</i>	Drill holes into shells	Govan (1992a,b)
<i>Muricodrupa fiscella</i>	Drill holes into shells	Govan (1992a)
<i>Thais aculeata</i>	Attack through valve gape	Govan (1992a,b)
<b>Family Octopodidae (Octopus)</b>		
<i>Octopus sp.</i>	Chip shells; pry valves apart to feed	Heslinga et al. (1984), Barker et al. (1988), Govan (1992b), Mercier and Hamel (1996)
<b>Family Pyramidellidae</b>		
<i>Turbonilla sp.</i>	Use their long, flexible proboscis to suck clams' body fluids, either from mantle edge or through byssal orifice	Govan (1992a,b)
<i>Tathrella iredalei</i>		Heslinga et al. (1990), Govan (1992b)
<b>Family Ranellidae (Tritons)</b>		
<i>Bursa granularis</i>	Insert proboscis between valves of prey	Govan et al. (1993)
<i>Cymatium aquatile</i>	Injection of an immobilizing fluid through mantle or byssal orifice, then feed on soft tissues	Abdon-Naguig and Alcazar (1989), Govan (1992a,b,1995)
<i>C. muricinum</i>		Perron et al. (1985), Govan (1992a,b,1995)
<i>C. nicobaricum</i>		Govan (1992a,b,1995)
<i>C. pileare</i>		Govan (1992a,b,1995)
<i>C. vespaceum</i>		Perio and Belda (1989), Govan (1992b)
<b>Family Volutidae (Volutes)</b>		
<i>Melo amphora</i>	–	Loch (1991)
<i>Melo sp.</i>	–	Govan (1992b)
<b>ECHINODERM</b>		
Seastar	Exert powerful suction and tire adductor muscles (pry open clam)	Weingarten (1991)
<b>CRUSTACEANS: Family Diogenidae (Hermit crabs)</b>		
<i>Dardanus deformis</i>	Crushed 26 juvenile <i>T. gigas</i> in 3 days	Heslinga et al. (1984)
<i>D. lagopodes</i>	Chip valve ends	Govan (1992a)
<i>D. pedunculatus</i>	Crush or chip valves of prey	Govan (1992a), Govan et al. (1993)
<b>Family Gonodactylidae (Mantis shrimps)</b>		
<i>Gonodactylus chiragra</i>	Smash shells	Govan (1992a)
<i>Gonodactylus sp.</i>	–	Govan (1992b)
<b>Family Portunidae (Swimming crabs)</b>		
<i>Thalamita admete</i>	Chip shells; attack via byssal orifice	Govan (1992a)
<i>T. coeruleipes</i>		Govan (1992a)
<i>T. crenata</i>	Crush shells; may pry clam open via ventral margin	Ling (2007)
<i>T. danae</i>	Crush or chip valves; attack via byssal orifice of clams	Govan et al. (1993)
<i>T. spinimana</i>	–	Richardson (1991)
<i>T. stephensoni</i>	Chip shells; attack via byssal orifice	Govan (1992a)
<i>T. cf. tenuipes</i>		Govan (1992a)
<i>Thalamita sp.</i>	Penetrate soft tissues of adults through either byssal orifice or the inhalant siphon	Alcazar (1986), Govan (1992b)
<b>Family Xanthidae (Stone crabs)</b>		
<i>Atergatis floridus</i>	Crush or chip valves	Richardson (1991), Govan et al. (1993)
<i>A. integerrimus</i>		Richardson (1991)
<i>Atergatis spp.</i>		Govan (1992b)
<i>Carpilius convexus</i>	Crush or chip valves of juvenile clams	Alcazar (1986), Govan (1992a,b), Govan et al. (1993)
<i>C. maculatus</i>	Crush shells	Govan (1992a,b)

Table 3 (continued)

Predator species	Method of predation	Literature source(s)
<i>Demania cultripes</i>	Crush shells of juvenile clams	Alcazar (1986), Govan (1992b)
<i>Leptodius sanguineus</i>	Crush shells	Govan (1992a,b)
<i>Lophozozymus pictor</i>	Crush or chip shells	Richardson (1991), Govan (1992b)
<i>Myomenippe hardwickii</i>	Crush shells; may attack via byssal orifice	Ling (2007)
<i>Zosimus aeneus</i>	Crush shells	Govan (1992a,b)
<i>FISH: Family Balistidae (Triggerfish)</i>		
<i>Balistapus undulatus</i>	Feed on mantle and the exposed byssus and foot of adult clams	Alcazar (1986), Perio and Belda (1989)
<i>Balistoides viridescens</i>	Crush or chip shells	Heslinga et al. (1990)
<i>Balistoides</i> sp.		Govan (1992b)
<i>Pseudobalistes flavimarginatus</i>		Heslinga et al. (1990), Chambers (2007)
<i>Pseudobalistes</i> sp.		Govan (1992b)
<i>Rhinecanthus</i> sp.		Govan (1992b)
<i>Family Lethrinidae (Emperors)</i>		
<i>Monotaxis grandoculis</i>	Directly consumed 50 juvenile <i>T. squamosa</i> in <2 h	Heslinga et al. (1984), Govan (1992b)
<i>Family Labridae (Wrasses)</i>		
<i>Cheilinus fasciatus</i>	–	Richardson (1991)
<i>Cheilinus</i> sp.	Crush or chip shells	Govan (1992b)
<i>Choerodon anchorago</i>	–	Richardson (1991)
<i>C. schoenleinii</i>	–	Richardson (1991)
<i>Choerodon</i> sp.	Crush or chip shells	Govan (1992b)
<i>Halichoeres</i> sp.	Feed only on the byssus and foot of unanchored clams	Alcazar (1986), Govan (1992b)
<i>Thalassoma hardwicke</i>	–	Richardson (1991)
<i>T. lunare</i>	–	Richardson (1991)
<i>Family Myliobatidae (Eagle rays)</i>		
<i>Aetobatis narinari</i>	Crush shells	Heslinga et al. (1990), Govan (1992b), Chambers (2007)
<i>Family Tetraodontidae (Pufferfish)</i>		
<i>Canthigaster solandri</i>	–	Richardson (1991)
<i>C. valentini</i>	Crush or chip shells	Perio and Belda (1989), Govan (1992b)
<i>Tetraodon stellatus</i>		Heslinga et al. (1990), Govan (1992b), Chambers (2007)
<i>TURTLES: Family Cheloniidae</i>		
<i>Caretta caretta</i>	–	Bustard (1972)
<i>Chelonia mydas</i>	Break off shell flakes and ingest as calcium carbonate dietary supplement	Weingarten (1991)

1977) that can make a significant dietary contribution to reef fish; the adult black damselfish (*Neoglyphidodon melas*), for instance (Chan, 2007).

#### 4. Giant clams as shelter

##### 4.1. Shelters for coral reef fish

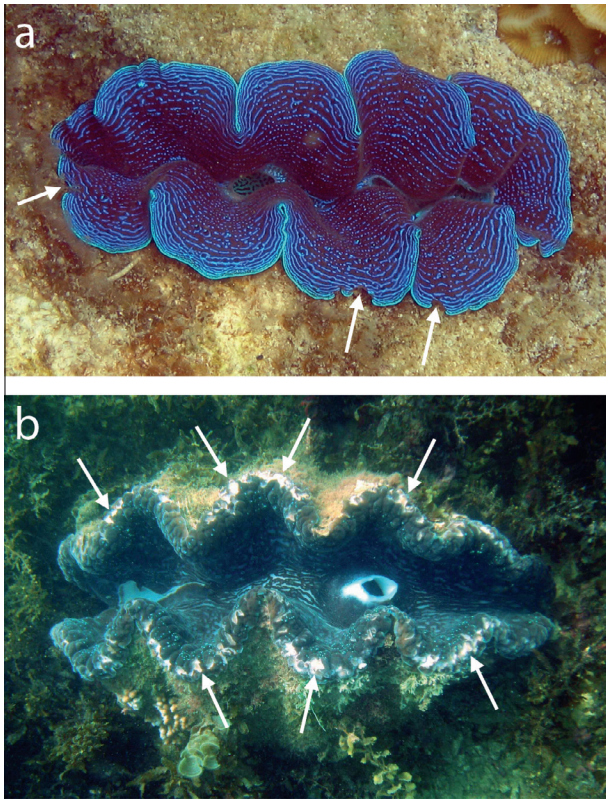
Coral reef fish diversity is related to coral cover (Bell and Galzin, 1984; Ault and Johnson, 1998) and substrate complexity (Gratwicke and Speight, 2005; Lingo and Szedlmayer, 2006). Dense aggregations of giant clams can increase topographic heterogeneity of the seabed and serve as nurseries and shelters 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).

##### 4.2. 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 harbour a variety of burrowing (Yonge, 1955; Turner and Boss, 1962) and encrusting (Roscoe, 1962; Rosewater, 1965) reef inhabitants, 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 (Fig. 3). 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, fouling algae on juvenile clams can reduce growth and lead to death by interfering with valve movement (unpublished data). Conversely, other epibionts may protect their hosts by contributing anti-predator defenses (Feiferak, 1987) and/or camouflage (Harder, 2008).

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 A1). 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) (see Fig. 3).



**Fig. 2.** Fish bite marks on the mantle edge of (a) *Tridacna crocea* (shell length ~14 cm) from Tioman Island, Malaysia and (b) *Tridacna gigas* (shell length ~80 cm) from Magnetic Island, Australia.

#### 4.3. Hosts for ectoparasites

Various cyclopoid copepods live within giant clams (Table A2). 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 been found within the same clam host (Humes, 1972, 1976). Ectoparasitic gastropods are also known to plague giant clams (also see Section 3.2.), and are especially severe in cultured juveniles (Cumming and Alford, 1994).

#### 4.4. 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. 4; Table A3) and pontoniid shrimps (Fig. 5; Table A4). Pea crabs are common within the mantle cavities of bivalves (Stauber, 1945; Schmitt et al., 1973), positioning themselves on the tenticular surface (gills) with their strong grip and gaining access to food aggregated by the host (Stauber, 1945). *Xanthasia murigera* (Fig. 3) is probably the most widespread, being found in five clam species (Table A3). Pontoniid 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 A4), *Anchistus gravieri* appears to be obligate to *Hippopus 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).

### 5. Reef-scale contributions of giant clams

#### 5.1. 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). The relict population of *T. gigas* from the Great Barrier Reef (Table 2) may only produce 356 kg ha<sup>-1</sup> yr<sup>-1</sup> of new shell material but Barker et al. (1988) estimated that a high-density cultured population of *T. gigas* could produce shell material in excess of 80 t ha<sup>-1</sup> yr<sup>-1</sup>. The natural *T. maxima* atoll populations in French Polynesia are capable of producing 23–37 t ha<sup>-1</sup> yr<sup>-1</sup> (Table 2) and are so dense that they create small islands called *mapiko* (Gilbert et al., 2006).

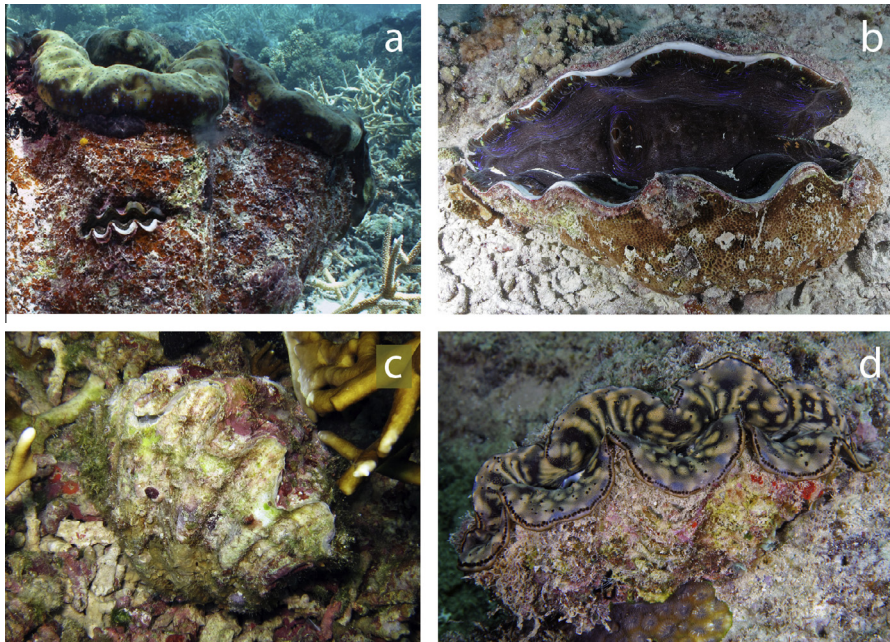
#### 5.2. Bioeroders

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 extending the pedal mantle tissue out of the byssal opening and dissolving the substrate under and around the clam via excreted solvents (Yonge, 1980; Fatherree, 2006). Given sufficient time and numbers of settling and growing/burrowing individuals, *T. crocea* will eventually erode away a dead coral head (Hamner and Jones, 1976; Glynn, 1997), but this erosive effect is limited to these habitats that are particular to *T. crocea*, 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.

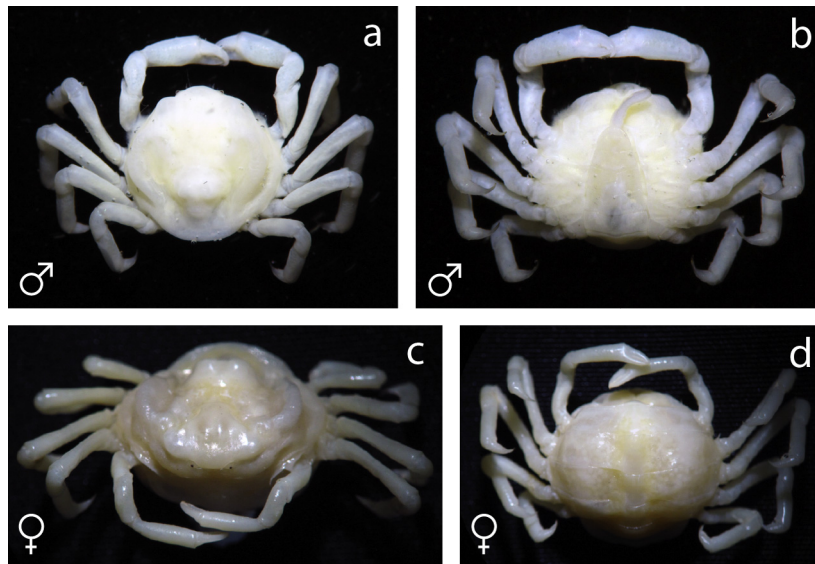
#### 5.3. Topographic enhancement

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





**Fig. 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.



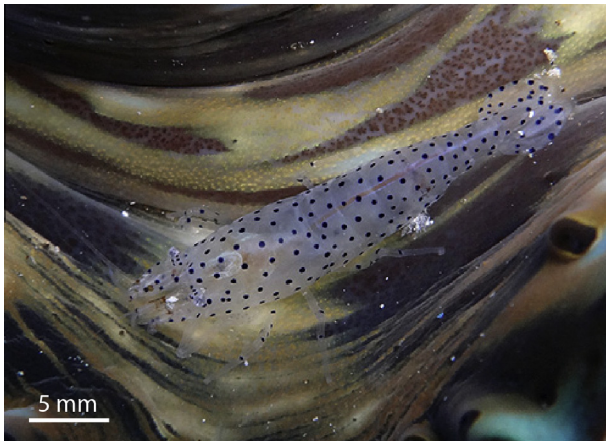
**Fig. 4.** Commensal pinnotherids (*Xanthasia murigera*; ZRC2013.0790) found within the mantle cavity of a fluted giant clam (*Tridacna squamosa*; shell length = 150 mm). (a and b) Carapace length (CL) = 5 mm. (c and d) CL = 11.5 mm.

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.

#### 5.4. 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 (Muscattine 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



**Fig. 5.** A commensal pontoniniid (*Anchistus* sp.; body length = 34 mm) found resting on the mantle of a fluted giant clam (*Tridacna squamosa*; shell length = 243 mm).

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  $4.9 \times 10^5$  cells clam<sup>-1</sup> d<sup>-1</sup> of intact zooxanthellae (Maruyama and Heslinga, 1997) and *T. gigas* can discharge  $4.7 \times 10^5$  cells clam<sup>-1</sup> d<sup>-1</sup> (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 and (possibly) types of zooxanthellae released from giant clams become available for other zooxanthellate-dependent species to ‘take up’, hence contributing to the wider coral reef ecosystem.

### 5.5. 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 (Klump and Griffiths, 1994). Giant clams filter large quantities of seawater; even a sparse population of mature *T. gigas* (0.04 clams m<sup>-2</sup>) on the Great Barrier Reef is capable of filtering over 28,000 l ha<sup>-1</sup> h<sup>-1</sup> (Table 2). Giant clams also clear water of algal cells efficiently, e.g. *Tridacna* species ingest 51–58% while *H. hippopus* ingests 81% (Klump 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), giant clams sequester them from the water where they could otherwise encourage macroalgae to flourish.

## 6. Conclusion

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, suggest 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 pontoniniid shrimp (*Paranchistus armatus*), are only found in tridacnine hosts. At the reef-scale, dense populations of giant clams can annually contribute 100s to 1,000s kg ha<sup>-1</sup> of shell material to a coral reef, far outweighing localized erosion by *T. crocea* and *T. maxima*. Giant clams provide their symbiotic *Symbiodinium* 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 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, however, 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. As mentioned in the Introduction, 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<sup>2</sup> 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 zoanths) 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. Similar research at different locations, and with other giant clam 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, plus one entirely new species, that have no official conservation status (Table 1). Giant clams should feature more prominently when planning marine protected areas and integrated coastal management schemes (van Wynsberge et al., 2013) 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 (for instance, fourteen cultured *T. gigas* are used in snorkel trails at Magnetic Island; Braley, pers. comm., 2014), 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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### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.11.004>.

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