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Assessment of spatiotemporal variability of giant clam populations (Cardiidae: *Tridacna*) from 11 years of monitoring at Koh Tao, Thailand

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ABSTRACT

Giant clams (Tridacninae) are an ecologically important species in coral reef habitats across the Indo-Pacific. Numerous examples of giant clam population declines of varying degrees of severity have been documented since the 1970s. These have been attributed to several reasons, such as overexploitation in regional fisheries and ornamental trades, extreme weather events and anomalous marine warming events leading to bleaching. In Thailand, this has led to extensive conservation efforts, such as legal protections and population restocking. Despite these strong measures, to date no long-term studies have been conducted on giant clam populations in Thai waters. We provide results from 11 years (2009–2019) of giant clam population monitoring, at Koh Tao, an island with a well-documented history of coral reef-associated stressors as well as conservation efforts. Surveys were conducted across two depth ranges at 18 reef sites around the island, revealing contrasting trends. Our findings indicate a significant population decline of *Tridacna crocea* from coral reefs in the 6–8 m depth range, from 1.41 (±0.47) individuals/100 m^2 in 2010 to 0.59 (±0.17) individuals/100 m^2 in 2019, with, however, no significant change in *T. squamosa* populations at this depth range. Data from the 3–5 m depth range indicate no significant change in the *T. crocea* population over the years, but a population increase of *T. squamosa* from 0.78 (±0.18) individuals/100 m^2 in 2009 to 2.07 (±0.38) individuals/100 m^2 in 2019. Abundance estimates from these sites indicate extensive heterogeneity in giant clam populations around the island, and highlight the importance of sufficient spatial resolution in identifying population trends.

INTRODUCTION

The importance of giant clams (Tridacninae) in coral reef ecosystems is increasingly being highlighted in recent research. Giant clams are large mixotrophic bivalves, utilizing endosymbiotic microalgae for photoautotrophic energy acquisition in combination with efficient, high-volume heterotrophic filter feeding to supplement their metabolic needs (Neo *et al.*, 2015). This combination has been associated with positive impacts on reef habitats. For example, species such as *Tridacna crocea* and *T. gigas* have been shown to be able to filter up to 8,144 and 28,121 l/h/hectare, respectively, feeding on dissolved and particulate nutrients (Pearson & Munro, 1991; Chantrapornsyl, Kittiwattanawong & Adulyanukosol, 1996). The mixotrophic nature of giant clams plays a vital role in their growth rates and their ability to achieve relatively large sizes (Klumpp, Bayne & Hawkins, 1992). This therefore may play a significant role in counteracting coral–macroalgal competition as driven by eutrophication, thus potentially having a positive impact on reef health (Neo *et al.*, 2015). Additionally, the reliance of giant clams on their microalgal symbionts is a feature shared by many scleractinian corals (Mies, 2019). The high-density release of intact microalgal cells in faecal pellets has been suggested to be available for uptake by nearby species such as corals and other clams (Neo *et al.*, 2015; Morishima *et al.*, 2019); however, further investigations are needed.

Giant clams are an important component to the fisheries of many countries (Davila *et al.*, 2017; Neo *et al.*, 2017). Unfortunately, overfishing and collection are leading threats for giant clams throughout their range, with clams being sold for their meat and their shells

(Munro, 1988; Planes *et al.*, 1993; Neo *et al.*, 2017). Recently, shells have also been found to be used in the production of imitation pearls (Zhou & Zhou, 2015), adding a further burden to threatened populations. Increasing temperatures and often the subsequent bleaching of giant clams have also been found to be a leading cause of decreases in population density throughout much of their range (Junchompoo *et al.*, 2012; Apte, Narayana & Dutta, 2019; Mies, 2019). Severe weather events such as typhoons have also been found to contribute to mass mortality, such as those recorded by Calumpong & Solis-Duran (1993), where 35% of over 20,000 restocked clams were lost due to typhoons in the Philippines. Furthermore, the negative impacts of tourism, while uncommon, have also been linked to reduction in clam populations, both directly due to collection (Planes *et al.*, 1993) and indirectly due to the effects of increased terrestrial development (Reef Check Malaysia, 2014; Ramah *et al.*, 2019).

The conservation status of clams is highly variable across their range (Gomez, 2015; Neo, 2020) with many areas being found to have legal support for conservation of giant clam species but lack sufficient enforcement of these policies. Furthermore, several regions throughout the Indo-Pacific have reported drastic declines in giant clam populations over the years (Othman, Goh & Todd, 2010). For example, Andréfouët *et al.* (2013) estimated a population decline of *T. maxima* by 83% in French Polynesia, which amounted to a loss of more than 18 ± 6 million individuals (mean estimate ± 95% confidence interval) between 2004 and 2012, believed to have been driven by highly variable temperatures. In Mauritius, surveys of *T. maxima* and *T. squamosa* populations between 1998 and 2016 revealed complete extirpation or declines of over 90% from numerous sites (Ramah *et al.*, 2019). Such declines have also been documented for several decades prior to the turn of the century, with Hirschberger (1980) recording drastic and continuous declines in populations of *T. gigas* and *T. derasa* due to overfishing. It was additionally reported that dead clam shells outnumbered living clams, acting as an indicator of fishing pressure, with living clams comprising as low as 40% of the total population.

Within the waters of Thailand, the majority of research on giant clams has been conducted along the coast of the Andaman Sea. Estimates of abundance from the southern islands have documented variable abundances of *T. crocea*, *T. maxima* and *T. squamosa*, with populations of *T. squamosa* being found to be the smallest and least connected (Chantrapornsyl *et al.*, 1996; Banchongmanee & Upanoi, 2000; Upanoi & Banchungmanee, 2000). Species-specific studies include growth rates of *T. squamosa* assessed *in situ* and *ex situ* (Adulyanukosol, 1997), and genetic indications of population divergence in *T. maxima* along the Andaman coast (Kittiwattanawong, 1997). Evidence has also been provided for historical populations of the threatened species *T. gigas* from the Andaman coast, with calls for reintroduction and conservation programmes focused on the species (Kittiwattanawong, 2001).

Comparatively little is known about the natural giant clam populations from the Gulf of Thailand (GOT), despite the location of the leading hatchery in Thailand being located within the GOT (Prachuap Khiri Khan province). Giant clams from this hatchery have been used in experiments in the Andaman Sea (Adulyanukosol, 1997) and in *ex situ* investigations on the biology of *T. squamosa* under varying levels of temperature, heavy metal load, sedimentation and light irradiance being conducted in the inner GOT (Tedengren, Blidberg & Elfwing, 2000; Elfwing *et al.*, 2001). Additionally, juvenile *T. squamosa* sourced from the same hatchery have been reared *in situ* at the islands of Koh Mun Nai and Koh Tao in the GOT, with survival rates strongly dependent on predation and hydrodynamic influences (Nugranad *et al.*, 1997; Charuchinda & Asawanghune, 2000; Scott, 2012a, 2013). Unsurprisingly, *T. squamosa* populations from the GOT have been found to be deeply divergent from the populations from the Andaman Sea (Kittiwattanawong, Nugranad & Srisawat, 2001). However, no comparisons have been made between giant clams in the GOT and the western Pacific. Limited data are available on the natural population abundances of giant clams within the GOT. Surveys at the island of Koh Mun Nai (Junchompoo *et al.*, 2012) documented abundances of 117 individuals of *T. crocea* per 200 m^2 and 12 individuals of *T. squamosa* per 200 m^2 (from historic restocking; Charuchinda & Asawanghune, 2000). Both species, however, were observed to suffer high mortality due to thermal bleaching of 60% and 67% for *T. crocea* and *T. squamosa*, respectively.

The most recent assessment of giant clam populations in Thailand was carried out by Chavanich *et al.* (2012), who compared the population change of various coral reef-associated vertebrate and invertebrate taxa between Koh Racha Yai (Andaman Sea) and Koh Tao (GOT) between 2007 and 2011. This study suggested a decline in giant clam numbers from Koh Tao, although it should be noted that only a single study site was surveyed from either island and giant clams were not differentiated by species. Koh Tao is an island of 19 km^2 hosting an extensive marine tourism industry and a high diversity of marine life (Scaps & Scott, 2014; Mehrotra & Scott, 2016). The island has, however, suffered from numerous stressors to its coral reef habitats, including widespread coral bleaching, disease and predation (Yeemin *et al.*, 1998; Chavanich *et al.*, 2012; Lamb *et al.*, 2014; Scott *et al.*, 2017b). The island has been supported by several years of marine conservation activities, including coral restoration and giant clam restocking programmes (Scott, 2013; Hein *et al.*, 2020). Giant clam restoration has involved transplantation of *T. squamosa* individuals into shallow coral reef areas at several sites around the island (the precise number of sites and surviving clams is unknown). Small-scale monitoring of transplants revealed high levels of mortality, believed to be due to natural predation; however, long-term monitoring of transplanted clams was not carried out.

As part of marine conservation activities at the island, regular monitoring of the abundances of invertebrate species has been carried out throughout the island for over a decade. However, population trends of important groups, such as giant clams, have not been assessed extensively till now. Here, we provide findings of a decade-long analysis of giant clam populations throughout Koh Tao and discuss trends in population structure.

MATERIAL AND METHODS

Temporal assessment

Belt transect (BT) surveys were conducted at coral reef habitats throughout the year between 2009 and 2019, following the protocol by Scott (2012b). Each BT was 5 m in width and 20 m in length, with the entire substrate within carefully checked for giant clams. Abundances of two species of giant clam were assessed at each site during BT surveys, *Tridacna crocea* and *T. squamosa*, with data for *T. crocea* abundances available only from 2010 onwards. Data from all sites were used to assess abundance of each species per year throughout the island. A total of 18 sites around Koh Tao were surveyed during this period at two depth ranges (Fig. 1), shallow (3–5 m) and deep (6–8 m).

Surveyed sites were divided into two categories, impermanent transect sites and permanent transect sites. Sites with a mean survey frequency of fewer than 12 BT surveys per year throughout the 11-year survey period were classified as impermanent sites for the purpose of our analyses. These sites, therefore, were used only to investigate general island-wide temporal variation across the survey period. The remaining six sites (Twins, Hin Wong Bay, Tanote Bay, Leuk Bay, Chalok Bay and Sai Nuan) were classified as permanent survey sites based on a mean survey frequency of greater than 12 BT surveys per year and were well dispersed around the coastline of the island. Permanent sites were used for site-specific temporal analysis of each species in addition to the overall island-wide

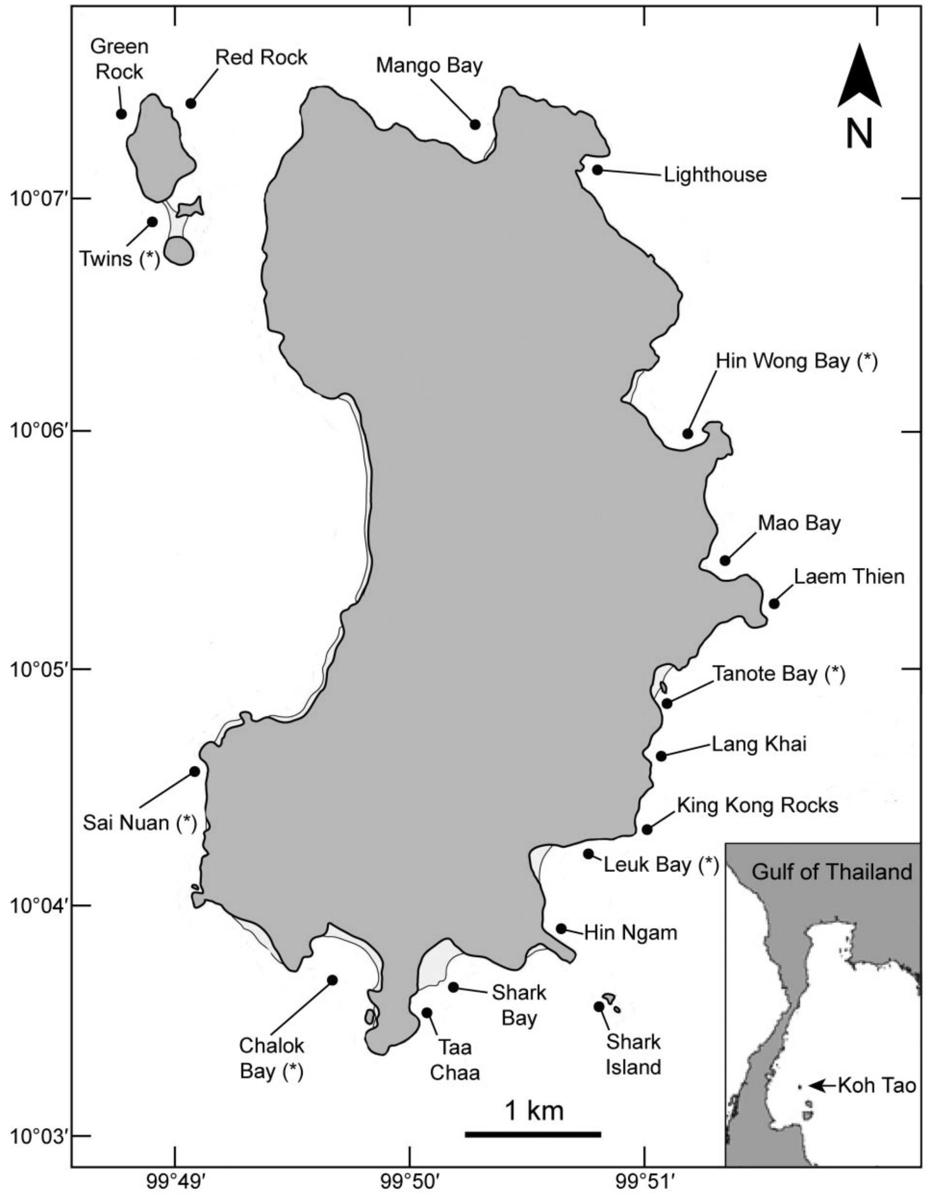

Figure 1. Sites surveyed at Koh Tao between 2009 and 2019. Sites used in site-specific analyses are designated with an asterisk.

investigation. Five of the six permanent sites were surveyed throughout the survey period, with a single site (Twins) being surveyed from 2012 onwards, resulting in a shorter dataset of 8 years as opposed to the 11 years for the remaining sites.

Spatial assessment

Variability in the abundance of each species at all sites was assessed via the same BT surveys, using only replicates from the year of most recent data collection. Of the 18 sites surveyed, data from 16 sites had been collected from the last year of data collection (2019), with the most recent data for 2 sites (Red Rock and Laem Thien) being from 2015 and 2016, respectively. As with temporal analysis, spatial analyses across sites assessed data from both species and depth ranges independently.

Statistical analyses

All analyses were run with RStudio v. 1.2.5033 (RStudio Team, 2015). Each survey consisted of multiple replications with the count data of clam abundance thus averaged based on these replications and used in the following analyses as 'clam abundance'. Temporal variation of clam abundance around the island was assessed using a linear mixed-effects model (LMM) on the log-transformed clam abundance of each species for each depth range, with year as a fixed effect and site as a random effect. Site-specific temporal variation was assessed using an LMM on the log-transformed clam abundance, with year as fixed and random effects. In both cases, year was set as a continuous variable to better describe the overall temporal trend.

RESULTS

Temporal variation

A total of 722 BT surveys were carried out throughout the survey period revealing two species of giant clam, *Tridacna squamosa* and *T. crocea*. Throughout the survey period, abundances of *T. squamosa* and *T. crocea* were found to vary considerably (Fig. 2). Overall, fewer

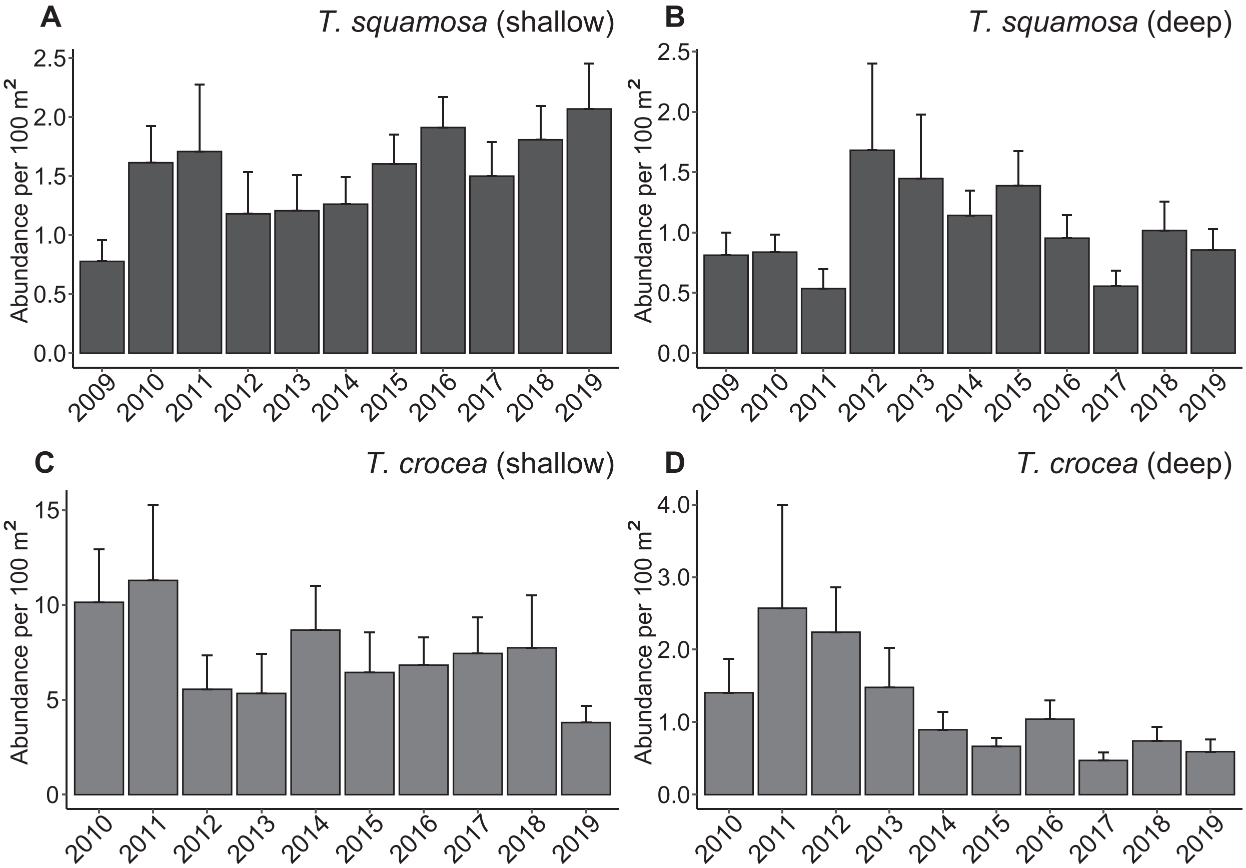

Figure 2. Annual mean abundance (mean number of individuals per 100 m^2) of *Tridacna squamosa* (**A** and **B**) and *T. crocea* (**C** and **D**) assessed in shallow (**A** and **C**) and deep (**B** and **D**) water at 18 sites around Koh Tao between 2009 and 2019 categorized by depth and species. Error bars represent standard error.

individuals of either species were recorded from the 6–8 m than the 3–5 m depth range. The lowest mean abundance of *T. squamosa* was found in 2011 with 0.54 (±0.16) individuals/100 m^2 and the lowest mean abundance of *T. crocea* was recorded in 2017 with 0.47 (±0.11) individuals/100 m^2, both at the 6–8 m depth range. The highest abundances for both species were 2.07 (±0.38) individuals/100 m^2 (*T. squamosa*) and 11.29 (±3.97) individuals/100 m^2 (*T. crocea*) in the 3–5 m depth range in 2019 and 2011, respectively. Analyses indicated that populations of *T. squamosa* in the shallow depth range increased significantly with time (LMM: estimate ± standard error = 0.035 ± 0.008, $P < 0.001$) from 0.78 (±0.18) individuals/100 m^2 in 2009 to 2.07 (±0.38) individuals/100 m^2 in 2019. Population change of *T. squamosa* at the 6–8 m depth range was nonsignificant (LMM: 0.004 ± 0.007, $P = 0.549$). Conversely, no significant difference was found in the 3–5 m populations of *T. crocea* (LMM: −0.008 ± 0.014, $P = 0.553$); however, a significant decline in population was recorded from the 6–8 m depth range (LMM: −0.025 ± 0.010, $P = 0.013$), from 1.41 (±0.47) individuals/100 m^2 in 2010 to 0.59 (±0.17) individuals/100 m^2 in 2019.

Of the 722 BT surveys, 490 were used to assess change over time for six sites. Site-specific analyses at the shallow depth range (3–5 m) revealed a significant increase (LMM: 0.093 ± 0.033, $P = 0.024$) in the mean abundance of *T. squamosa* at a single site (Tanote Bay) throughout the survey period from 0 (±0) individuals/100 m^2 in 2009 to 2 (±0) individuals/100 m^2 in 2019, with all other sites showing no significant difference for either species (Figs 3, 4). There was no significant change in the abundance of either species at the deeper range (6–8 m) at any of the six sites (see Supplementary Material Tables S1, S2).

Spatial variation

Assessment of the most recent clam abundances across the 16 sites revealed extensive variability between sites (Supplementary Material Table S1). At depths between 3 and 5 m, *T. squamosa* abundances varied from 0.17 (±0.11) individuals/100 m^2 (Chalok Bay) to 12 (±0) individuals/100 m^2 (Lang Khai). No individuals were recorded from the 6–8 m depth range at three sites and a maximum abundance of 4.17 (±0) individuals/100 m^2 was recorded in 2019 (Hin Ngam). Data from Red Rock in 2015 indicated a higher abundance of *T. squamosa* from the 6–8 m depth range, 4.5 (±2.5) individuals/100 m^2. However, more recent data are unavailable. No individuals of *T. crocea* were recorded from three sites in 2019, with a maximum abundance at the 3–5 m depth range of 22.25 (±9.38) individuals/100 m^2 (Tanote Bay) and a maximum abundance of 2.38 (±1.56) individuals/100 m^2 (Mango Bay) from the 6–8 m depth range.

DISCUSSION

These findings represent the first overview of trends in giant clam populations at Koh Tao. Intriguingly, the trends supported in our data suggest distinct and contrasting population changes

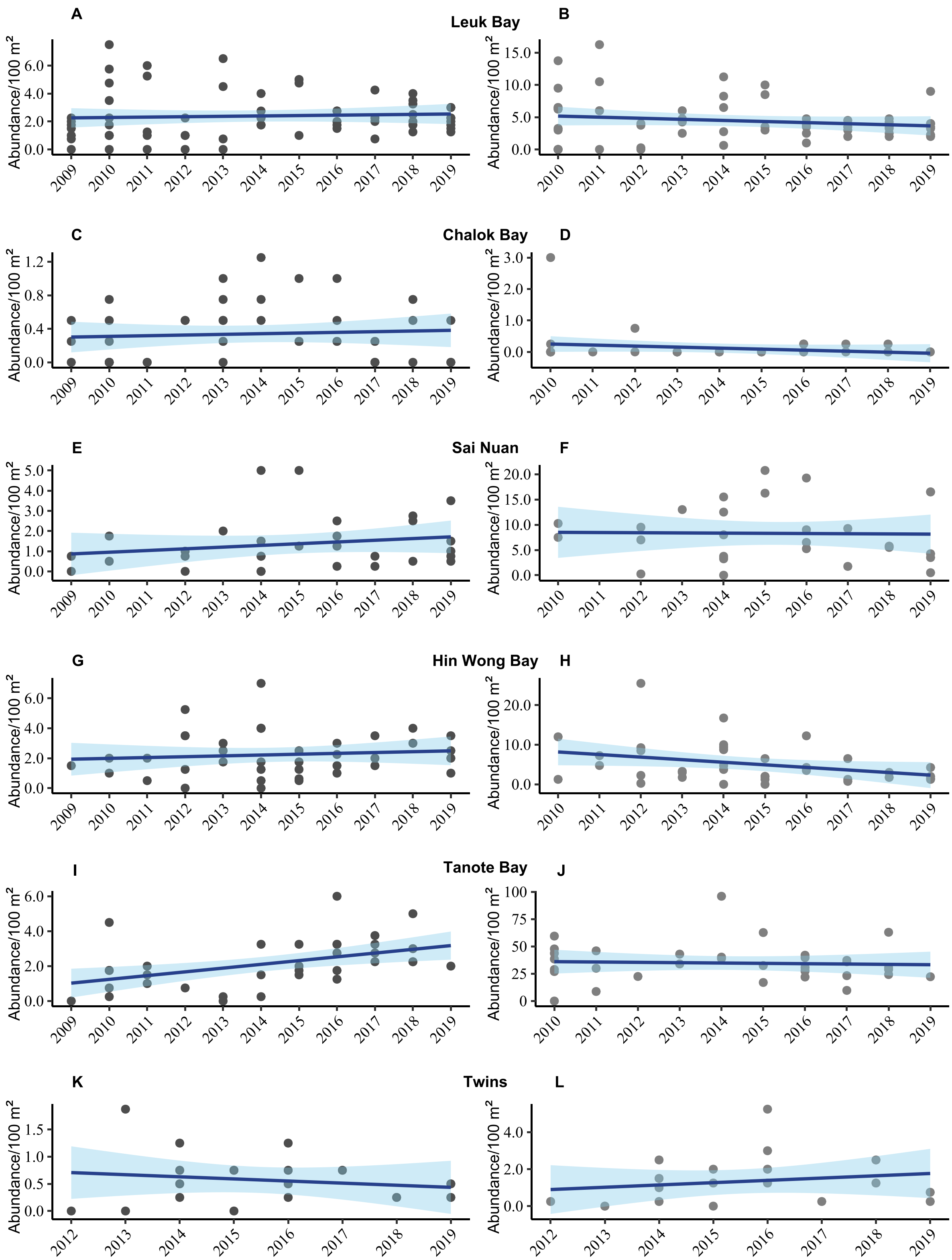

Figure 3. Mean annual abundance of *Tridacna squamosa* (**A**, **C**, **E**, **G**, **I** and **K**) and *T. crocea* (**B**, **D**, **F**, **H**, **J** and **L**) at six specific sites of Koh Tao over the past decade at shallow (3–5 m) fringing reefs. **A, B.** Leuk Bay. **C, D.** Chalok Bay. **E, F.** Sai Nuan. **G, H.** Hin Wong Bay. **I, J.** Tanote Bay. **K, L.** Twins. Estimated trends (from linear mixed-effects models) are displayed in solid lines with 95% confidence level intervals displayed in blue.

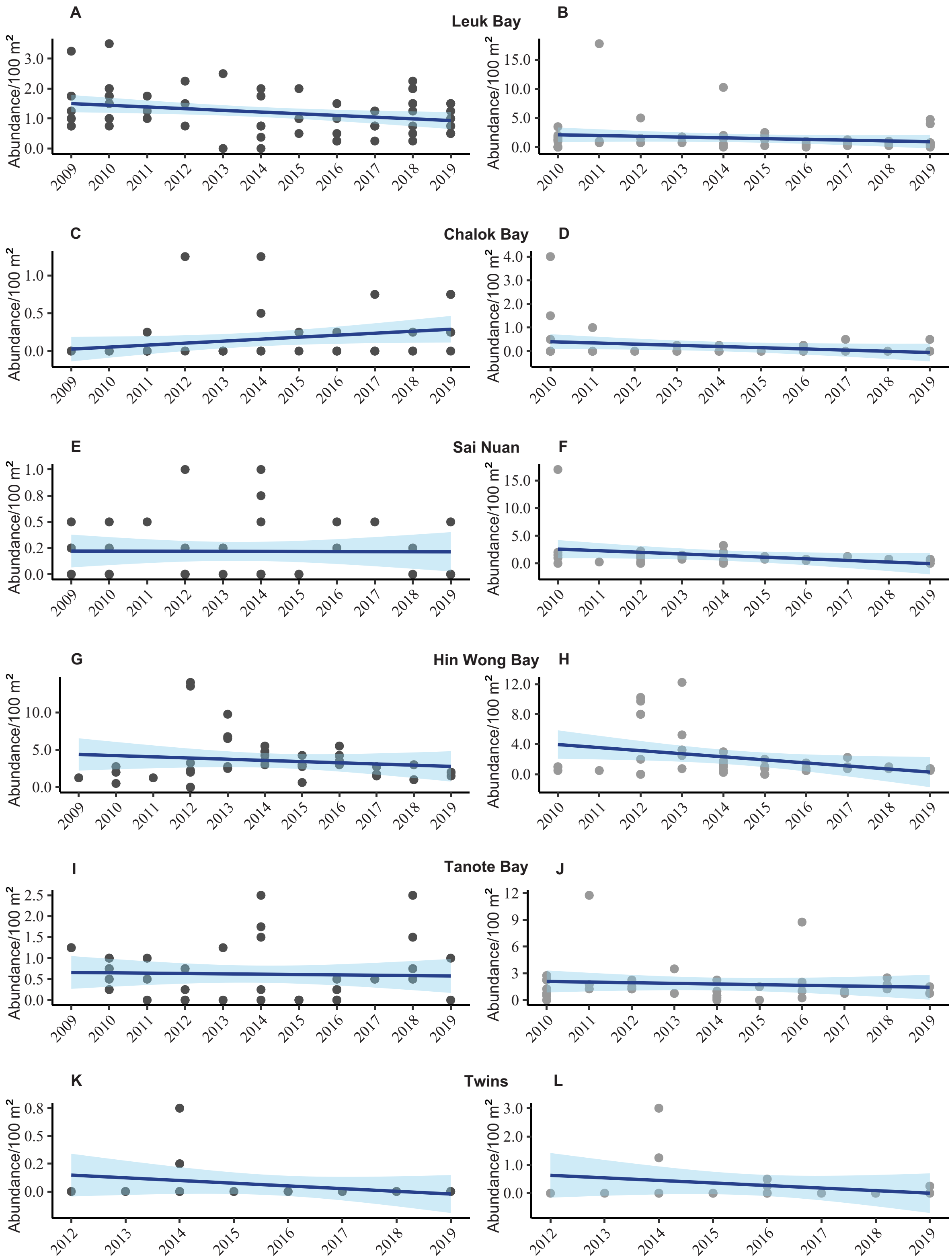

Figure 4. Mean annual abundance of *Tridacna squamosa* (**A, C, E, G, I** and **K**) and *T. crocea* (**B, D, F, H, J** and **L**) at six specific sites of Koh Tao over the past decade at deep (6–8 m) fringing reefs. **A, B.** Leuk Bay. **C, D.** Chalok Bay. **E, F.** Sai Nuan. **G, H.** Hin Wong Bay. **I, J.** Tanote Bay. **K, L.** Twins. Estimated trends (from linear mixed-effects models) are displayed in solid lines with 95% confidence level interval displayed in blue.

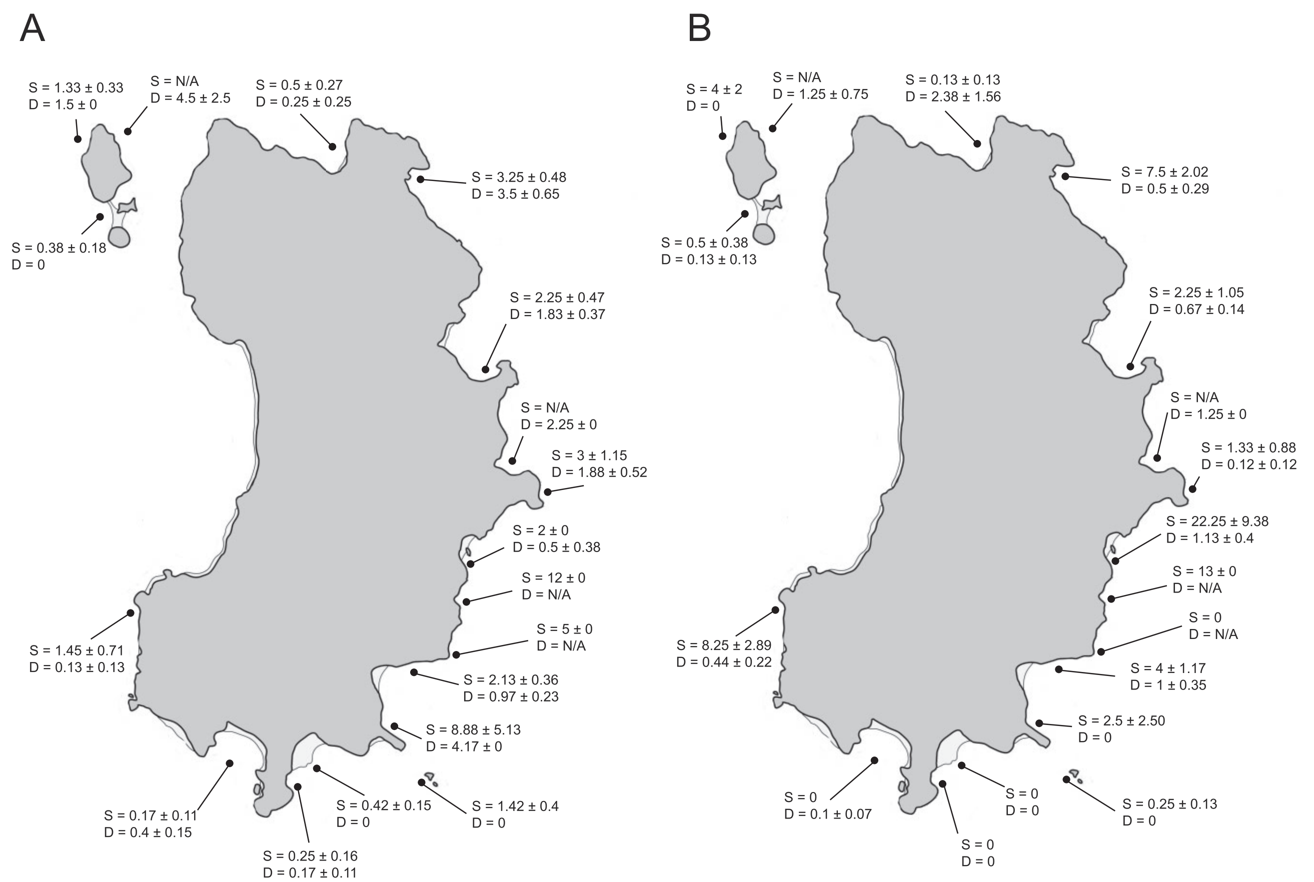

Figure 5. Distribution of *Tridacna squamosa* (**A**) and *T. crocea* (**B**) around Koh Tao showing mean abundance per species per 100 m^2 (including standard error) based on most recently available data. Data show shallow (S) and deep (D) surveys at 3–5 and 6–8 m depth ranges, respectively.

between *Tridacna* species at Koh Tao, a population growth of *Tridacna squamosa* in shallow water and decline of *T. crocea* in deeper water. Site-specific analyses, however, indicated only one significant change: an increase in shallow *T. squamosa* populations in Tanote Bay, agreeing with the island-wide trends observed. Spatial variability between sites was found to be dramatic for both species with multiple reefs showing a complete absence of individuals across both depth ranges. Interestingly, the lowest abundances of either species at either depth range were found to be along the southern reefs of the island, such as Chalok Ban Kao, Taa Chaa and Shark Bay. Even within specific sites, contrasts in population density were recorded, such as those in Mango Bay in the north, where the highest density of *T. crocea* was recorded in the 6–8 m depth range, whereas shallow water abundances were among the lowest. Giant clam populations at Mango Bay have historically been assessed (2007–2011) by Chavanich *et al.* (2012), who documented a decline in *Tridacna* spp. at the site before and after the 2010 coral bleaching event. The present findings, in contrast, suggest an increase in the abundance of *T. squamosa* and *T. crocea* across the island between 2010 and 2011, with the exception of *T. squamosa* from the 6–8 m depth range, which decreased. This highlights the importance of spatially comprehensive sampling to provide an accurate assessment of population from a given location. This is further supported by site-specific analyses documented here, which were largely unable to resolve the trends visible when each of the 6 sites were considered in isolation (Figs 3, 4) but were found when all 18 sites were analysed. This may partly be due to the unique history of each site, with many reefs along the southern part of the island suffering an almost complete loss of coral in the 1998 bleaching event (Yeemin, Sutthacheep & Pettongma, 2006) and Tanote Bay being inundated with 1.5–2 m of sediment following the construction of a reservoir in the overlying water shed in 2006–2007 (Larpnun, Scott & Surasawadi, 2011).

Stratification by depth was apparent in clam populations across the island, with most *T. crocea* being recorded from the shallower depth range, dropping steeply beyond 5 m. In contrast, *T. squamosa* populations, while also higher in the shallower depth range, remained well represented in the 6–8 m depth range. No individuals of either species were recorded deeper than 8 m at the island. We suggest that the overall constraint in depth is driven by the relatively high turbidity of the GOT, as a basin into which multiple large rivers flow. Meanwhile, the reduced abundance of individuals at the topographically shallower sites at the south of the island in comparison to the steeper reefs of the north may be attributed to thermally induced stressors recorded from these sites. This largely agrees with previous research, highlighting the influence of turbidity and irradiance in influencing phototrophic capacity in clams throughout the Indo-Pacific, with environmental conditions in many regions facilitating clam communities distinctly different from those at Koh Tao (Hardy and Hardy 1969; Guest *et al.*, 2008; Jantzen *et al.*, 2008). Thermal anomalies and subsequent bleaching have been linked to mortality in giant clams, as in scleractinian corals, in Thailand. Sangmanee & Sutthacheep (2010) and Junchompoo *et al.* (2012) have documented bleaching in giant clams (associated with the 2010 event) from the Andaman and Gulf coasts of Thailand, respectively. In the latter case, mortality of *T. squamosa* and *T. crocea* attributed to the bleaching was 67% and 60%, respectively. While widespread bleaching and mortality were recorded among corals at Koh Tao during 2010 (Chavanich *et al.*, 2012; Hoeksema, 2012;

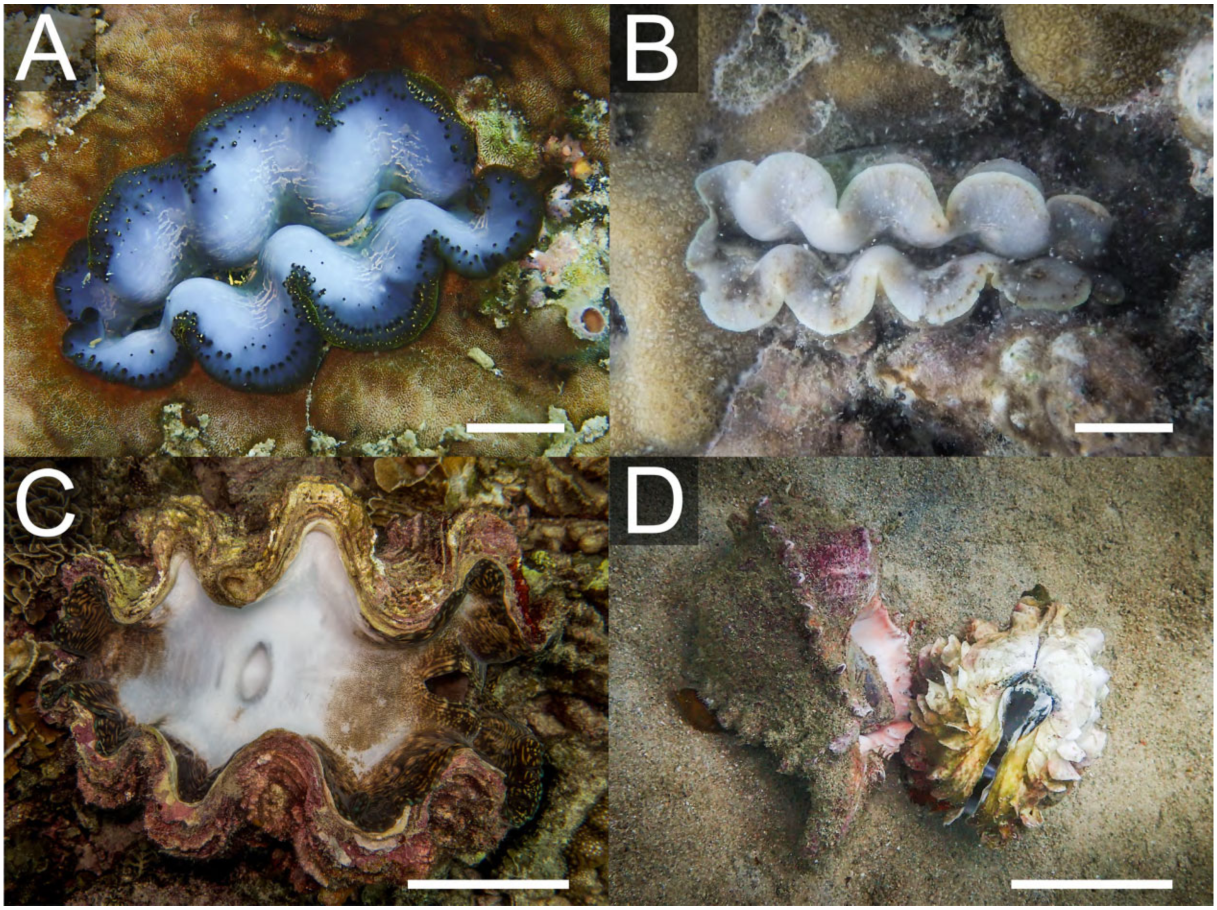

Figure 6. Indications of threats to giant clams at Koh Tao. **A.** Partial bleaching of *Tridacna crocea* in 2018. **B.** Complete bleaching of *T. crocea* in 2014. **C.** Partial bleaching of *T. squamosa* in 2016. **D.** Displaced individuals of *Chicoreus ramosus* and *T. squamosa*, left exposed in shallow sandy environments. Scale bars: **A** = 20 mm; **B** = 10 mm; **C** = 10 cm; **D** = 15 cm. Image credits: **A**, Elouise Haskin; **C**, Pau Urgell Plaza.

Scott *et al.*, 2017b), neither site-specific analyses nor island-wide analyses revealed dramatic mortality associated with bleaching at Koh Tao. It should be noted that while bleaching in giant clams was found to be common during the mass coral bleaching events of 2010, 2014 (Scott *et al.*, 2017a), 2016 and 2018, this was not quantified for this study (Fig. 5A–C). With the increasing regularity of mass coral bleaching events, further investigations are needed to determine whether these are responsible for the observed decline in population of *T. crocea* from deeper reefs.

A possible threat to giant clams at Koh Tao appears to be negative interactions (i.e. displacement and consumption) or removal of clams by locals and opportunistic tourists (Fig. 6). Observations of intrusive interactions between tourists and giant clams, while rare, were made during the surveys carried out. In addition, multiple observations of overturned or displaced individuals of *T. squamosa* were recorded, often still alive in groups, in the absence of active anthropogenic interaction (Fig. 5D). Education and awareness were increased through a community-based giant clam nursery project on the island starting in 2009. After pressure from a local community group, enforcement of the national regulations concerning the collection or consumption of giant clams under Thailand's Wild Animal Reservation and Protection Act of 1992 was increased, with the first local arrest made in 2014. The legal status and enforcement against collection, in combination with the present findings of a population increase in *T. squamosa* from shallow reefs, suggest that negative interactions by tourists are likely decreasing.

Throughout their Indo-Pacific range, giant clam abundances vary considerably by location and species, and in particular over time (Othman *et al.*, 2010). Recent mean population estimates for *T. squamosa* range from 0.53 individuals/100 m^2 in Mauritius (Ramah *et al.*, 2019), 0.13–1.3 individuals/100 m^2 in parts of Indonesia (Naguit, Tisera & Calumpong, 2012; Harahap, Yanuar & Ilham, 2018) to 0.06 individuals/100 m^2 at the Ryukyu Archipelago, Japan (Neo *et al.*, 2019). Historic abundances closer to the GOT include 2.52 individuals/100 m^2 from Tioman Island, Malaysia (Tan *et al.*, 1998) and 0.16 individuals/100 m^2 from Singapore (Guest *et al.*, 2008). While mean populations from 2019 at Koh Tao are relatively high, in comparison, at 2.78 individuals/100 m^2 (3–5 m) and 1.38 individuals/100 m^2 (6–8 m), the spatial variation across the island encompasses an extensive range in abundances. Similarly, mean population estimates for *T. crocea* vary drastically across its modern range from 10–2,500 individuals/100 m^2 in Vietnam (Selin & Latypov, 2011), 767 individuals/100 m^2 at Tubbataha, Philippines (Conales, Bundal & Dolorosa, 2015), 0–8.7 individuals/100 m^2 in parts of Indonesia (Naguit *et al.*, 2012; Harahap *et al.*, 2018) to 3.63 individuals/100 m^2 at the Ryukyu Archipelago, Japan (Neo *et al.*, 2019). Historic abundances closer to the GOT include 24.4 individuals/100 m^2 from Koh Lipe, Thailand (Chantrapornsyl *et al.*, 1996), 0.99 individuals/100 m^2 from Tioman Island, Malaysia (Tan *et al.*, 1998) and 0.07 individuals/100 m^2 from Singapore (Guest *et al.*, 2008). Mean abundances for Koh Tao in 2019 were found to be 4.12 individuals/100 m^2 (3–5 m) and 0.56 individuals/100 m^2 (6–8 m).

The variability in population distributions of *Tridacna* spp. across their range is determined by numerous influencing factors and threats that are just as variable. For example, large-scale coastal development and land reclamation projects have been found to be a dramatic threat to clams in Singapore (Guest *et al*., 2008), and habitat loss due to destructive fishing practices has been attributed to declines in Indonesia (Harahap *et al*., 2018). Overfishing and collection for the aquarium industry are documented from Mauritius to Japan and Indonesia (Naguit *et al*., 2012; Neo *et al*., 2019; Ramah *et al*., 2019), and indeed from Thailand (Chantrapornsyl *et al*., 1996). While there have not been many long-term monitoring efforts to assess giant clam populations in Thai waters, prior surveys have played a significant role in driving legal protection and conservation efforts for clams in Thailand (Chantrapornsyl *et al*., 1996; Boonprakob, Asawangkoon & Charunchinda, 2001).

Koh Tao has been a key site for *T. squamosa* restocking efforts (Nugranad *et al*., 1997; Scott, 2012a, 2013), which has continued at varying scales into the present, with more than 10,000 juvenile clams being brought to the island over the last 15 years. Unfortunately, little quantifiable information is available on the site-specific population change of restocking efforts as tracking and long-term monitoring of the clams have proven difficult. Most of the stocking efforts have been carried out by untrained volunteers, and no efforts to tag or track transplanted clams have been taken, except in more recent efforts conducted by the authors. However, due to a lack of monitoring data, it is unclear whether the community-based clam transplantation projects were carried out in the vicinity of our BT surveys. Nonetheless, this may account for, or contribute towards, the observed population growth in some shallow reefs. We note, however, that transplantation is believed to have been carried out only at a small number of sites. Additionally, anecdotal evidence and unpublished survey data from these sites indicate high levels of post-transplantation mortality. Future studies could verify this with molecular techniques (i.e. microsatellites), as all restocked clams have been sourced from a single hatchery in Prachuap Khiri Khan province, GOT. Giant clam restocking efforts have been carried out at several locations, utilizing a variety of species (Neo *et al*., 2017). Population recovery of giant clams may be limited due to anthropogenic threats or due to environmental constraints limiting dispersal between source and sink populations, such as those in Singapore (Neo *et al*., 2013). In such cases, restocking programmes may be the only viable option to promote population recovery (Neo *et al*., 2013). It is therefore important that variables influencing population dispersal potential and key source and sink sites be identified within the GOT to maximize the impact of conservation measures.

Closer investigations and continued monitoring are required to assess the cause and prognosis of *T. crocea* populations at Koh Tao, which show signs of significant decline in deeper reefs. The legal protections afforded to reef habitats around Koh Tao specifically and to giant clams in Thai waters have likely reduced active anthropogenic threats to giant clams at the island and, combined with the nursery and transplantation programmes, may be responsible for a population increase of *T. squamosa* in shallow reefs. With growing evidence for dramatic changes to the coral reefs of the island (Scott *et al*., 2017a, b), the ecological benefit of giant clams in reef habitats (Neo *et al*., 2015) is likely of greater importance now than ever before. The GOT has remained underrepresented in investigations regarding population connectivity and dispersal (Hui *et al*., 2016; Keyse *et al*., 2018) for *Tridacna*. As one of the geologically youngest regions in the west Pacific (Voris, 2000; Keyse *et al*., 2018), a deeper investigation into population biology and ecology of giant clams in the GOT is warranted.

SUPPLEMENTARY MATERIAL

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

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