

University of Groningen

Variation in epibiont communities among restocked giant clam species (Cardiidae: Tridacninae) and across different habitat types

de Guzman, Ian Joseph A.; Cabaitan, Patrick C.; Hoeksema, Bert W.; Sayco, Sherry Lyn G.; Conaco, Cecilia

Published in:
Marine Biodiversity

DOI:
[10.1007/s12526-023-01363-y](https://doi.org/10.1007/s12526-023-01363-y)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2023

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

de Guzman, I. J. A., Cabaitan, P. C., Hoeksema, B. W., Sayco, S. L. G., & Conaco, C. (2023). Variation in epibiont communities among restocked giant clam species (Cardiidae: Tridacninae) and across different habitat types. *Marine Biodiversity*, 53, Article 51. <https://doi.org/10.1007/s12526-023-01363-y>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.



Variation in epibiont communities among restocked giant clam species (Cardiidae: Tridacninae) and across different habitat types

Ian Joseph A. de Guzman¹ · Patrick C. Cabaitan¹ · Bert W. Hoeksema^{2,3} · Sherry Lyn G. Sayco¹ · Cecilia Conaco¹

Received: 18 February 2021 / Revised: 2 May 2023 / Accepted: 16 May 2023

© The Author(s), under exclusive licence to Senckenberg Gesellschaft für Naturforschung 2023

Abstract

Giant clam shells provide a solid substrate for various species of epibionts. Yet, it is not well known how epibiont communities vary among populations of different giant clam species and in giant clams restocked in different habitat types. Here, we examined differences in the epibiont communities of three species of giant clams with different shell morphology (*Tridacna gigas*, *Tridacna derasa*, and *Hippopus hippopus*), and characterized the epibiont communities on *T. gigas* from three different habitat types (sandy reef flat, seagrass bed, and coral reef). *Tridacna gigas* had higher species richness, abundance, and cover of epibionts compared to the other two species. *Tridacna gigas* in coral reef habitat also displayed higher species richness and cover of sessile epibionts, while the same species in the sandy reef flat had higher species richness and abundance of mobile epibionts. Epibiont communities were more variable across habitat types than among different giant clam species restocked in a similar area. Differences in abundance of *Trochus* sp., *Pyramidella* sp., and crustose coralline algae contributed to the variability in epibiont communities among the giant clam species and across habitats. A few taxa were observed only on specific giant clam species and sites. For instance, *Diadema* sp. and *Echinometra* sp. were found only on *T. gigas*, and *Diadema* sp. was present only in the sandy reef flat. Both the complexity of the giant clam shells and habitat type contribute to differences in associated epibiont communities. This further emphasizes the ecological importance of giant clams as habitats for other invertebrates.

Keywords Coral reefs · *Hippopus* · Philippines · Seagrass · *Tridacna*

Introduction

In marine ecosystems, any free space or substrate, such as the surfaces of rocks and living or dead corals and shells, will soon be colonized by an array of epibionts, including invertebrates (mobile and sessile) and algae (Lescinsky 2001; Wahl 2008). Epibionts can have variable impacts on host biology. For example, barnacles attached to the shells of periwinkle snails (Littorinidae) or sea turtles act as ballast to their hosts, increasing weight, water drag, and energy

required for movement (Warner 1997; Fuller et al. 2010). Tubeworms of the families Serpulidae and Sabellidae are known to cause damage to the polyps of their host corals (Hoeksema et al. 2019b, 2022a), while excavating animals, such as boring sponges and boring mussels destroy the interior parts of coral skeletons (de Bakker et al. 2018; Hoeksema et al. 2022b). Conversely, algae on turban snails in intertidal habitats protect the organism against thermal stress during air exposure at low tide (Kagawa and Chiba 2018), while small symbiotic hydroids protect their host corals against predation and diseases (Montano et al. 2017). Similarly, the sponge and hydroid epibionts of the octocoral *Bebryce* cf. *grandivalyx* protect the octocoral and each other from multiple sources of predation (Maggioni et al. 2020). Epibionts may also influence relationships among organisms (e.g., predator–prey). For example, the presence of barnacles on mussels decreases their palatability to predatory asteroids (Gutiérrez and Palomo 2016) and the epiphytes on oysters provide camouflage that decreases predation pressure (Laudien and Wahl 1999). On the other hand, fouling organisms such as bryozoans or encrusting sponges on red algae (*Cryptonemia seminervis*) attract herbivores that otherwise would

Communicated by C. Chen

✉ Patrick C. Cabaitan
pcabaitan@msi.upd.edu.ph

¹ The Marine Science Institute, University of the Philippines, Diliman, 1101 Quezon City, Philippines

² Naturalis Biodiversity Center, P.O. Box 9517, 2300 Leiden, The Netherlands

³ Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands

not feed on the seaweed (da Gama et al. 2008). Epibionts may also increase the structural complexity of their benthic hosts. Examples of this include Christmas tree worms that form tubes in coral, which can be occupied by hermit crabs and cryptobenthic fishes after the worms die (Schuhmacher 1977; Böhm and Hoeksema 2017; Hoeksema et al. 2019a).

Several factors are known to influence epibiont composition. These include substrate-specific properties, such as surface roughness, complexity, and wettability (Berntsson et al. 2000; Qian et al. 2000; Scardino et al. 2008). Environmental parameters such as irradiation (Maida et al. 1994), hydrodynamics (Mullineaux and Butman 1991; Koehl 2007), and eutrophication (Stuhldreier et al. 2015; van der Schoot and Hoeksema 2022), also affect epibiont associations and determine regional and seasonal variability in the quantity and composition of colonizers (Chiavelli et al. 1993; Davis and White 1994; Reiss et al. 2003; Fernandez-Leborans and Gabilondo 2006). Moreover, secreted chemical cues and anti-fouling compounds (Wahl 2008) will influence recruitment of certain organisms. In a limited space, interspecific interactions play an important role in defining the overall epibiont assemblage attached to a host (Wahl and Mark 1999). Interspecific competition and microhabitat preferences of different epibionts can result in a certain degree of space partitioning in benthic hosts (Korringa 1951; Gutt and Schickan 1998; Hoeksema and Fransen 2011; Hoeksema et al. 2012, 2017).

Organisms like giant clams which possess large and complex calcium carbonate shells, support reef biodiversity by providing substrate and microhabitat for associated fauna (Mekawy 2014; Vicentuan et al. 2014; Neo et al. 2015; van

der Schoot et al. 2016; de Gier and Becker 2020; Fig. 1). Giant clams (Tridacninae) are the largest bivalves, with 12 extant species (Neo et al. 2017; Fauvelot et al. 2020; Tan et al. 2021), eight of which are found in Philippine waters (Junio et al. 1989; Gomez and Mingo-Licuanan 2006; Lizano and Santos 2014; Ecube et al. 2019). However, populations of giant clams throughout much of the Indo-Pacific, specifically the Philippines, have been depleted to the point where they have limited potential for replenishment (Lucas 1994; Lyons et al. 2018; Neo et al. 2019). This is especially alarming in the context of climate change, with stress caused by rising seawater temperature and ocean acidification exhibiting negative effects on the health and survival of juvenile, as well as adult, giant clams (Adessi 2001; Andréfouët et al. 2013; Watson et al. 2012; Dubousquet et al. 2016; Enricuso et al. 2019).

To help initiate recovery of declining giant clam populations, restocking of individuals reared in hatcheries is being conducted. The University of the Philippines Marine Science Institute (UP MSI) has been at the forefront of such conservation efforts in the Philippines since the early 1980s. To date, thousands of individuals of the giant clam, *Tridacna gigas*, as well as *T. derasa*, *T. squamosa*, *T. crocea*, *T. maxima*, and *Hippopus hippopus*, have been restocked at more than 40 sites all over the archipelago, with some reefs already showing signs of natural recruitment from restocked clams (Gomez and Mingo-Licuanan 2006; Cabaitan and Conaco 2017). Reintroduction of giant clams is expected to bring ecosystem benefits, such as the enhancement of biodiversity through provision of microhabitats for reef organisms and food for predators and scavengers (Cabaitan et al. 2008; Neo et al. 2015).

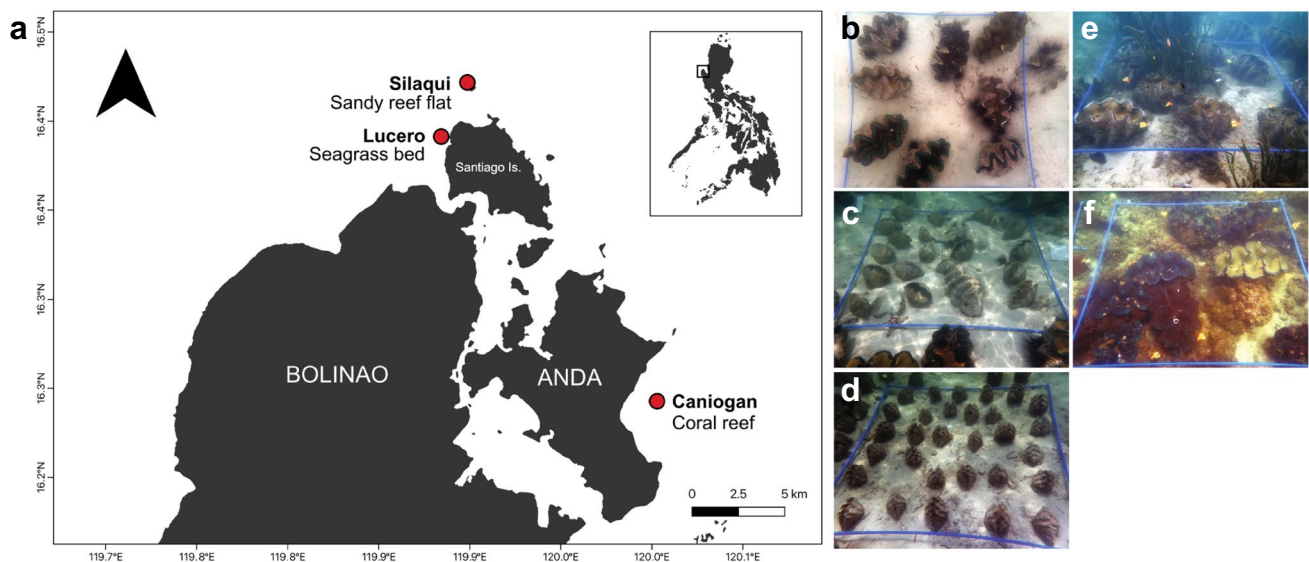


Fig. 1 a Location of study sites, Silaqui (sandy reef flat), Lucero (seagrass bed), and Caniogan (coral reef) in Pangasinan, northwestern Philippines (inset). Hatchery-bred giant clams, b *Tridacna gigas*, c *Tridacna*

derasa, and d *Hippopus hippopus*, restocked in the Silaqui giant clam ocean nursery are arranged in well-spaced clusters according to species. *Tridacna gigas* individuals restocked in e Lucero and f Caniogan

Giant clams have been observed to host a wide variety of epibionts on their shells (Vicentuan et al. 2014; Neo et al. 2015; van der Schoot et al. 2016). The fluted giant clam, *Tridacna squamosa*, has been shown to be colonized by a diverse community of epibionts comprising at least 49 species belonging to a minimum of 36 families, including macroalgae, ascidians, bivalves, ophiuroids, crustaceans, chitons, gastropods, polychaetes, and sponges (Vicentuan et al. 2014). The shell of *T. squamosa* is characterized by large elaborate scales (scutes) on its surface (Neo and Todd 2011; Andréfouët et al. 2014), which make it an ideal microhabitat for epibionts. Whether other giant clams, which differ in their shell morphology and size, will recruit a similarly diverse community of epibionts remains unknown.

In this study, we aimed to investigate the epibiont communities associated with three species of giant clams with varying shell size and morphology. The species we compared are the true giant clam, *Tridacna gigas*, which has 4–5 vertical folded ribs with triangular inward projections at the upper margins of its shell and can grow up to 120 cm in length; the smooth giant clam, *T. derasa*, which has a smooth shell with 6–7 vertical folds and grows up to 60 cm; and the strawberry clam, *H. hippopus*, which has a thick, heavy shell with triangular, horse-hoof like valves and can grow up to 40 cm (Braley 1988; Neo et al. 2017). We also examined site-specific differences in the epibionts associated with *T. gigas* translocated to a coral reef, a sandy reef flat, and a seagrass area, to approximate the typical habitats at restocking sites around the country. We hypothesize that giant clam species with variable shell morphology would host contrasting epibiont communities, and that giant clams in different habitats would have variable epibiont communities.

Materials and methods

Study site and organisms

Comparison of epibiont communities among three giant clam species

This study was conducted at the Silaqui Giant Clam Ocean Nursery on Silaqui Island, Bolinao, Pangasinan, in north-western Philippines (Fig. 1a). It is situated on a reef flat characterized by a sandy and rubble bottom in a depth range of 3–5 m. The nursery was established in the early 1980s and currently houses more than 25,000 hatchery-bred giant clams comprised of six species. Three groups or aggregations of *Tridacna gigas* (shell length 50–60 cm), *T. derasa* (30–40 cm), and *H. hippopus* (20–30 cm) individuals were identified within the ocean nursery. These giant clam species were chosen because of distinct differences in their shell sizes and morphologies, abundance in the ocean nursery,

and presence of suitable aggregations (at least 30 cm apart between clam individuals). Plots containing each group of giant clams were delineated with 2 × 2 m² PVC frames (Fig. 1b–d) (n = 3 plots per species). The coordinates and depth of each plot were recorded, and temperature and light intensity were monitored using submersible data loggers (Onset HOBO UA-002–64). The number of clam individuals per plot varied among the three giant clam species. The plots for *T. gigas* and *T. derasa* contained fewer individuals, while the plots for *H. hippopus* had more individuals. However, the overall shell surface area within each plot was comparable among the three species (Table 1).

Comparison of epibiont communities on *T. gigas* across different habitats

To explore the effect of site on giant clam epibiont communities, we selected three groups of *T. gigas* individuals (length 50–60 cm) restocked at three sites within the Bolinao-Anda Reef Complex (Silaqui Giant Clam Ocean Nursery, Lucero, and Caniogan Marine Sanctuary) with distinct habitat characteristics (Fig. 1a). Silaqui has been described above. Lucero is a seagrass bed with a depth range of 3–5 m with giant clams restocked in the years 1990–2006 (Gomez and Mingoa-Licuanan 2006). The Caniogan Marine Sanctuary is a coral reef with a depth range of 3–5 m and was established as a restocking site around 2002–2004 (Gomez and Mingoa-Licuanan 2006). We only used adult *T. gigas* for this study as there were not enough individuals of the other species for comparison. Plots containing each group of clams were delineated with 2 × 2 m² PVC frames for monitoring (Fig. 1b, e, f) (n = 3 plots per site). The coordinates and depth of each plot were recorded and temperature and light intensity were monitored using submersible data loggers (Onset HOBO UA-002–64). The number and sizes of *T. gigas* individuals were comparable among the three study sites (Table 2).

Epibiont community sampling

The shells of giant clam individuals within each plot were photographed on 2 sides with a size reference scale. The shell length of each giant clam and the approximate total surface area of the valves, based on the 2D planar view of the shell,

Table 1 Number of giant clam individuals per plot and the mean shell surface area of the giant clams in all plots per species

Species	Plot 1	Plot 2	Plot 3	Total	Mean shell surface area
<i>Tridacna gigas</i>	8	8	8	24	18,538 ± 558 cm ²
<i>Tridacna derasa</i>	25	37	17	79	17,475 ± 2,949 cm ²
<i>Hippopus hippopus</i>	31	30	23	84	14,857 ± 1,567 cm ²

Table 2 Number of *T. gigas* individuals per plot and the mean shell surface area of the giant clams in all plots per site

Site	Habitat	Plot 1	Plot 2	Plot 3	Total	Mean shell surface area
Silaqui	Sandy reef flat	8	8	8	24	18,537 ± 557 cm ²
Lucero	Seagrass bed	8	8	8	24	17,102 ± 783 cm ²
Caniogan	Coral reef	6	8	8	22	18,087 ± 1427 cm ²

were estimated from the photographs using the software ImageJ (Schneider et al. 2012). This method of estimation does not account for the curvature of the shells and therefore the data obtained would be an underestimate of shell size. To determine species richness, all visible epibionts (diameter > 3 mm) on each giant clam were photographed individually and identified to the highest taxonomic resolution (Fig. 2). Epibiont taxa were then classified as mobile (gastropods, echinoderms, crustaceans, bivalves, and foraminifera) or sessile (algae, crustose coralline algae, bivalves, hydroids, corals, sponges, and ascidians). Abundance of mobile epibionts was determined by counting individuals of each species, while abundance of sessile epibionts was determined by measuring the amount of shell surface covered by each organism (in cm²), based on the photographs analyzed on ImageJ. The same method of epibiont enumeration was used for the inter-species and inter-habitat studies.

Data analysis

To account for differences in giant clam shell sizes, the actual values of species richness, counts, and cover of epibionts were divided by the estimated shell surface area of individual clams, and then multiplied by 1000 cm² to obtain normalized values. We use 1000 cm² to standardize surface area as this value approximates the average shell surface area across the 3 species (*Hippopus hippopus*: 530 cm², *Tridacna derasa*: 664 cm², *Tridacna gigas*: 2335 cm²; average for the three species: 1176 cm²). The normalized data was analyzed using the following statistical tests to compare the mobile and sessile epibionts for both inter-species and inter-habitat studies: (1) Shapiro–Wilk

Test and Levene’s Test to assess the normality and heteroscedasticity of the data, (2) Kruskal–Wallis tests and Dunn’s Test were used to determine significant pairwise differences in species richness, abundance, and surface cover of epibionts between giant clam species and between different habitat types, (3) Non-Metric Multidimensional Scaling (nMDS) was used to visualize the similarity of epibiont community composition among the giant clam species and between habitats, (4) ANOSIM (Analysis of Similarity) was used to determine if there is a significant difference among the epibiont communities, (5) Pairwise ANOSIM was used to further compare significant difference of the epibiont communities between giant clam species and habitat types, and (6) SIMPER (Similarity percentage) was used to identify epibiont taxa that distinguish the community associated with each giant clam species or habitat. Kruskal–Wallis tests were conducted on R statistical software (R Core Team 2018), whereas all the multivariate tests were done on PRIMER (Plymouth Routines In Multivariate Ecological Research; Clarke and Gorley 2001).

Results

Species richness and abundance of epibionts

Inter-species variability

Species richness and abundance of epibionts, which was expressed as counts of mobile organisms or cover of sessile organisms, were significantly variable among giant clam species (Fig. 3; Supplementary Table 1). Specifically,

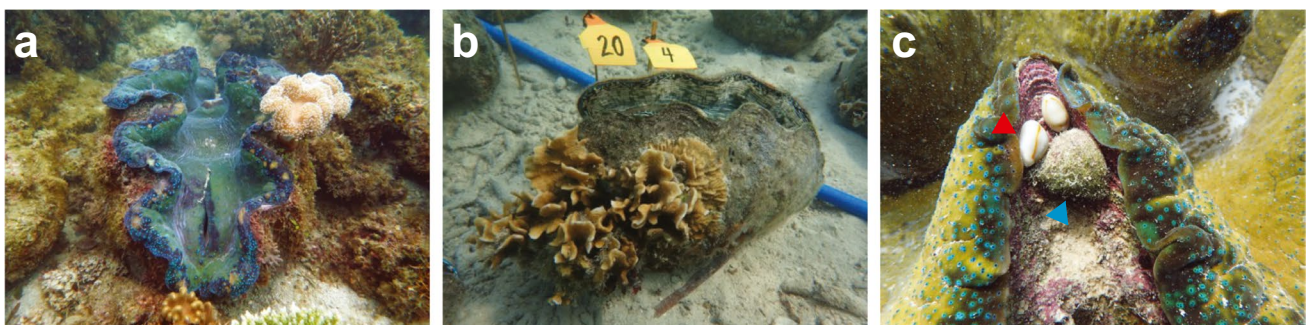


Fig. 2 Giant clams with epibionts attached to their calcium carbonate shells. **a** *Sarcophyton* sp. and macroalgae attached to *Tridacna gigas*, **b** *Pavona* cf. *cactus* attached to the shell of *T. derasa*, and **c**

marine snails, *Monetaria annulus* (red arrowhead) and *Trochus* sp. (blue arrowhead), attached to *T. gigas*

species richness and abundance of mobile epibionts (Fig. 3a, c), as well as surface cover of sessile epibionts (Fig. 3d), were significantly higher in *T. gigas* than in the other giant clam species (Supplementary Table 2). On the other hand, species richness of sessile epibionts was significantly higher in *H. hippopus* than in *T. gigas* (Fig. 3b).

Inter-site variability

Species richness and abundance of epibionts also varied significantly across sites (Fig. 3; Supplementary Table 1). Species richness of mobile epibionts was significantly higher in the sandy reef flat and seagrass bed than in the coral reef site (Fig. 3e; Supplementary Table 3), whereas the opposite pattern was observed for species richness of sessile epibionts (Fig. 3f). Abundance of mobile epibionts was significantly higher in the sandy reef flat compared to the seagrass bed and coral reef (Fig. 3g). Surface cover of sessile epibionts was highest in the coral reef site but was not significantly different from the surface cover of sessile epibionts in the sandy reef flat (Fig. 3h).

Epibiont community composition

Community composition of mobile and sessile epibionts among giant clam species, and of mobile epibionts among

sites, were not distinctly different (Global $R < 0.2$; Fig. 4a, b, c). In contrast, sessile epibiont community composition showed greater difference across sites (Global $R = 0.530$; Fig. 4d). Pairwise tests showed that these differences were most apparent between the coral reef site in comparison to the other habitats (Global $R > 0.5$; Table 3).

Inter-species variability

Gastropods and corals were the most common epibionts found on all giant clam species (Fig. 5a, b). Gastropods, echinoderms (sea urchins and sea cucumbers), and crustaceans were significantly more abundant on *T. gigas* clams than on the other clam species (Fig. 5a; Supplementary Table 4 and 5). Sponges were also abundant on *T. gigas* and *T. derasa* (Fig. 5b).

Epibiont members that contributed most to similarities amongst giant clam species were identified using SIMPER tests (Table 4; Supplementary Table 7). About 90% of the entire epibiont community on different giant clam species were dominated by one to six taxa of mobile or sessile organisms. Some of the epibiont taxa observed in one giant clam species were also observed in the others, but at varying abundance, which explains why the clustering of samples in the MDS plots is not so apparent. *Trochus* sp. and *Pyramidella* sp. were among the most dominant mobile epibiont

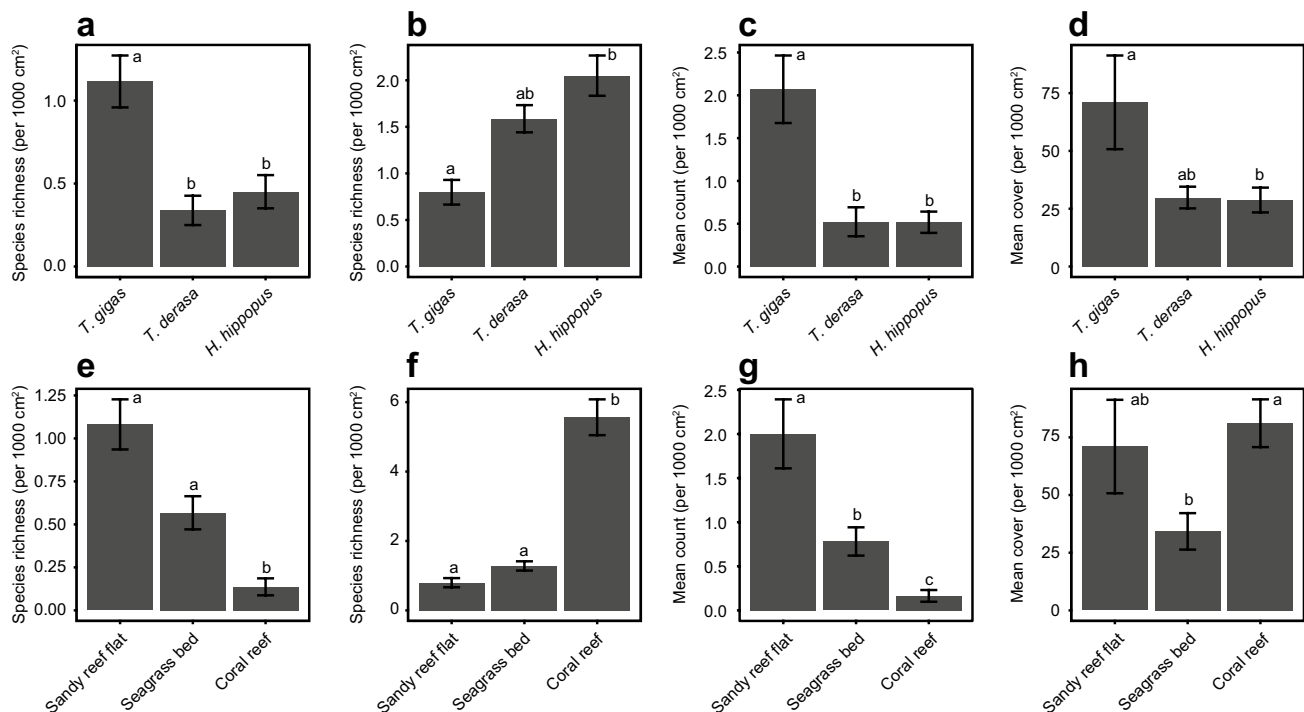
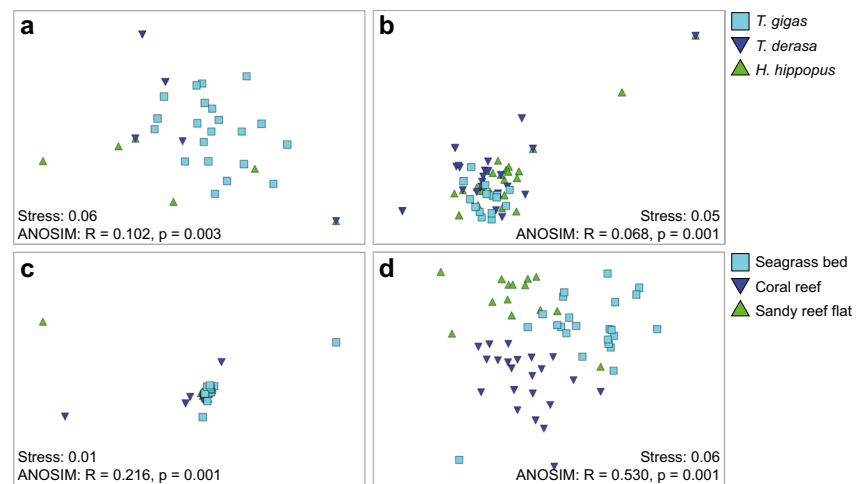


Fig. 3 Species richness (mean \pm standard error) of **a** mobile and **b** sessile epibionts, and abundance of **c** mobile and **d** sessile epibionts on the shells of different giant clam species. Species richness of **e** mobile and **f** sessile epibionts, and abundance of **g** mobile and **h** ses-

sile epibionts on the shells of *T. gigas* restocked in different habitats. Similar letters above the bars indicate that values of species richness or abundance do not vary between samples based on the results of the Kruskal–Wallis tests

Fig. 4 Non-metric multidimensional scaling (MDS) plots comparing the community composition of **a** mobile and **b** sessile epibionts on *Tridacna gigas* (square), *T. derasa* (inverted triangle), and *Hippopus hippopus* (triangle); and community composition of **c** mobile and **d** sessile epibionts on *Tridacna gigas* restocked in a seagrass bed (square), coral reef (inverted triangle), and sandy reef flat (triangle)



taxa associated with the three giant clam species. On the other hand, crustose coralline algae was the dominant sessile epibiont on *T. gigas*, while the other two giant clam species were dominated by *Porites* sp.

Epibiont taxa that contributed to the differences in community composition between two giant clam species were also identified using SIMPER pairwise tests (Table 4; Supplementary Table 7). Mobile epibionts such as *Trochus* sp., *Pyramidella* sp., *Vexillum* sp., *Diadema* sp., and hermit crab consistently provided a greater percentage contribution when *T. gigas* was compared with *H. hippopus* and *T. derasa*. Sessile epibionts such as *Porites* sp., *Hymeniacidon* sp., crustose coralline algae, *Pavona* sp., and *Haliclona* sp. consistently provided a greater percentage contribution when *H. hippopus* was compared with *T. gigas* and *T. derasa*.

Inter-site variability

Gastropods, coral, crustose coralline algae, and sponges were the most common epibionts observed in giant clams at the three sites (Fig. 5c, d). Gastropods and echinoderms were significantly more abundant in the sandy reef flat and seagrass

bed compared to the coral reef site (Fig. 5c; Supplementary Table 4 and 6). Crustose coralline algae were significantly more abundant in the sandy reef flat compared to the seagrass bed (Fig. 5d). On the other hand, sponge cover was higher in the seagrass bed and coral reef than the sandy reef flat. Algae and ascidians were found at greater abundance in the coral reef site.

Epibiont members that contributed most to similarities amongst sites were identified using SIMPER tests (Table 5; Supplementary Table 8). About 90% of the entire epibiont community on *T. gigas* giant clams at different sites were dominated by one to six taxa of mobile or sessile organisms. *Trochus* sp. and *Pyramidella* sp. were the most dominant mobile epibionts on clams from the sandy reef flat and seagrass bed. Foraminiferans comprised a major proportion of the mobile epibiont community on clams from the coral reef. Crustose coralline algae was the dominant sessile epibiont in the sandy reef flat and *Padina* and *Hymeniacidon* in the seagrass bed. In contrast, giant clams in the coral reef had a greater diversity of contributing sessile taxa.

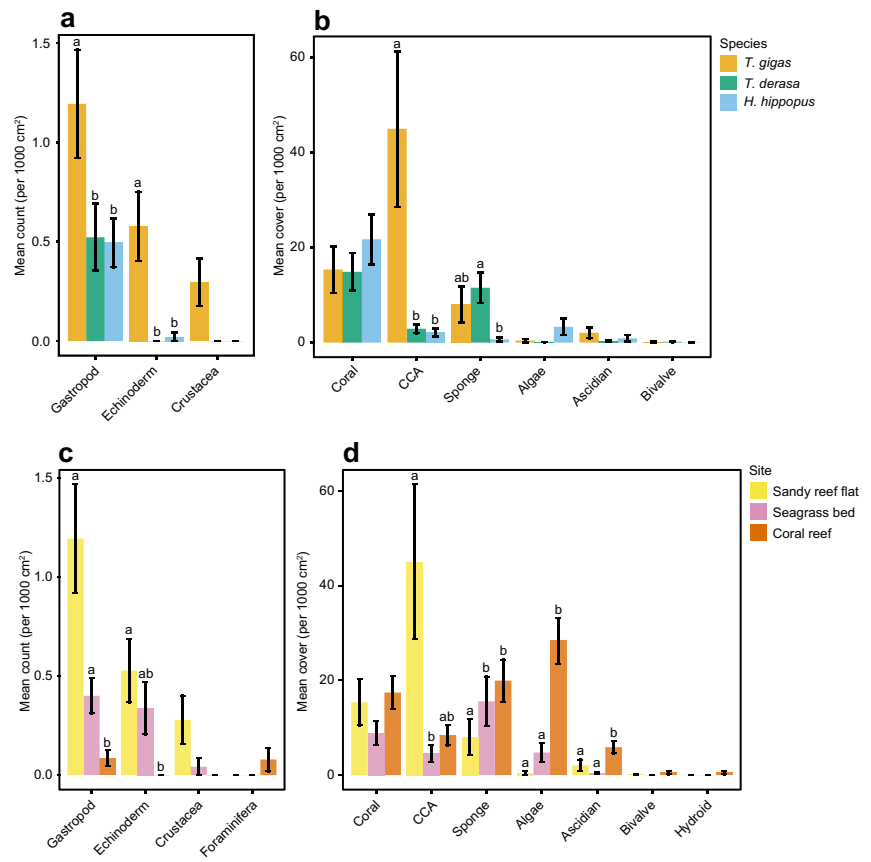
Epibiont taxa that contributed to the differences in community composition between two sites were also identified using SIMPER pairwise tests (Table 5; Supplementary Table 8).

Table 3 Summary of analyses of similarity (ANOSIM) pairwise comparisons of **a** mobile and sessile epibiont communities between giant clam species, and of **b** mobile and sessile epibiont communities between habitats

a Pairwise comparisons	Inter-species variability (count of mobile epibionts)		Inter-species variability (cover of sessile epibionts)	
	R	p	R	p
<i>T. gigas</i> vs <i>T. derasa</i>	0.144	0.008*	-0.020	0.710
<i>T. gigas</i> vs <i>H. hippopus</i>	0.099	0.007*	0.153	0.003*
<i>T. derasa</i> vs <i>H. hippopus</i>	0.049	0.090	0.066	0.001*
b Pairwise comparisons	Inter-site variability (count of mobile epibionts)		Inter-site variability (cover of sessile epibionts)	
	R	p	R	p
Silaqui vs Lucero	0.15	0.002*	0.472	0.001*
Silaqui vs Caniogan	0.402	0.001*	0.561	0.001*
Lucero vs Caniogan	0.247	0.001*	0.596	0.001*

Significant comparisons are indicated by bold font and asterisks

Fig. 5 Abundance (mean \pm standard error) of **a** mobile and **b** sessile epibionts on the shells of different giant clam species. Abundance of **c** mobile and **d** sessile epibionts on the shells of *T. gigas* restocked in different habitats. Similar letters above the bars indicate that values of abundance do not vary between samples based on the results of the Kruskal–Wallis tests



Pyramidella sp. consistently provided high percentage contribution when comparing the three sites. *Trochus* sp. provided a greater percentage contribution when sandy reef flat was compared with the coral reef and seagrass bed. Foraminiferans contributed to the difference between coral reef and seagrass bed and sandy reef flat, and *Synapta* sp. showed high percentage contribution when comparing the seagrass bed to the sandy reef flat and coral reef. For sessile epibionts, *Hymeniacidon perlevis* and crustose coralline algae contributed to differences across all three sites. *Padina* sp. provided a high percent contribution when comparing the seagrass bed to coral reef and sandy reef flat, and *Halimeda* sp. contributed to the difference between the coral reef site and the seagrass bed and sandy reef flat.

Discussion

Giant clam restocking has been conducted to help restore depleted populations of giant clams. Restocked clams are known to provide additional substrate for other organisms to live in (Vicentuan et al. 2014; Neo et al. 2015; van der Schoot et al. 2016). However, differences in the epibiont communities associated with different giant clam species or on giant clams restocked in different habitat types are not yet well-studied. Here, we show that giant clams host

diverse types of mobile and sessile epibionts on their shells. We further revealed that epibiont communities were more variable across habitat types than among different giant clam species restocked in a similar area.

Species richness and abundance of epibionts

Inter-species variability

In general, *T. gigas* had higher species richness and abundance of mobile epibionts, and surface cover of sessile epibionts than *T. derasa* and *H. hippopus*. Species richness and abundance of both mobile and sessile epibionts were comparable between *T. derasa* and *H. hippopus*. This trend may be due to overall differences in shell morphology that translates to varying levels of habitat complexity. Although detailed differences in shell shape and structural complexity were not measured in the current study, *Tridacna gigas* shells are large and have well-defined ribs and folds and are likely to provide a more complex substrate. In contrast, *T. derasa* possesses medium sized, smooth, and minimally ribbed shells, and *H. hippopus* has smaller, triangular, smooth shells (Lucas 1988). Previous studies have documented greater species diversity in complex habitats (Heck and Wetstone 1977; St. Pierre and Kovalenko 2014) as these provide more

Table 4 Summary results of SIMPER (Similarity percentage) analyses, showing the top 5 **a** mobile and **b** sessile epibiont taxa that characterize the epibiont community per giant clam species, and **c** mobile and **d** sessile epibiont taxa that contributed to the differences in epibiont communities between giant clam species. Full results are in Supplementary Table 7

a Inter-species variability (count of mobile epibionts)			
Species	Ave. abundance	% contribution	
<i>T. gigas</i> (Ave. sim.: 19.61)			
<i>Trochus</i> sp. (gastropod)	0.44	38.54	
<i>Pyramidella</i> sp. (gastropod)	0.30	14.83	
<i>Diadema</i> sp. (echinoderm)	0.43	13.88	
Hermit crab	0.32	12.11	
<i>Vexillum</i> sp. (gastropod)	0.09	7.49	
<i>T. derasa</i> (Ave. sim.: 15.34)			
<i>Coralliophila neritoidea</i> (gastropod)	0.53	28.06	
<i>Trochus</i> sp. (gastropod)	1.07	24.46	
<i>Hexaplex</i> sp. (gastropod)	0.35	21.49	
<i>Pyramidella</i> sp. (gastropod)	0.72	21.49	
<i>H. hippopus</i> (Ave. sim.: 17.06)			
<i>Monetaria annulus</i> (gastropod)	0.88	59.32	
<i>Trochus</i> sp. (gastropod)	0.46	27.00	
<i>Pyramidella</i> sp. (gastropod)	0.46	11.49	
b Inter-species variability (cover of sessile epibionts)			
Species	Ave. abundance	% contribution	
<i>T. gigas</i> (Ave. sim.: 41.96)			
Crustose coralline algae	54.00	85.71	
<i>Porites</i> sp. (coral)	4.99	5.91	
<i>T. derasa</i> (Ave. sim.: 16.39)			
<i>Porites</i> sp. (coral)	7.37	34.06	
<i>Hymeniacidon perlevis</i> (sponge)	6.78	29.94	
Crustose coralline algae	3.90	18.43	
<i>Haliclona</i> sp. (sponge)	8.17	12.17	
<i>H. hippopus</i> (Ave. sim.: 25.30)			
<i>Porites</i> sp. (coral)	10.95	79.46	
<i>Pavona</i> sp. (coral)	17.14	7.41	
<i>Padina pavonica</i> (algae)	3.75	5.82	
c Pairwise inter-species variability (count of mobile epibionts)			
	<i>T. gigas</i>	<i>T. derasa</i>	
<i>T. gigas</i> vs <i>T. derasa</i> (Ave. dis.: 87.62)	Ave. abundance	Ave. abundance	% contribution
<i>Trochus</i> sp. (gastropod)	0.44	1.07	15.63
<i>Pyramidella</i> sp. (gastropod)	0.30	0.72	13.81
<i>Vexillum</i> sp. (gastropod)	0.09	0.21	9.86
<i>Coralliophila neritoidea</i> (gastropod)	0.00	0.53	9.54
<i>Hexaplex</i> sp. (gastropod)	0.02	0.35	9.39
	<i>T. gigas</i>	<i>H. hippopus</i>	
<i>T. gigas</i> vs <i>H. hippopus</i> (Ave. dis.: 85.81)	Ave. abundance	Ave. abundance	% contribution
<i>Trochus</i> sp. (gastropod)	0.44	0.46	16.59
<i>Monetaria annulus</i> (gastropod)	0.12	0.88	15.34
<i>Pyramidella</i> sp. (gastropod)	0.30	0.46	13.19
<i>Diadema</i> sp. (echinoderm)	0.43	0.10	9.95
<i>Vexillum</i> sp. (gastropod)	0.09	0.10	8.53
	<i>T. derasa</i>	<i>H. hippopus</i>	
<i>T. derasa</i> vs <i>H. hippopus</i> (Ave. dis.: 87.14)	Ave. abundance	Ave. abundance	% contribution
<i>Monetaria annulus</i> (gastropod)	0.08	0.88	19.31
<i>Trochus</i> sp. (gastropod)	1.07	0.46	18.37
<i>Pyramidella</i> sp. (gastropod)	0.72	0.46	16.73
<i>Hexaplex</i> sp. (gastropod)	0.35	0.12	13.43

Table 4 (continued)

<i>Coralliophila neritoidea</i> (gastropod)	0.53	0.00	12.69
d Pairwise inter-species variability (cover of sessile epibionts)			
	<i>T. gigas</i>	<i>T. derasa</i>	
<i>T. gigas</i> vs <i>T. derasa</i> (Ave. dis.: 81.44)	Ave. abundance	Ave. abundance	% contribution
Crustose coralline algae	54.00	3.90	29.68
<i>Porites</i> sp. (coral)	4.99	7.37	15.36
<i>Hymeniacidon perlevis</i> (sponge)	5.04	6.78	14.11
<i>Pavona</i> sp. (coral)	7.00	8.22	9.15
<i>Haliclona</i> sp. (sponge)	0.00	8.17	7.20
	<i>T. gigas</i>	<i>H. hippopus</i>	
<i>T. gigas</i> vs <i>H. hippopus</i> (Ave. dis.: 83.40)	ave abundance	ave abundance	% contribution
Crustose coralline algae	54.00	3.20	29.22
<i>Porites</i> sp. (coral)	4.99	10.95	20.61
<i>Pavona</i> sp. (coral)	7.00	17.14	10.73
<i>Hymeniacidon perlevis</i> (sponge)	5.04	0.39	8.33
<i>Padina pavonica</i> (algae)	0.00	3.75	6.08
	<i>T. derasa</i>	<i>H. hippopus</i>	
<i>T. derasa</i> vs <i>H. hippopus</i> (Ave. dis.: 83.73)	Ave. abundance	Ave. abundance	% contribution
<i>Porites</i> sp. (coral)	7.37	10.95	24.48
<i>Hymeniacidon perlevis</i> (sponge)	6.78	0.39	13.90
Crustose coralline algae	3.90	3.20	12.90
<i>Pavona</i> sp. (coral)	8.22	17.14	10.79
<i>Haliclona</i> sp. (sponge)	8.17	0.00	7.81

opportunities for attachment of various sessile organisms, such as algae (Callow et al. 2002; Scardino et al. 2008), corals (Whalan et al. 2015; Hata et al. 2017), ascidians (Chase et al. 2016), and bivalves (Czarnecki et al. 2004; Praeger et al. 2012). Moreover, a more complex structure decreases the foraging efficiency of predators (Chaffey 2010) and thus increases the survival rate of inhabitants.

Apart from shell morphology, stability of the giant clam shells may also influence epibiont succession. Individuals of *H. hippopus*, *T. derasa*, and *T. gigas* live byssally anchored as juveniles but are free-living on coral rubble or hard-packed sand as adults, which may cause them to roll over during wave action, after which they may right themselves (Fankboner 1971). Large *T. gigas* offer a stable substrate as they are heavy enough to resist mobility, whereas *H. hippopus* have a greater tendency to roll over because they have smaller and rounder shells.

Another factor that may contribute to differences in giant clam-associated epibiont communities is the possible presence of biochemical cues or anti-fouling properties of different giant clam species. Giant clams, like *T. gigas* and *T. maxima*, produce bioactive compounds such as sterols that may act as chemical defensive substances (Withers et al. 1982; Wang et al. 2008; Guibert et al. 2019). Specifically, a pigment called peridinin (a carotenoid) found in the zooxanthellae symbionts of giant clams has been shown to have cytotoxic activity (Ishikawa et al. 2016; Guibert et al. 2019). The production of these

types of compounds by different giant clam species and their effects on epibiont associates remains unknown but present an interesting avenue for further investigation.

Inter-site variability

Tridacna gigas clams that were restocked in a coral reef site had significantly higher species richness and surface cover of sessile epibionts compared to conspecifics in the sandy reef flat and seagrass bed habitats. This result is within expectations as coral reefs are one of the most diverse marine ecosystems (Hughes 1991) and thus, the potential pool of colonizers (e.g., hard corals) is much more diverse compared to the other habitat types. Seagrass habitats, on the other hand, while home to a wide variety of potential colonizing organisms (Moncreiff and Sullivan 2001), are not as diverse and are mostly comprised of epiphytic algae and various grazing invertebrates. Sandy bottom habitats are the least diverse and support mostly burrowing and benthic organisms and various grazing fishes (Moyle and Cech 2004; Bellwood et al. 2018). Surprisingly, however, *T. gigas* in the sandy reef flat habitat showed the highest species richness and abundance of mobile epibionts. The lack of substrate complexity within the sandy habitat may have driven the aggregation of mobile epibionts towards the giant clams, which are the only complex structures present in an area mostly dominated by sand and rubble. In contrast, sites such as the coral reef

Table 5 Summary results of SIMPER (Similarity percentage) analyses, showing the top 5 **a** mobile and **b** sessile epibiont taxa that characterize the epibiont community on *T. gigas* per habitat type, and **c** mobile and **d** sessile epibiont taxa that contributed to the differences in epibiont communities between habitats. Full results are in Supplementary Table 8

a Inter-site variability (count of mobile epibionts)			
Species	Ave. abundance	% contribution	
Silaqui (Ave. sim.: 17.28)			
<i>Trochus</i> sp. (gastropod)	0.42	42.25	
<i>Pyramidella</i> sp. (gastropod)	0.29	15.37	
<i>Diadema</i> sp. (echinoderm)	0.35	10.69	
Hermit crab	0.29	10.14	
<i>Vexillum</i> sp. (gastropod)	0.09	7.76	
Lucero (Ave. sim.: 14.10)			
<i>Pyramidella</i> sp. (gastropod)	0.21	40.42	
<i>Synapta</i> sp. (echinoderm)	0.14	34.30	
<i>Trochus</i> sp. (gastropod)	0.09	9.77	
<i>Holothuria scabra</i> (echinoderm)	0.14	9.05	
Caniogan (Ave. sim.: 6.67)			
Foraminifera	0.29	100.00	
b Inter-site variability (cover of sessile epibionts)			
Species	Ave. abundance	% contribution	
Silaqui (Ave. sim.: 41.96)			
Crustose Coralline Algae	54.00	85.71	
<i>Porites</i> sp. (coral)	4.99	5.91	
Lucero (Ave. sim.: 34.86)			
<i>Padina</i> sp. (algae)	8.70	53.19	
<i>Hymeniacidon perlevis</i>	13.09	32.37	
Crustose coralline algae	4.85	10.78	
Caniogan (Ave. sim.: 23.79)			
<i>Halimeda</i> sp. (algae)	8.41	18.58	
Crustose coralline algae	8.47	16.87	
<i>Hymeniacidon perlevis</i> (sponge)	3.29	12.70	
<i>Halymenia macroloba</i> (algae)	9.61	12.05	
<i>Didemnum moseleyi</i> (ascidian)	1.40	4.59	
c Pairwise inter-site variability (count of mobile epibionts)			
	Silaqui	Lucero	
Silaqui vs Lucero (Ave. dis.: 90.49)			
	Ave. abundance	Ave. abundance	% contribution
<i>Trochus</i> sp. (gastropod)	0.42	0.09	14.01
<i>Pyramidella</i> sp. (gastropod)	0.29	0.21	13.30
<i>Synapta</i> sp. (echinoderm)	0.02	0.14	10.13
<i>Diadema</i> sp. (echinoderm)	0.35	0.00	6.48
Hermit crab	0.29	0.00	6.35
Silaqui vs Caniogan (Ave. dis.: 99.40)			
	Silaqui	Caniogan	
	Ave. abundance	Ave. abundance	% contribution
<i>Trochus</i> sp. (gastropod)	0.42	0.00	12.41
Foraminiferan	0.00	0.29	12.26
<i>Pyramidella</i> sp. (gastropod)	0.29	0.00	8.24
<i>Nassarius</i> sp. (gastropod)	0.15	0.09	7.33
<i>Diadema</i> sp. (echinoderm)	0.35	0.00	6.52
Lucero vs Caniogan (Ave. dis.: 100.00)			
	Lucero	Caniogan	
	Ave. abundance	Ave. abundance	% contribution
Foraminiferan	0.00	0.29	14.48
<i>Pyramidella</i> sp. (gastropod)	0.21	0.00	12.08
<i>Synapta</i> sp. (echinoderm)	0.14	0.00	11.69
<i>Nassarius</i> sp. (gastropod)	0.00	0.09	7.24
<i>Turritella</i> sp. (gastropod)	0.00	0.07	7.24

Table 5 (continued)

d Pairwise inter-site variability (cover of sessile epibionts)			
	Silaqui	Lucero	
Silaqui vs Lucero (Ave. dis.: 84.01)	Ave. abundance	Ave. abundance	% contribution
Crustose coralline algae	54.00	4.85	19.92
<i>Padina</i> sp. (algae)	0.00	8.70	18.68
<i>Hymeniacidon perlevis</i> (sponge)	5.04	13.09	15.52
<i>Porites</i> sp. (coral)	4.99	0.00	6.30
<i>Pavona</i> sp. (coral)	7.00	0.00	4.84
	Silaqui	Caniogan	
Silaqui vs Caniogan (Ave. dis.: 87.73)	Ave. abundance	Ave. abundance	% contribution
Crustose coralline algae	54.00	8.47	8.60
<i>Halimeda</i> sp. (algae)	0.52	8.41	6.67
<i>Hymeniacidon perlevis</i> (sponge)	5.04	3.29	6.00
<i>Halymenia macroloba</i> (algae)	0.00	9.61	5.27
<i>Porites</i> sp. (coral)	4.99	0.25	3.43
	Lucero	Caniogan	
Lucero vs Caniogan (Ave. dis.: 88.30)	Ave. abundance	Ave. abundance	% contribution
<i>Padina</i> sp. (coral)	8.70	0.00	8.84
<i>Hymeniacidon perlevis</i> (sponge)	13.09	3.29	6.79
<i>Halimeda</i> sp. (algae)	0.58	8.41	6.06
Crustose coralline algae	4.85	8.47	5.88
<i>Didemnum mole</i> (ascidian)	0.00	9.61	4.92

area in Caniogan present countless other alternative structures (e.g., corals) for mobile epibionts to explore.

Many organisms prefer habitats with higher structural complexity because this confers better protection against predators and ensures better survival (Crowder and Cooper 1982; Chaffey 2010). This preference for structurally complex habitats is well documented in other organisms (Johns and Mann 1987; Noonan 2012; Brooker et al. 2013). For example, juvenile lobsters have a preference for habitats with the seaweed, *Chondrus crispus*, versus habitats without any structures at all, and increasing habitat complexity by adding seaweeds and bricks increased lobster survivability (Johns and Mann 1987). Similarly, fish have been shown to prefer corals with higher structural complexity (Noonan 2012; Brooker et al. 2013).

Epibiont community composition

Inter-species variability

Epibiont community composition, especially of mobile epibionts, was not distinctly different among giant clam species. Among the most abundant were gastropods, including *Pyramidella* sp., which are ectoparasites of molluscs and known natural predators of giant clams, *Drupella* and *Coralliophila neritoidea*, which are corallivores that feed on corals growing on the giant clam shells, and the top shell, *Trochus* sp., a grazer of algae that grow on hard substrates like rocks and boulders (Boglio and Lucas 1997; Moerland et al. 2016).

Larger mobile epibionts such as *Diadema setosum* and *Echinometra* sp. were only observed on *T. gigas*, likely because this species has the largest shell area.

Future studies should observe a wider range of sizes of the different giant clam species to determine whether there is an association between shell size and epibiont community composition. More studies are also needed on possible harmful effects of epibionts on *Tridacna* shells, especially invertebrates that settle on the shell surface and bore into its interior (Mekawy 2014), such as sponges of the family Clionidae (Hoeksema 1983), mussels of the subfamily Lithophaginae (Appukuttan 1976), and polychaetes of the genus *Polydora* (Zottoli and Carriker 1974; Waser et al. 2021).

Inter-site variability

Epibiont communities on the shells of *T. gigas* showed some distinct differences across sites, which was most apparent for sessile epibionts. The community observed on the giant clam shells likely reflects the benthic community at each habitat. For example, mobile epibionts such as *Holothuria scabra* and *Echinotrix diadema* were only observed on *T. gigas* in the seagrass bed, which may be due to the habitat preference of *H. scabra* and the seagrass grazing preference of *E. diadema* (Kinch et al. 2008; Hamel et al. 2013; Floren et al. 2021). Sessile epibionts such as the corals, *Porites* sp. and *Pavona* sp., were only observed on *T. gigas* in the sandy reef flat in Silaqui, while the sponge, *Phorbos* sp., was only

found in the seagrass bed. The sponge, *Tedania ignis*, and corals, *Goniopora* sp. and *Pectinia* sp., were observed only in the coral reef site. The presence of reef-associated organisms, such as corals and crustose coralline algae, on giant clam shells at all three habitats is to be expected given that these sites are in proximity to coral reef areas (less than 300 m). It should be noted, however, that this study did not compare the surrounding benthic communities in each habitat type against the epibiont communities observed on the giant clams but warrants further investigation.

Most of the epibionts likely make use of giant clam shells as settlement substrate, shelter, or feeding grounds. Epibiont communities observed at any one time may reflect interactions amongst organisms. Some mobile epibionts that were identified are known predators of the sessile epibionts that settle on giant clam shells. One such example is *Drupella* sp., which are predators of corals (Moerland et al. 2016). Moreover, the abundance of certain sessile epibionts may indicate the absence of natural predators or that the shells afford effective protection. For instance, there were more algae that settled on the shells of *T. gigas* restocked on a seagrass bed where no *Diadema*, an herbivore, were observed. Long-term monitoring studies are needed to identify whether there are epibiont taxa that are specifically associated with giant clam species or habitats, as well as to reveal patterns of settlement and succession on giant clams.

Potential implications

This study highlights the important role of giant clams as hosts to a diverse community of mobile and sessile epibionts. Giant clam shells provide available substrate and serve as a complex structure that attracts epibiont communities, reflecting the biodiversity of a specific habitat. There does not appear to be a difference in terms of the epibiont community that forms on the shells of different giant clam species. Hence, in the context of restoration and restocking efforts with the goal of biodiversity enhancement, the largest giant clam, *Tridacna gigas*, would provide the greatest advantage because they have the largest shell surface area per individual and can attract the highest species richness, abundance, and cover of epibionts.

Conclusion

All giant clams investigated in this study were associated with a diverse community of epibionts. The structure of the epibiont communities appeared to be influenced by the size and complexity of the giant clam shell, as well as by the habitat type of the restocking site. This highlights the important ecological role of giant clams in the provision of viable settlement substrates and suitable habitats for recruitment of many organisms. These findings further underline the

utility of giant clams in enhancing biodiversity at restocking sites, especially on degraded reefs where substrates are not suitable for settlement. Restocking of giant clams may help kickstart recovery of degraded reef communities, which is one of the aims of reef conservation.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12526-023-01363-y>.

Acknowledgements The authors acknowledge Jun Castrence and the staff of Bolinao Marine Laboratory for assistance with field work. We also acknowledge the assistance of Edwin Dumalagan with coral and algae identification, Timothy Quimpo for his assistance and advice on statistical analysis, and Elizabeth Gomez for her assistance in generating the map of study sites. Lastly, we would like to thank members of the Coral Reef Ecology Laboratory (CoRE) for their helpful comments and suggestions on the study. This study was supported by a grant from the Philippine Council for Agriculture, Aquatic, and Natural Resources Research and Development of the Department of Science and Technology to PCC and CC (QMSR-MRRD-MEC-314-1542) and a Department of Science and Technology ASTHRDP Scholarship and University of the Philippines Marine Science Institute Thesis Writing Grant 2020 to ID. We thank the reviewers for the suggestions that helped improve our paper.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the “**Acknowledgements**”, if applicable.

Data availability All data generated or analyzed during this study are included in this published article. For requests, please contact Patrick Cabaitan (pcabaitan@msi.upd.edu.ph).

Author contributions ID, PCC, BWH, SGS, CC conceived and designed the research and analysis; ID performed the experiments; ID, PCC, BWH, SGS, CC analyzed the data; PCC, CC provided materials and funds; PCC, BWH, CC provided supervision; ID wrote the first draft of the manuscript; ID, PCC, BWH, SGS, CC edited the manuscript and approved its submission.

References

- Adessi L (2001) Giant clam bleaching in the lagoon of Takapoto atoll (French Polynesia). *Coral Reefs* 19:220. <https://doi.org/10.1007/PL00006957>
- Andréfouët S, Van Wynsberge S, Gaertner-Mazouni N, Menkes C, Gilbert A, Remoissenet G (2013) Climate variability and massive mortalities challenge giant clam conservation and management efforts in French Polynesia atolls. *Biol Conserv* 160:190–199. <https://doi.org/10.1016/j.biocon.2013.01.017>
- Andréfouët S, Van Wynsberge S, Fauvelot C, Bruckner AW, Remoissenet G (2014) Significance of new records of *Tridacna squamosa* Lamarck, 1819, in the Tuamotu and Gambier Archipelagos (French Polynesia). *Molluscan Res* 44:277–284. <https://doi.org/10.1080/13235818.2014.940662>

- Appukkuttan KK (1976) On *Lithophaga (Diberus) bisulcata* a mytilid borer causing damage to the commercially important gastropod shells. *Ind J Fish* 23:194–200
- Bellwood DR, Tebbett SB, Bellwood O, Mihalitsis M, Morais RA, Streit RP, Fulton CJ (2018) The role of the reef flat in coral reef trophodynamics: past, present, and future. *Ecol Evol* 8:4108–4119. <https://doi.org/10.1002/ece3.3967>
- Berntsson KM, Jonsson PR, Lejhall M, Gatenholm P (2000) Analysis of behavioral rejection of micro-textured surfaces and implications for recruitment by the barnacle *Balanus improvisus*. *J Exp Mar Biol Ecol* 251:59–83. [https://doi.org/10.1016/S0022-0981\(00\)00210-0](https://doi.org/10.1016/S0022-0981(00)00210-0)
- Boglio EG, Lucas JS (1997) Impacts of ectoparasitic gastropods on growth, survival, and physiology of juvenile giant clams (*Tridacna gigas*), including a simulation model of mortality and reduced growth rate. *Aquaculture* 150(1–2):25–43
- Böhm T, Hoeksema BW (2017) Habitat selection of the coral-dwelling spinyhead blenny, *Acanthemblemaria spinosa*, at Curaçao, Dutch Caribbean. *Mar Biodivers* 47:17–25. <https://doi.org/10.1007/s12526-016-0543-9>
- Bralely RD (1988) Recruitment of the giant clams *Tridacna gigas* and *T. derasa* at four sites on the Great Barrier Reef. In: Copland JW and Lucas JS (eds) *Giant Clams in Asia and Pacific*, ACIAR Monograph no. 9, Australian Centre for International Agricultural Research, Canberra. pp 73–77
- Brooker RM, Munday PL, McLeod IM, Jones GP (2013) Habitat preferences of a coralivorous reef fish: Predation risk versus food quality. *Coral Reefs* 32:613–622. <https://doi.org/10.1007/s00338-013-1057-6>
- Cabaitan PC, Conaco CG (2017) Bringing back the giants: juvenile *Tridacna gigas* from natural spawning of restocked giant clams. *Coral Reefs* 36:519. <https://doi.org/10.1007/s00338-017-1558-9>
- Cabaitan PC, Gomez ED, Aliño PM (2008) Effects of coral transplantation and giant clam restocking on the structure of fish communities on degraded patch reefs. *J Exp Mar Biol Ecol* 357(1):85–98
- Callow ME, Jennings AR, Brennan AB, Seegert CE, Gibson A, Wilson L, Feinberg A, Baney R, Callow JA (2002) Microtopographic cues for settlement of zoospores of the green fouling alga *Enteromorpha*. *Biofouling* 18:229–236. <https://doi.org/10.1080/08927010290014908>
- Chaffey N (2010) *Encyclopedia of Ecology*. *Ann Bot* 105:vi–viii. <https://doi.org/10.1093/aob/mcp308>
- Chase AL, Dijkstra JA, Harris LG (2016) The influence of substrate material on ascidian larval settlement. *Mar Pollut Bull* 106(1–2):35–42. <https://doi.org/10.1016/j.marpolbul.2016.03.049>
- Chiavelli DA, Mills EL, Threlkeld ST (1993) Host preference, seasonality, and community interactions of zooplankton epibionts. *Limnol Oceanogr* 38:574–583. <https://doi.org/10.1007/s10452-004-5001-2>
- Clarke KR, Gorley RN (2001) *PRIMER v5: User Manual / Tutorial*. PRIMER-E: Plymouth
- Crowder LB, Cooper WE (1982) Habitat structural complexity and the interaction between Bluegills and their prey. *Ecology* 63:1802–1813. <https://doi.org/10.2307/1940122>
- Czarnoleski M, Michalczyk Ł, Pajdak-Stós A (2004) Substrate preference in settling zebra mussels *Dreissena polymorpha*. *Arch Hydrobiol* 159:263–270. <https://doi.org/10.1127/0003-9136/2004/0159-0263>
- da Gama BAP, Rodrigo PD, Santos A, Pereira RC (2008) The effect of epibionts on the susceptibility of the red seaweed *Cryptonemia seminervis* to herbivory and fouling. *Biofouling* 24:209–218. <https://doi.org/10.1080/08927010802041253>
- Davis AR, White GA (1994) Epibiosis in a guild of sessile invertebrates in South-Eastern Australia – a quantitative survey. *J Exp Mar Biol Ecol* 177:1–14. [https://doi.org/10.1016/0022-0981\(94\)90140-6](https://doi.org/10.1016/0022-0981(94)90140-6)
- de Gier W, Becker C (2020) A review of the ecomorphology of pinnotherine pea crabs (Brachyura: Pinnotheridae), with an updated list of symbiont-host associations. *Diversity* 12:431. <https://doi.org/10.3390/d12110431>
- de Bakker DM, Webb AE, van den Bogaart LA, van Heuven SMAC, Meesters EH, van Duyl FC (2018) Quantification of chemical and mechanical bioerosion rates of six Caribbean excavating sponge species found on the coral reefs of Curaçao. *PLoS One* 13:e0197824. <https://doi.org/10.1371/journal.pone.0197824>
- Dubousquet V, Gros E, Berteaux-Lecellier V, Viguier B, Raharivomanana P, Bertrand C, Lecellier GJ (2016) Changes in fatty acid composition in the giant clam *Tridacna maxima* in response to thermal stress. *Biol Open* 5(10):1400–1407. <https://doi.org/10.1242/bio.017921>
- Ecube KMA, Villanueva E, Dolorosa RG, Cabaitan PC (2019) Notes on the first record of *Tridacna noae* (Röding, 1798) (Cardiidae: Tridacninae) in Palawan, Philippines. *Palawan Scientist* 11:112–115
- Enricuso O, Conaco C, Sayco SL, Neo ML, Cabaitan PC (2019) Elevated seawater temperatures affect embryonic and larval development in the giant clam *Tridacna gigas* (Cardiidae: Tridacninae). *J Molluscan Stud* 85:66–72. <https://doi.org/10.1093/mollusc/eyy051>
- Fankboner PT (1971) Self righting by tridacnid clams. *Nature* 230:579–580. <https://doi.org/10.1038/230579a0>
- Fauvelot C, Zuccon D, Borsa P, Daphné G, Magalon H, Riquet F, Andréfouët S, Berumen ML, Sinclair-Taylor TH, Gelin P, Behivoke F, ter Poorten JJ, Strong EE, Bouchet P (2020) Phylogeographical patterns and a cryptic species provide new insights into Western Indian Ocean giant clams phylogenetic relationships and colonization history. *J Biogeogr* 47:1086–1105. <https://doi.org/10.1111/jbi.13797>
- Fernandez-Leborans G, Gabilondo R (2006) Inter-annual variability of the epibiotic community on *Pagurus bernhardus* from Scotland. *Estuar Coastal Shelf Sci* 66:35–54. <https://doi.org/10.1016/j.ecss.2005.07.016>
- Floren AS, Hayashizaki K, Putchakarn S, Tuntiprapas P, Prathep A (2021) A Review of Factors Influencing the Seagrass-Sea Cucumber Association in Tropical Seagrass Meadows. *Front Mar Sci* 8:696134. <https://doi.org/10.3389/fmars.2021.696134>
- Fuller WJ, Broderick AC, Enever R, Thorne P, Godley BJ (2010) Motile homes: A comparison of the spatial distribution of epibiotic communities on Mediterranean Sea turtles. *J Nat Hist* 44:25–28. <https://doi.org/10.1080/00222931003624820>
- Gomez ED, Mingoa-Licuanan SS (2006) Achievements and lessons learned in restocking giant clams in the Philippines. *Fish Res* 80:46–52. <https://doi.org/10.1016/j.fishres.2006.03.017>
- Guibert I, Bonnard I, Pochon X, Zubia M, Sidobre C, Gael L, Berteaux-Lecellier V (2019) Differential effects of coral-giant clam assemblages on biofouling formation. *Sci Rep* 9:2675. <https://doi.org/10.1038/s41598-019-39268-1>
- Gutiérrez JL, Palomo MG (2016) Increased algal fouling on mussels with barnacle epibionts: A fouling cascade. *J Sea Res* 112:49–54. <https://doi.org/10.1016/j.seares.2016.04.002>
- Gutt J, Schickan T (1998) Epibiotic relationships in the Antarctic benthos. *Antarctic Sci* 10:398–405. <https://doi.org/10.1017/s0954102098000480>
- Hamel JF, Mercier A, Conand C, Purcell S, Toral-Granda V, Gamboa R (2013) *Holothuria scabra*, golden sandfish. IUCN Red List Threat Species 2013:8235. <https://doi.org/10.2305/IUCN.UK.2013-1.RLTS.T180257A1606648.en>
- Hata T, Madin JS, Cumbo V, Denny M, Figueiredo J, Harii S, Thomas CJ, Baird A (2017) Coral larvae are poor swimmers and require fine-scale reef structure to settle. *Sci Rep* 7:2249. <https://doi.org/10.1038/s41598-017-02402-y>
- Heck KL, Wetstone GS (1977) Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *J Biogeogr* 4(2):135–142. <https://doi.org/10.2307/3038158>
- Hoeksema BW (1983) Excavation patterns and spiculae dimensions of the boring sponge *Cliona celata* from the SW Netherlands. *Senckenb Marit* 15:55–85

- Hoeksema BW, Fransen CHJM (2011) Space partitioning by symbiotic shrimp species cohabitating in the mushroom coral *Heliofungia actiniformis* at Semporna, eastern Sabah. *Coral Reefs* 30:519. <https://doi.org/10.1007/s00338-011-0736-4>
- Hoeksema BW, van der Meij SET, Fransen CHJM (2012) The mushroom coral as a habitat. *J Mar Biol Assoc UK* 92:647–663. <https://doi.org/10.1017/S0025315411001445>
- Hoeksema BW, van Beusekom M, ten Hove HA, Ivanenko VN, van der Meij SET, van Moorsel GWNM (2017) *Helioseris cucullata* as a host coral at St. Eustatius. *Dutch Caribbean Mar Biodivers* 47:71–78. <https://doi.org/10.1007/s12526-016-0599-6>
- Hoeksema BW, van der Schoot RJ, Wels D, Scott C, ten Hove HA (2019a) Filamentous turf algae on tube worms intensify damage in massive *Porites* corals. *Ecology* 100:e02668. <https://doi.org/10.1002/ecy.2668>
- Hoeksema BW, Wels D, van der Schoot RJ, ten Hove HA (2019b) Coral injuries caused by *Spirobranchus* opercula with and without epibiotic turf algae at Curaçao. *Mar Biol* 166:60. <https://doi.org/10.1007/s00227-019-3504-6>
- Hoeksema BW, Smith-Moorhouse A, Harper CE, van der Schoot RJ, Timmerman RF, Spaargaren R, Langdon-Down SJ (2022a) Black mantle tissue of endolithic mussels (*Leiosolenus* spp.) is cloaking borehole orifices in Caribbean reef corals. *Diversity* 14:401. <https://doi.org/10.3390/d14050401>
- Hoeksema BW, Timmerman RF, Spaargaren R, Smith-Moorhouse A, van der Schoot RJ, Langdon-Down SJ, Harper CE (2022b) Morphological modifications and injuries of corals caused by symbiotic feather duster worms (*Sabellidae*) in the Caribbean. *Diversity* 14:332. <https://doi.org/10.3390/d14050332>
- Hughes RN (1991) Reefs In: Barnes RSK, Mann KH (ed) *Fundamentals of aquatic ecology*, 2nd edn. Blackwell Publishing, England. pp 221–229. <https://doi.org/10.1002/9781444314113>
- Ishikawa C, Jomori T, Tanaka J, Senba M, Mori N (2016) Peridinin, a carotenoid, inhibits proliferation and survival of HTLV-1-infected T-cell lines. *Int J Oncol* 49:1713–1721. <https://doi.org/10.3892/ijo.2016.3648>
- Johns PM, Mann KH (1987) An experimental investigation of juvenile lobster habitat preference and mortality among habitats of varying structural complexity. *J Exp Mar Biol Ecol* 109:275–285. [https://doi.org/10.1016/0022-0981\(87\)90058-X](https://doi.org/10.1016/0022-0981(87)90058-X)
- Juinio MA, Meñez LA, Villanoy C, Gomez ED (1989) Status of giant clam resources in the Philippines. *J Molluscan Stud* 55:431–440. <https://doi.org/10.1093/mollus/55.4.431>
- Kagawa O, Chiba S (2018) Snails wearing green heatproof suits: the benefits of algae growing on the shells of an intertidal gastropod. *J Zool* 307:256–263. <https://doi.org/10.1111/jzo.12641>
- Kinch J, Purcell S, Uthicke S, and Friedman, K (2008) Population Status, Fisheries and Trade of Sea Cucumbers in the Western Central Pacific. In V. Toral-Granda, A. Lovatelli and M. Vasconcellos. *Sea cucumbers. A Global Review of Fisheries and Trade*. FAO Fisheries and Aquaculture Technical Paper. No. 516. Rome: FAO, 7–55
- Koehl M (2007) Mini review: Hydrodynamics of larval settlement into fouling communities. *Biofouling* 23:357–368. <https://doi.org/10.1080/08927010701492250>
- Korringa P (1951) The shell of *Ostrea edulis* as a habitat. *Arch Néerl Zool* 10:32–152. <https://doi.org/10.1163/036551654X00122>
- Laudien J, Wahl M (1999) Indirect effects of epibiosis on host mortality: seastar predation on differently fouled mussels. *Mar Ecol* 20:35–47. <https://doi.org/10.1046/j.1439-0485.1999.00063.x>
- Lescinsky HL (2001) Epibionts. In: Derek Briggs and Peter Crowther (ed.). *Palaeobiology II*. Wiley-Blackwell, United Kingdom, pp. 460–463. <https://doi.org/10.1002/9780470999295.ch112>
- Lizano AM, Santos M (2014) Updates on the status of giant clams *Tridacna* spp. and *Hippopus hippopus* in the Philippines using mitochondrial CO1 and 16S rRNA genes. *Phil Sci Lett* 7:187–200
- Lucas JS (1988) Giant clams: description, distribution and life history. In: Copland JW and Lucas JS (eds) *Giant clams in Asia and the Pacific*. ACIAR Monograph 9: 21–32
- Lucas JS (1994) The biology, exploitation, and mariculture of giant clams (*Tridacnidae*). *Rev Fish Sci* 2:181–223. <https://doi.org/10.1080/10641269409388557>
- Lyons Y, Cheong D, Neo ML, Wong HF (2018) Managing Giant Clams in the South China Sea. *Int J Mar Coast Law* 33(3):467–494. <https://doi.org/10.1163/15718085-13301048>
- Maggioni D, Montano S, Voigt O, Seveso D, Galli P (2020) A mesophotic hotel: the octocoral *Beubryce* cf. *grandicalyx* as a host. *Ecology* 101:e02950. <https://doi.org/10.1002/ecy.2950>
- Maida M, Coll JC, Samarco PW (1994) Shedding new light on scleractinian coral recruitment. *J Exp Mar Biol Ecol* 180:189–202. [https://doi.org/10.1016/0022-0981\(94\)90066-3](https://doi.org/10.1016/0022-0981(94)90066-3)
- Mekawy MS (2014) Environmental factors controlling the distribution patterns and abundance of sclerobionts on the shells of *Tridacna maxima* from the Egyptian Red Sea coast. *Arab J Geosci* 7:3085–3092. <https://doi.org/10.1007/s12517-013-0966-6>
- Moerland MS, Scott CM, Hoeksema BW (2016) Prey selection of corallivorous muricids at Koh Tao (Gulf of Thailand) four years after a major coral bleaching event. *Contrib Zool* 85:291–309. <https://doi.org/10.1163/18759866-08503003>
- Moncreiff CA, Sullivan M (2001) Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analyses. *Mar Ecol Prog Ser* 215:93–106. <https://doi.org/10.3354/meps215093>
- Montano S, Fattorini S, Parravicini V, Berumen ML, Galli P, Maggioni D, Arrigoni R, Seveso D, Strona G (2017) Corals hosting symbiotic hydrozoans are less susceptible to predation and disease. *Proc R Soc B* 284:20172405. <https://doi.org/10.1098/rspb.2017.2405>
- Moyle PB, Cech JJ (2004) *Fishes, an introduction to ichthyology*. Prentice Hall, Upper Saddle River, NJ, USA. 726 pp. <https://doi.org/10.1007/BF01313096>
- Mullineaux LS, Butman CA (1991) Initial contact, exploration and attachment of barnacle (*Balanus amphrite*) cyprids settling in flow. *Mar Biol* 110:93–103. <https://doi.org/10.1007/BF01313096>
- Neo ML, Todd PA (2011) Predator-induced changes in fluted giant clam (*Tridacna squamosa*) shell morphology. *J Exp Mar Biol Ecol* 397:21–26. <https://doi.org/10.1016/j.jembe.2010.11.008>
- Neo ML, Eckman W, Vicentuan K, Teo S, Todd P (2015) The ecological significance of giant clams in coral reef ecosystems. *Biol Conserv* 181:111–123. <https://doi.org/10.1016/j.biocon.2014.11.004>
- Neo ML, Wabnitz CCC, Braley RD, Heslinga GA, Fauvelot C, Van Wynsberge S, Andrefouët S, Waters C, Tan ASH, Gomez ED, Costello MJ, Todd PA (2017) Giant clams (*Bivalvia*: *Cardiidae*: *Tridacninae*): A comprehensive update of species and their distribution, current threats and conservation status. *Oceanogr Mar Biol Ann Rev* 55:87–388
- Neo ML, Kheng Lim K, Yang SY, Soong GY, Masucci GD, Biondi P, Wee HB, Kise H, Reimer JD (2019) Status of giant clam resources around Okinawa-jima Island, Ryukyu Archipelago, Japan. *Aquat Conserv Mar Freshw Ecosyst* 29:1002–1011. <https://doi.org/10.1002/aqc.3033>
- Noonan S (2012) Coral size, health and structural complexity: effects on the ecology of a coral reef damselfish. *Mar Ecol Prog Ser* 456:127–137. <https://doi.org/10.3354/meps09687>
- Praeger C, Poole AJ, Sexton BA, Glenn FL, Vucko MJ, Williams MR, Whalan S, de Nys R (2012) Enhancing the settlement and attachment strength of pediveligers of *Mytilus galloprovincialis* by changing surface wettability and microtopography. *Biofouling* 28:175–186. <https://doi.org/10.1080/08927014.2012.662676>
- Qian PY, Rittschof D, Sreedhar B (2000) Macrofouling in unidirectional flow: miniature pipes as experimental models for studying the interaction of flow and surface characteristics on the attachment of barnacle, bryozoan and polychaete larvae. *Mar Ecol Prog Ser* 207:109–112. <https://doi.org/10.3354/meps207109>

- R Core Team (2018) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Reiss H, Knauper S, Kroncke I (2003) Invertebrate associations with gastropod shells inhabited by *Pagurus bernhardus* (Paguridae) – secondary hard substrate increasing biodiversity in North Sea soft-bottom communities. *Sarsia* 88:404–414. <https://doi.org/10.1080/00364820310003235>
- Scardino AJ, Guenther J, de Nys R (2008) Attachment point theory revisited: The fouling response to a microtextured matrix. *Biofouling* 24:45–53. <https://doi.org/10.1080/08927010701784391>
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nat Methods* 9:671–675. <https://doi.org/10.1038/nmeth.2089>
- Schuhmacher H (1977) A hermit crab, sessile on corals, exclusively feeds by feathered antennae. *Oecologia* 27:371–374. <https://doi.org/10.1007/BF00346831>
- St. Pierre J, Kovalenko KE (2014) Effect of habitat complexity attributes on species richness. *Ecosphere* 5:1–10. <https://doi.org/10.1890/ES13-00323.1>
- Stuhldreier I, Bastian P, Schoenig E, Wild C (2015) Effects of simulated eutrophication and overfishing on algae and invertebrate settlement in a coral reef of Koh Phangan, Gulf of Thailand. *Mar Pollut Bull* 92:35–44. <https://doi.org/10.1016/j.marpolbul.2015.01.007>
- Tan EYW, Quek ZBR, Neo ML, Fauvelot C, Huang D (2021) Genome skimming resolves the giant clam (Bivalvia: Cardiidae: Tridacninae) tree of life. *Coral Reefs*. <https://doi.org/10.1007/s00338-020-02039-w>
- Van der Schoot RJ, Hoeksema BW (2022) Abundance of coral-associated fauna in relation to depth and eutrophication along the leeward side of Curaçao, southern Caribbean. *Mar Environ Res* 181:105738. <https://doi.org/10.1016/j.marenvres.2022.105738>
- Van der Schoot R, Scott CM, Ten Hove HA, Hoeksema BW (2016) Christmas tree worms as epibionts of giant clams at Koh Tao, Gulf of Thailand. *Mar Biodivers* 46:751–752. <https://doi.org/10.1007/s12526-015-0439-0>
- Vicentuan K, Neo ML, Eckman W, Teo S, Todd P (2014) Giant clam shells host a multitude of epibionts. *Bul Mar Sci* 90. <https://doi.org/10.5343/bms.2014.1010>
- Wahl M (2008) Ecological lever and interface ecology: epibiosis modulates the interactions between host and environment. *Biofouling* 24:427–438. <https://doi.org/10.1080/08927010802339772>
- Wahl M, Mark O (1999) The predominantly facultative nature of epibiosis: experimental and observational evidence. *Mar Ecol Prog Ser* 187:59–66. <https://doi.org/10.3354/meps187059>
- Wang C, Liu H, Chang-Lun S, Wang Y (2008) Chemical defensive substances of soft corals and gorgonians. *Acta Ecol Sin* 28:2320–2328. [https://doi.org/10.1016/S1872-2032\(08\)60048-7](https://doi.org/10.1016/S1872-2032(08)60048-7)
- Warner GF (1997) Occurrence of epifauna on the periwinkle, *Littorina littorea* (L), and interactions with the polychaete *Polydora ciliata* (Johnston). *Hydrobiologia* 355:41–47. https://doi.org/10.1007/978-94-017-1907-0_5
- Waser AM, Knol J, Dekker R, Thielges DW (2021) Invasive oysters as new hosts for native shell-boring polychaetes: Using historical shell collections and recent field data to investigate parasite spillback in native mussels in the Dutch Wadden Sea. *J Sea Res*. 175:102086. <https://doi.org/10.1016/j.seares.2021.102086>
- Watson SA, Southgate PC, Miller GM, Moorhead JA, Knauer J (2012) Ocean acidification and warming reduce juvenile survival of the fluted giant clam, *Tridacna squamosa*. *Molluscan Res* 32:177–180
- Whalan S, Wahab MAA, Sprungala S, Poole AJ, de Nys R (2015) Larval settlement: the role of surface topography for sessile coral reef invertebrates. *PLoS ONE* 10:e0117675. <https://doi.org/10.1371/journal.pone.0117675>
- Withers NW, Kokke WC, Fenical W, Djerassi C (1982) Sterol patterns of cultured zooxanthellae isolated from marine invertebrates: Synthesis of gorgosterol and 23-desmethylgorgosterol by aposymbiotic algae. *Proc Natl Acad Sci USA* 79:3764–3768. <https://doi.org/10.1073/pnas.79.12.3764>
- Zottoli RA, Carriker MR (1974) Burrow morphology, tube formation, and microarchitecture of shell dissolution by the spionid polychaete *Polydora websteri*. *Mar Biol* 27:307–316. <https://doi.org/10.1007/BF00394366>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.