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Recruitment of hard coral communities on giant clam shells (Cardiidae: *Tridacna*) differ from surrounding reef habitats at a tourist destination in the Gulf of Thailand

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ABSTRACT

Giant clams are organisms of significant ecological importance on coral reefs. They are known to help maintain oligotrophic conditions on reefs, to act as potential reservoirs of symbiotic dinoflagellates and as a consequence of their large, dense shells, to contribute to reef structural complexity. Despite this, little work has been done to investigate the utility of giant clam shells for coral recruitment. Here, we quantify scleractinian coral growth on living and dead giant clams around the Thai island of Koh Tao, a site with a history of environmental and anthropogenic pressure related to tourism. Transect surveys at 15 reefs around the island yielded 739 clams, of which 120 were found to support coral recruits. A total of 270 distinct corals were recorded between depths of 2.1 and 8 m (none were found at depths shallower than 2 m), with 29% found on dead shells and 71% on living clams. Differences were found in the community structure of hard corals found on clam shells *vs* those found in surrounding reef environments, with mushroom corals (Fungiidae) and *Stylocoeniella* being significantly more abundant on clam shells than on the natural reef. In contrast, corals abundant on surrounding reefs (e.g. *Acropora* and *Porites*) were disproportionately better represented on the reef than on clam shells. This suggests that giant clam shells may play a significant role in the succession of coral reefs with certain corals being preferentially supported over others.

INTRODUCTION

Much of the research on giant clams in Thailand has been conducted over the last three decades. This work has been recently reviewed by Mehrotra *et al.* (2021a), who found that most studies were from the Andaman coast (i.e. Chantrapornsyl *et al.*, 1996; Kittiwattanawong, 1997; Kittiwattanawong, 2001). Studies from the Gulf of Thailand have largely focused on *ex situ* investigations of giant clam biology (Tedengren *et al.*, 2000; Elfwing *et al.*, 2001) and restocking efforts of natural populations (Nugranad *et al.*, 1997; Charuchinda & Asawanghune, 2000). Long-term monitoring of *Tridacna* spp. on the island of Koh Tao, Gulf of Thailand, has indicated that over the past 11 years, populations of *Tridacna crocea* have appeared to be stable in the shallower parts of their depth range (3–5 m) but have been declining at greater depths (6–8 m) (Mehrotra *et al.*, 2021a). In contrast, populations of *T. squamosa* appear stable at depths of 6–8 m but are increasing across the 3–5 m depth range; it has been suggested that this is a possible result of historic giant clam restocking efforts at Koh Tao. Despite this, little has been done to investigate the ecological function and ecosystem services of giant clams found in Thai waters.

Investigations on the ecology of giant clams outside of Thai waters can broadly be divided into those examining trophic dynamics and those exploring shell function. In the former case, it has been shown that the heterotrophic capacity of giant clams via filter feeding may help maintain oligotrophic conditions within reef environments (Pearson & Munro, 1991; Neo *et al.*, 2015), while the symbiosis between clams and endosymbionts (Symbiodiniaceae) may benefit nearby zooxanthellate corals (Neo *et al.*, 2015; Morishima *et al.*, 2019). The shells of Tridacnine species have been shown to be effective in assessing historic climate variability (Driscoll *et al.*, 2014; Arias-Ruiz *et al.*, 2017; Gannon *et al.*, 2017). Additionally, the shells of giant clams have also been shown to host a diverse array of epibionts. Macroalgae, sponges, ascidians, brittlestars, crustaceans, polychaetes and various molluscs, including other bivalves, have been found to use the shells of living *T. squamosa* as substrata in Singapore (Vicentuan-Cabaitan *et al.*, 2014). Clam shell substrata have additionally been found to host coral reef competitors. For example, damselfish of the genera *Dischistodus* and *Stegastes* were observed using giant clam shells as substrate (*T. gigas*, *T. derasa* and *Hippopus hippopus*), and manipulating (via biting) the mantles of *T. gigas*, to maximize the growth of turf algae (Cabaitan *et al.*, 2018).

Dead clam shells are also reportedly used to support the growth of a variety of calcifying organisms. For instance, the internal surface of shells belonging to dead giant clams was found to be utilized by juvenile *T. maxima* individuals in French Polynesia after a dramatic population loss (Andréfouët *et al.*, 2013).

Despite extensive evidence of giant clam shells being used as substrata for a diverse array of colonizers, few records exist of these shells hosting reef-building corals. In the Philippines, Dizon *et al.* (2008) documented the efficacy of dead *T. gigas* shells as a substratum for a variety of transplanted reef-building corals attached with different adhesives. Similarly, Cabaitan *et al.* (2008) assessed the role of coral transplants on reef fish communities, finding that transplants on *T. gigas* shells were able to significantly promote fish species richness over controls (i.e. absence of shells). At present, the only detailed documentation of reef-building corals naturally growing on the shells of giant clams is that of Mekawy (2014), who recorded various species encrusting on *T. maxima*, alongside numerous other invertebrate taxa, in the Red Sea. Additionally, the rare skeleton-forming octocoral *Nanipora* was recorded growing on the shell of a living *T. squamosa* at Koh Tao (Urgell Plaza *et al.*, 2018). Both studies, however, did not quantify these epibionts nor distinguish between incidental growth of nearby colonies and recruits or coral growth independent of the reef benthos.

A recent study of the island of Koh Tao found significant differences between the community structure of corals on natural and on artificial reefs (Monchanin *et al.*, 2021). These differences could not be explained by a range of different variables including depth, duration *in situ* and distance from reefs. The prevalence of certain coral types (as divided by genus, reproductive mode, structural complexity and more) on artificial structures that were less abundant or even rare on natural reefs raised questions about the possible dynamics of coral recruitment and coral reef succession on the island. The reefs of the island, which have been shown to be impacted by a wide range of threats such as coral disease associated with tourism pressure (Lamb *et al.*, 2014), coral predation (Scott *et al.*, 2017a) and coral bleaching (Scott *et al.*, 2017b), among others, nonetheless have been shown to host a high diversity of marine life (Scaps & Scott, 2014; Mehrotra *et al.*, 2021b). Here, we conduct an in-depth assessment quantifying the role of giant clam shells *in situ* as substrata for coral recruitment. We compare the community structure of hard corals on giant clam shells with those of the surrounding reefs. Finally, we compare our findings with those of Monchanin *et al.* (2021), thus exploring the role of both natural and artificial substrata, on and off coral reefs, in the successional dynamics of coral reefs.

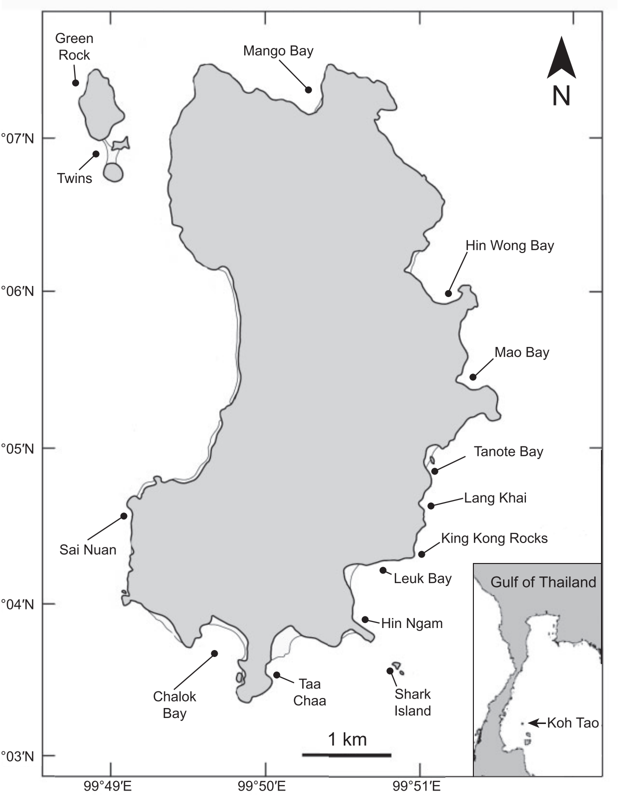

Figure 1. Sites surveyed at Koh Tao for giant clam epibionts and natural reef scleractinian coral community structure.

MATERIAL AND METHODS

Field surveys

Belt transect (BT) surveys were conducted following the protocols described by Mehrotra *et al.* (2021a). The entire substrata of each BT (width 5 m, length 20 m) was carefully checked for giant clams. Between May–August 2019, BT surveys were carried out at 15 sites at Koh Tao (Fig. 1) to assess the growth of scleractinian corals on the shells of living and dead *Tridacna* spp. Species identification was carried out *in situ*, with underwater photography utilized for further clarification where required. To maximize the number of clams assessed, the resolution of depth ranges surveyed was increased from previous spatiotemporal surveys to include depths of 0–2 m, 2.1–4 m, 4.1–6 m and 6.1–8 m. Each coral recruit was counted if they were found to be using clam shells as their primary substrate, and thus not attached to any other benthic substrate. Corals were counted based on each individual recruit (colonies for colonial corals, individuals for solitary), regardless of size. For boring clams (*Tridacna crocea* and some juvenile *T. squamosa*), corals were included if they were encrusting upon any visible part of the shell and no part was growing on the host substrata of the clams. Therefore, coral colonies hosting boring clams were discounted from the analysis.

The total abundance of scleractinian corals on the clam shell substratum per site was counted, with the corals being identified to genus level and recruits being assessed per clam. Fungiidae identification however was limited to the family level due to the difficulty of identifying fungiid recruits on the basis of morphology. We used a range of literature for identifying genera and family-specific groups, with Veron (2000) used as a basis; taxon names follow Hoeksema & Cairns (2021). Shell substrata were divided by species (*T. crocea* or *T. squamosa*) and whether specimens were living or dead. For living clams, both shell valves of an individual clam were treated as a single unit. Dead clams for which only a single shell valve was found were considered as 0.5 unit; however, these were in the minority. Hard corals on dead clam shells were divided into those found growing on the external surface or internal surface. Orientation of shells was not assessed in this study, where exposed and unexposed surfaces being treated equally based on external (high rugosity) or internal (low rugosity) surfaces. Therefore, no distinction was made between the upward-facing internal and external surfaces of dead clams. Neither size nor growth of corals was accounted for in this study.

Alongside each BT survey at each of the 15 sites, a 20 m point-intercept transect (PIT) survey was carried out on the coral reef and data on the proportional abundance of each genus of scleractinian coral were assessed. The PIT surveys were carried out at shallow (3–5 m) and deep (6–8 m) depth ranges, following the protocol by Monchanin *et al.* (2021). Proportional abundances of coral genera on the reef were compared with corals growing on the shells of *Tridacna* spp. PIT surveys overlapped precisely with BT surveys in at least two depth ranges at each site, such that natural reef coral communities and recruits on *Tridacna* shells were from identical habitats, thus allowing for direct comparisons.

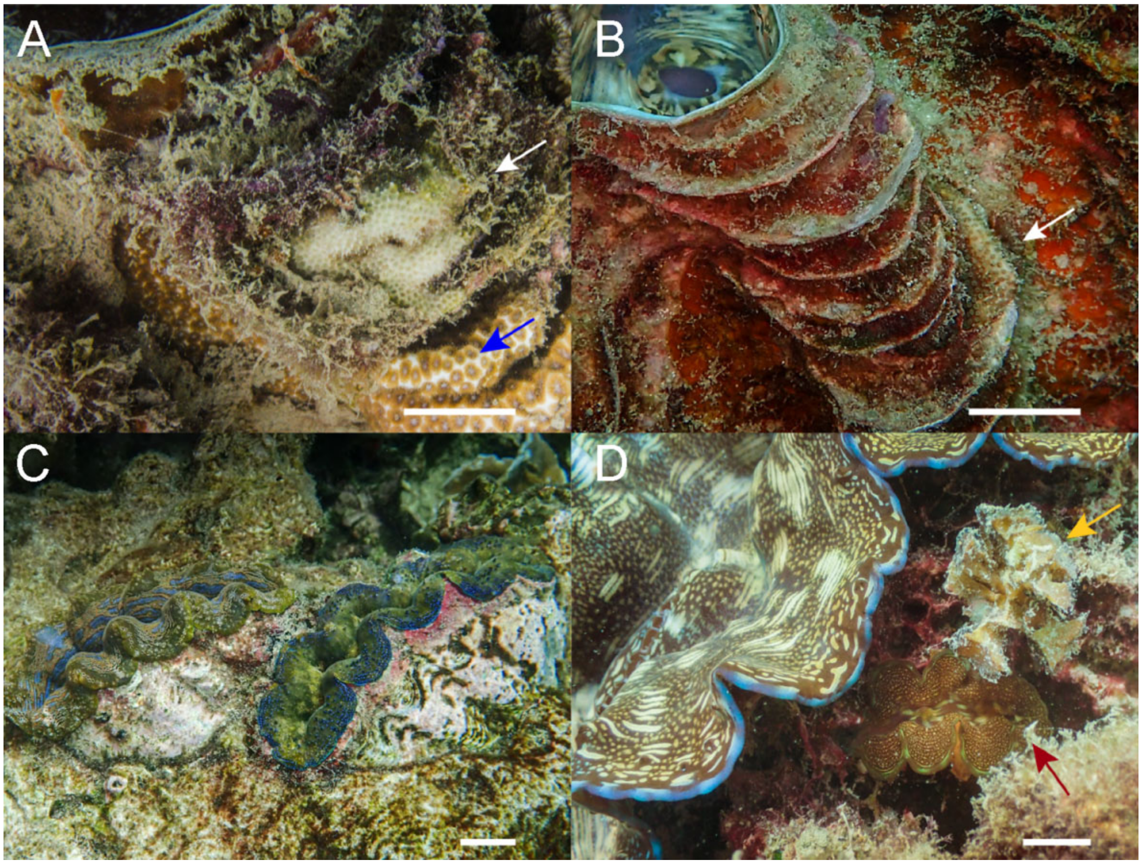

Figure 2. Giant clams and their epibionts. **A.** *Stylocoeniella armata* (white arrow) and *Leptastrea purpurea* (blue arrow) growing on the scutes of *Tridacna squamosa*. **B.** Encrustation of *S. armata* (white arrow) over scutes surrounded by cyanobacteria and other epibionts. **C.** The exposed shells of *T. crocea* on a dead coral with growth of filamentous algae. **D.** Space competition on *T. squamosa* between a juvenile *T. squamosa* (red arrow) and the macroalgae *Turbinaria* sp. (yellow arrow). Scale bars: **A**, **B**, 15 mm; **C**, **D**, 20 mm.

Statistical analyses

All statistical analyses were carried out in R v.1.2.5033 (RStudio Team, 2019). The proportions of clam shells hosting corals were compared using a proportion test (package RVAideMemoire v. 0.9–73 Hervé, 2020). The mean number of corals per clam was tested between categories (i.e. living or dead clam shells; all clams at 2.1–4, 4.1–6 or 6.1–8 m depth ranges) using Fisher's exact test. The relative abundances of coral genera between categories (i.e. on clam shells at 2.1–4, 4.1–6 or 6.1–8 m depth ranges and on coral reef at 3–5 and 6–8 m depth ranges) were compared using Fisher's exact test followed by pairwise comparisons using the R package RVAideMemoire.

RESULTS

A total of 739 clams were surveyed, of which 120 were found to host 270 corals. Similar numbers of clams were surveyed for each species with 363 individuals of *Tridacna squamosa* and 376 individuals of *T. crocea* being included in the analysis. In both species, corals were observed encrusting both directly on and between scutes (i.e. lateral projections of the external shell structure; see Figure 2). The total surveyed area from which clams were counted was 16,400m^2. The proportion of clams hosting corals was significantly higher ($\chi^2 = 15.776$, df = 1, $P < 0.001$) for shells of dead individuals (33.33%) than for living individuals (14.39%). Additionally, corals were found on a far greater number of shells belonging to *T. squamosa* than *T. crocea* (Table 1), regardless of clam mortality (Fisher's exact test: $P < 0.001$). We found only 9 individuals of dead *T. crocea* shells whereas for *T. squamosa* we recorded 63. The mean number of corals per clam was found to be highest among dead shells of *T. squamosa* (1.21 corals per individual), that is *c.* twice as many as those hosted by living individuals (0.63) (Fisher's exact test: $P < 0.001$). A far greater proportion of dead *T. crocea* shells were also found to be supporting corals (a mean of 0.22 corals per clam) than living individuals (0.01 corals per clam) (Fisher's exact test: $P = 0.004$). Notably, a single juvenile *T. squamosa* was observed growing directly on the shell of a larger living individual of the same species (Fig. 2D). A number of other bivalves were documented growing on the shells of living and dead giant clams, but these were not quantified.

Assessment of the shells of 667 living and 72 dead *Tridacna* spp. revealed abundant utilization by multiple genera of scleractinian corals, but the majority of clams surveyed did not host corals. Significant differences were found in the proportion of clams hosting corals ($\chi^2 = 71.939$, df = 3, $P < 0.001$) and the mean number of corals per clam (Fisher's exact test: $P < 0.001$) at the different depth ranges. Most notably, no corals were recorded growing on clam shells at depths shallower that 2 m. At all other depth ranges, coral epibionts were found growing on clam shells. A total of ~28.26% of clams between 2.1–4 m were found to be hosting corals, with a mean density of 0.96 corals per clam across the depth range. In contrast, 15.05% of clams at the 4.1–8 m depth range supported coral growth at a mean density of 0.28 clams per coral. The greatest proportion of clams hosting corals was at 6.1–8 m (33.48% of clams); the mean density of corals per clam was 0.84. Pairwise analyses found no significant difference in the proportion of clams hosting corals or the mean number of corals per clam between the 2.1–4

Table 1. Numbers of giant clams and corals on giant clams that were assessed for scleractinian growth.

Clam species/category	No. of clams	No. of corals	No. of clams with coral epibionts	Mean no. of corals per clam
Tridacna squamosa				
Dead	63	76	23	1.21
Alive	300	190	94	0.63
Both	363	266	117	0.73
Tridacna crocea				
Dead	9	2	1	0.22
Alive	367	2	2	0.01
Both	376	4	3	0.01
Species combined				
Dead	72	78	24	1.08
Alive	667	192	96	0.29
Total	739	270	120	0.37
Depth range (m)				
0–2	123	0	0	0
2.1–4	46	44	13	0.96
4.1–6	455	129	68.5	0.28
6.1–8	115	97	38.5	0.84

Clams are categorized by species, living/dead state and depth. The mean number of corals per clam are provided.

and 6.1–8 m depth ranges. Regarding external versus internal shell use, a total of 6 corals were found growing on the internal surface across 4 dead clam shells whereas 72 corals were found growing on the external surface of 20 dead clams.

Comparison of the coral community structure between clams and the surrounding reef revealed further differences. A total of 16 non-Fungiidae scleractinian coral genera were recorded from giant clams at Koh Tao. Proportions of corals in the genus *Stylocoeniella* and those of the monostamatous Fungiidae growing on clam shells were found to be significantly different between 2.1–4 and 6.1–8 m depth ranges (Fig. 3). The proportion of *Stylocoeniella* was significantly higher at 6.1–8 m (32.29%) than at 2.1–4 m (2.27%), whereas the proportion of Fungiidae corals was found to be significantly lower at 6.1–8 m (31.25%) than at 2.1–4 m (65.91%). The proportion of both coral groups growing on giant clam shells was also found to be significantly higher than was recorded from the coral reef ($P < 0.047$), with *Stylocoeniella* being absent from reef PIT surveys (Fig. 4). Conversely, the genera *Acropora* and *Porites* were found to be significantly more abundant on the reef than on clam shells ($P < 0.017$), except for the *Acropora* on shallow clams (2.1–4 m) and the deep reef (6.1–8 m), between which no significant difference was found. Shallow reefs were found to host a greater proportion of *Pocillopora* than those found on clam shells ($P < 0.012$), but no significant difference was found between deeper reefs and clam shells. *Diploastrea* corals were found to be abundant on the coral reef but were absent from giant clam shells, thus preventing further analysis. No significant differences were found between the proportions of *Montipora*, *Pavona*, *Lobophyllia*, *Favites*, *Goniastrea*, *Merulina* and *Platygyra* corals growing on clam shells and on the surrounding reef. All other coral genera were found in proportions of <1% in all surveyed groups (see Supplementary Material) of the comparison of living and dead clam shells showed that *Pavona* and *Porites* corals occurred on dead clam shells in significantly greater proportions (Fisher test: $P = 0.031$ and $P = 0.009$, respectively). In contrast, *Pocillopora* corals were significantly better represented on living clam shells ($P = 0.04$). No significant difference was found between the other coral types.

DISCUSSION

The species, live/dead state and depth of giant clams appeared to influence the abundance or diversity of scleractinian epibionts. Given that living *Tridacna crocea* typically have only a fraction of their shells exposed to light or potential coral larvae, it is unsurprising that only 2 of the 367 clams were found to host coral recruits. It also therefore explains why the mean number of corals per clam was found to be lower for living (0.01) compared to dead (0.22) clams, as the few dead *T. crocea* shells assessed ($n = 9$) were separated from the substrata (or burrows) and thus had the entire surface of the shell exposed to the environment. While the available shell surface area for supporting epibiont growth was not quantified in our study, this is undoubtedly likely to be a prominent factor in determining the abundance of epibionts found on a given shell. This is further suggested by the significantly higher abundance of corals colonizing shells of *T. squamosa*; this species grows to a greater size than *T. crocea* and is characterized by large prominent external scutes that further increase the available surface area (Ling *et al.*, 2008). Unlike the boring nature of *T. crocea*, individuals of *T. squamosa* were found to be more exposed, suggesting that both dead and living *T. squamosa* shells would potentially support higher abundances of corals.

The shells of giant clams at Koh Tao have been shown to host a multitude of epibionts (van der Schoot *et al.*, 2016; Urgell Plaza *et al.*, 2018), including the hard corals that formed the focus of the present study. The only previous study to document scleractinian coral growth on Tridacninae shells (Mekawy, 2014) assessed a total of 25 individuals of *T. maxima* along several hundred kilometers of coastline in the Egyptian Red Sea. In that study, the diversity (but not abundance) of epibionts, including scleractinians, was found to be positively associated with what was broadly defined as ‘contamination’; however, this was largely treated as a binary factor with some specific causes being hypothesized. While in our Koh Tao study we were able to quantify and compare factors that may influence scleractinian growth on the shells of giant clams, the role of substrata competition was not assessed. However, we found firm evidence that living clam shells support coral competitors, including cyanobacteria and algae (Fig. 2B–D).

Giant clam shells may offer a variety of advantages for hard coral growth. This includes the endosymbiont-rich faecal pellets produced by the clams (Neo *et al.*, 2015; Morishima *et al.*, 2019), which may support faster recovery during times of coral bleaching, though more study is needed. Additionally, Guibert *et al.* (2019) provide evidence for aggregations of the giant clam *T. maxima*, particularly when combined with scleractinian corals, as effective deterrents of biofouling organisms via the mechanism of filter feeding. While the surveys conducted in the present study did not specifically

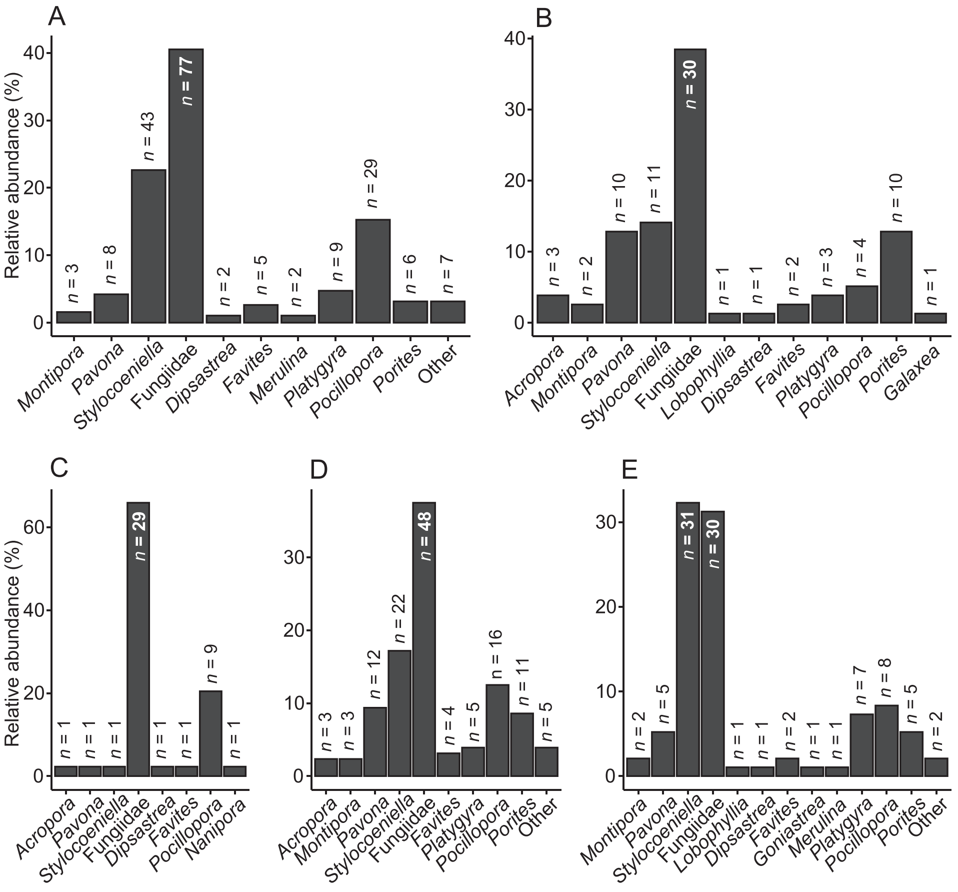

Figure 3. Coral community structure in relation to variation in substrates and habitats. Relative abundance of corals on living clam shells (**A**), dead clam shells (**B**) and all clam shells at depths of 2.1–4 (**C**), 4.1–6 (**D**) and 6.1–8 m (**E**). Corals comprising less than 1% in all analyses were grouped together as 'other'.

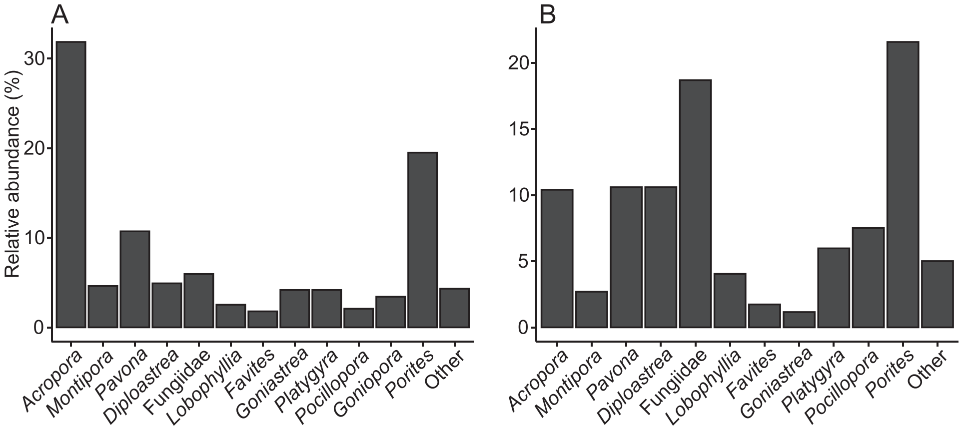

Figure 4. Coral community structure in shallow reef (**A**) and deeper reef (**B**) environments. Corals comprising <1% in all analyses were grouped together as 'other'.

assess the aggregation of giant clams, the presence of cyanobacterial and algae on clam shells may indicate that these offer significant competition to coral recruits. Furthermore, the observation of more corals being found on dead than living clam shells suggests that the rugosity and large surface area of clam shells is the prominent factor in promoting coral settlement, while the vertical versus horizontal orientations of living clams relative to the seabed are likely to influence recruitment patterns. It has been shown that the shells of living *T. squamosa* may offer up to 26 times more settlement substrate than the footprint they occupy (Vicentuan-Cabaitan *et al.*, 2014). It is likely that this value is significantly reduced for dead clams, as our results suggest that coral recruits strongly prefer external over internal surfaces of dead clam shells. However, Calumpong *et al.* (2003) documented that juvenile *T. squamosa* showed no preference between dead coral, dead clam shells and concrete substrata. The proportional prevalence of *Pavona* and *Porites* corals on dead clams suggest that there may be a localized preference for more direct light, but this requires further study.

Several differences were found between the proportion of particular corals growing on clam shells and those on the surrounding reef environment, such as the high abundances of the genus *Stylocoeniella* on clam shells. Roving diver surveys that were done following our study revealed that *Stylocoeniella* colonies (*S. armata*) were small and sparse throughout the reef habitat, being predominantly found among dense rubble or under overhanging corals and this explains why they were not observed in our PIT surveys. These observations agree with Dinesen (1983) who documented *Stylocoeniella* (*S. armata* specifically) as cavernicolous and preferring shaded habitats. The increasing abundance of *Stylocoeniella* found on giant clam shells with depth in our findings indicates a preference for substrata exposed to less light. The community structure of corals found on the natural reef in our study agrees with the most recent assessment of coral reef communities at Koh Tao (Monchanin *et al.*, 2021). This is not surprising given the overlap in some of the data and sites assessed.

The significant differences in the coral communities between the surrounding reef and those found on the shells of *Tridacna* in this study echo the contrasts seen in communities of natural versus artificial reefs by Monchanin *et al.* (2021). For example, the proportion of Fungiidae corals observed on artificial reefs and *Tridacna* shells was significantly greater than on natural reefs. In contrast, Merulinids and corals of the genus *Leptastrea* are not well represented on artificial reefs. Similarly, *Stylocoeniella* was not recorded in any significant abundance on artificial reefs although it occurs prominently on giant clam shells. While it should be noted that giant clams are not found deeper than 8 m at Koh Tao and no shallow artificial reefs were assessed by Monchanin *et al.* (2021), the community of coral recruits on giant clam shells may provide valuable insights on the dynamics of coral reef succession. New recruits on both natural (giant clam shells) and artificial (concrete and metal) substrata showed an enrichment of Fungiidae corals, which have been shown to be competitive colonizers of substrata as well as contributing to the expansion of reef slopes in sandy areas (Chadwick-Furman & Loya, 1992; Hoeksema, 2012). Free-living Fungiidae corals have been found to be prominent players in the coral reefs at Koh Tao, both as prey of corallivorous gastropods and as predators of algivorous ones (Hoeksema *et al.*, 2013; Mehrotra *et al.*, 2019). Both types of substrates also showed relatively low levels of recruitment by Acroporidae corals as compared with natural reefs, possibly suggesting a tendency towards later colonization in the successional pathways in reef development. Many Acroporidae species are considered to be 'high structural complexity' species on reefs (Monchanin *et al.*, 2021) and their absence may have significant ecological impacts. However, in our study high-structural-complexity genera, such as *Pocillipora* and *Pavona*, were relatively well-represented on giant clam shells in shallow depths but poorly represented on deeper artificial reefs, indicating that the coral succession at Koh Tao may be particularly influenced by depth.

Our findings showing that giant clam shells offer viable and potentially advantageous substrata for hard coral growth and recruitment contribute to the growing evidence underlining the importance of giant clams to the resilience and sustainability of coral reefs. These findings thus clearly further highlight the benefits of continuing giant clam restoration and population restocking for the conservation of coral reefs in Thailand (Mehrotra *et al.*, 2021a). The observation of juvenile *T. squamosa* and other bivalves growing on the shells of living *T. squamosa* adds further credence to this and suggests that assessments of the capacity of *Tridacna* spp. in maintaining oligotrophic conditions (via nutrient and plankton removal) on reefs should incorporate investigations into the contribution of bivalve epibionts. Further studies into shifting coral community structure and substratum preferences are needed to prioritize targeted management plans for conservation efforts of reef environments. The Gulf of Thailand has remained underrepresented in studies of population connectivity and dispersal (Hui *et al.*, 2016; Keyse *et al.*, 2018) for *Tridacna*, as well as in research on the role of photosymbionts in the dynamics of the host–symbiont relationships (Mies, 2019). As one of the geologically youngest regions in the west Pacific (Voris, 2000; Keyse *et al.*, 2018), a deeper investigation into the population biology and ecology of giant clams in the Gulf of Thailand is warranted.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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