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Review

The ecological significance of giant clams in coral reef ecosystems

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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.

Contents

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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. (Huelsken 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; Chantrapornsyl 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