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Contrasting coral community structures between natural and artificial substrates at Koh Tao, Gulf of Thailand

Coline Monchanin[a,b,c], Rahul Mehrotra[a,c,d,*], Elouise Haskin[a,e], Chad M. Scott[a], Pau Urgell Plaza[a], Alyssa Allchurch[a,f], Spencer Arnold[a], Kirsty Magson[a,g], Bert W. Hoeksema[h,i]

[a] *Conservation Diver, 7321 Timber Trail Road, Evergreen, CO, 80439, USA*
[b] *Research Center on Animal Cognition (CRCA), Center for Integrative Biology (CBI), CNRS, University Paul Sabatier – Toulouse III, France*
[c] *Aow Thai Marine Ecology Center, Love Wildlife Foundation, FREC Bangkok, 77 Nakhon Sawan Rd, Wat Sommanat, Pom Prap Sattru Phai, Bangkok, 10100, Thailand*
[d] *Reef Biology Research Group. Department of Marine Science, Faculty of Science, Chulalongkorn University, Bangkok, 10330, Thailand*
[e] *The University of Western Australia, 35 Stirling Hwy, Crawley, WA, 6009, Australia*
[f] *School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC, Canada*
[g] *New Heaven Reef Conservation Program, 48 Moo 2, Chalok Ban Kao, Koh Tao, Suratthani, 84360, Thailand*
[h] *Taxonomy, Systematics, and Geodiversity Group, Naturalis Biodiversity Center, P.O. Box 9517, 2300, RA, Leiden, the Netherlands*
[i] *Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, 9700, CC, Groningen, the Netherlands*

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ABSTRACT

Concrete cubic frames and decommissioned steel naval vessels have been deployed in Thailand liberally to act as artificial substrates for coral restoration and marine recreation. We assessed recruitment at such substrate types at Koh Tao, Gulf of Thailand, and compared the community structure of scleractinian corals between artificial substrates and nearby natural reefs. Our results from a sample of 2677 recruits from nine sites highlighted significant differences in community structure between both reef types. Investigations of variables including time since deployment, distance from the natural reef, and seafloor depth revealed only the latter as a possible influencing factor. The diversity of recruits could not be explained by dynamics in coral spawning, and were found to represent groups with lower structural complexity. Our results suggest that coral community structure on artificial and natural reefs differs and supports distinct ecological and functional roles.

1. Introduction

Multiple studies of coral reef community successions have been published over the past decades (Connell, 1973; Karlson and Hurd, 1993; Rogers, 1993). In recent years they focused on the impacts of severe and frequent disturbance events and the resulting shift in benthic communities throughout coral reefs worldwide (Nyström et al., 2000; Riegl and Purkis 2009; Doropoulos et al., 2017). However, the relatively slow growth of scleractinian corals and rates of change in undisturbed reefs has provided challenges in monitoring gradual shifts in their community structure. Additionally, assessments of coral recruitment often fail to provide corresponding data on nearby reefs or reefs of parent colonies, thereby preventing comparisons of community structure. Meanwhile the prevalence of algal colonisers as dominant players and key competitors in succession within coral reefs is relatively well documented (Lirman, 2001; Doropoulos et al., 2017). Comparatively less is known, however, about the slow development of reefs from the perspective of communities of coral recruits. Multiple studies have investigated this, including one by Edmunds (2000), who found a non-linear relationship between the overall coral community structure of reefs in the US Virgin Islands and the juvenile corals therein. Jackson (1991) reviewed the diversity and community structure in Caribbean Reefs, expressing that, while many ecological factors influence coral community structure, few studies have had consistent results. This supports the idea that species differ greatly in the ways they exploit resources and their habitat. These studies further highlight the need to better understand factors that shape how coral recruitment contributes to reef development. Investigations into the influence of reproduction in reef scleractinians have again shown variation in the resulting coral communities. For example, Hughes et al. (1999) presented

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* Corresponding author. Aow Thai Marine Ecology Center, Love Wildlife Foundation, FREC Bangkok, 77 Nakhon Sawan Rd, Wat Sommanat, Pom Prap Sattru Phai, Bangkok, 10100, Thailand.
E-mail address: rahul-m@hotmail.co.uk (R. Mehrotra).

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comprehensive analyses of coral communities across Australia's Great Barrier Reef. Their findings showed dramatic differences in the proportions of broadcast-spawning corals and brooding corals across reefs with similar and dissimilar coral cover.

The use of tiles as artificial substrate to study *in situ* recruitment of marine organisms has been standard practice in various spatial and temporal scales across the world's reefs. These are typically comprised of ceramic, concrete or terracotta, however various other substrates have also been applied (i.e. Fitzhardinge and Bailey-Brock, 1989; Schuhmacher, 2002; Lam, 2003; Arnold and Steneck, 2011; Hylkema et al., 2021). Many such substrates have also been used in the construction of artificial reefs, some of which in turn have been used in the study of coral recruitment (Ng et al., 2017; Higgins et al., 2019; Subhan et al., 2019). However, there is growing evidence for significant divergences in the community structure of corals recruiting onto artificial reefs, and those of nearby natural reefs (Budd and Pandolfi, 2010; Kramer et al., 2019; Hill et al., 2021). The need for detailed comparisons of species assemblages between artificial and natural reefs to assess the impact of artificial reefs has been highlighted repeatedly over the years (Carr and Hixon, 1997; Perkol-Finkel and Benayahu, 2004; Blakeway et al., 2013; Hill et al., 2021).

The majority of investigations into coral community structure in the Gulf of Thailand have focused on variations and changes among natural reef areas. Apart from localised assessments and comparisons between reefs (Sakai et al., 1986; Chou et al., 1991; Latypov, 2003), multiple studies in the Gulf of Thailand have attempted to document responses in community structure to chronic or singular disturbance events. Coral reef stressors attributed to the characteristic riverine input into the Gulf include chronic sedimentation and freshwater inundation due to flooding (Nakano et al., 2009; Yeemin et al., 2013). As has been seen throughout much of the tropical Indo-Pacific, documentation of changes to coral community structure driven by thermal bleaching has been a focus in the Gulf of Thailand (Yeemin et al., 2009; Pengsakun et al., 2012; Phongsuwan et al., 2013). Some commonalities emerge from these assessments, including the dominance of *Porites* throughout much of the near-shore Gulf (attributed to resilience to sedimentation and thermal bleaching), and the high mortality of specific coral types (i.e. *Acropora* spp.) due to bleaching and localised reductions in coral recruitment (Sutthacheep et al., 2018, 2019). Despite these important findings, none of these studies have attempted to provide insights into shifting coral community structure through the lens of ecosystem successional pathways.

The island of Koh Tao sits approximately 65 km offshore in the western Gulf of Thailand. The island is a popular tourist destination and has been the subject of several investigations into coral reef threats including disease associated with tourism pressure (Lamb et al., 2014) and outbreaks of coral predators (Hoeksema et al., 2013; Scott et al., 2015, 2017b, 2017c; Moerland et al., 2016). Surveys from 2002 represent some of the earliest data on coral communities at Koh Tao (Yeemin et al., 2006) where high mortality of *Acropora* corals following the 1998 bleaching event was observed, and Fungiidae, *Porites* and *Pavona* corals were found to be among the most abundant juvenile corals. Subsequent surveys of reefs throughout the island between 2006 and 2014 (Scott et al., 2017a) revealed an overall reduction in abundances of genera considered locally vulnerable to anthropogenic and environmental stressors (i.e. *Acropora, Montipora* and *Diploastrea*) and an increase in corals considered more locally resistant (i.e. *Pavona, Porites* and Fungiidae).

Throughout this period, Koh Tao has been subject to extensive coral conservation efforts that may be divided into proactive and reactive coral restoration. Reactive coral restoration efforts have involved transplantation and securement of naturally fragmented corals back onto stable substrates, both synthetic (i.e. concrete, glass and steel rebar) and natural (dead coral skeletons), and have been shown to be successful in terms of diversity, coverage and survival rates (Hein et al., 2017, 2020). Proactive efforts have included protection measures within zonation strategies (Hein et al., 2015), and an emphasis on large-scale deployment of artificial substrate structures between 2011 and 2017. The structures deployed throughout this period included the intentional sinking of the 50-m long *HTMS Sattakut* by the Royal Thai Navy in June 2011 to act as an alternative dive site for recreational SCUBA diving at depths of 26–31 m, and placement of approximately 3000 concrete cubic frames (sometimes called 'concrete dice') by the Department of Marine and Coastal Resources of Thailand. These were situated on soft-sediment habitats with varying degrees of proximity to nearby coral reefs. The concrete cubic frames (ca. 1.5 m^3) have been a popular artificial reef structure in Thailand (Kheawwongjan and Kim, 2012), and were deployed at irregular intervals between 2013 and 2017, either a single tier or a stack of two tiers at depths ranging from 8.5 to 20 m.

The objective of the present study is to investigate possible relationships between the community composition on natural reef sites and those on nearby artificial reefs, and some of the variables that may influence these. Specifically, our hypotheses are as follows: i) there is a direct relationship between depth and the community structure of corals on artificial reefs and natural reefs; ii) distance between artificial reefs and their nearest natural reef has a significant influence on the community of coral recruits on artificial reefs; iii) the time since deployment of artificial substrates has a significant influence on coral community structure; iv) there is a direct relationship in the community structure between artificial and natural reefs, which can be explained by the influence of depth, distance and time as mentioned in i-iii). To test these, we conducted a comprehensive assessment of coral recruitment on these artificial substrates from locations throughout Koh Tao. We provide detailed comparisons between scleractinian coral communities growing on these synthetic substrate types and those on the natural reefs, and express these findings as possible insights into localised coral reef succession. We provide detailed comparisons between scleractinian coral communities growing on these synthetic substrate types and those on the natural reefs, and also consider depth, distance, time since deployment of artificial substrates as possible influencing covariates. We express these findings as possible insights into localised coral reef succession. In addition, we provide original data on coral spawning events which we use to support analyses investigating if and how sexual reproductive dynamics influence coral recruitment on artificial substrates (i.e. brooding vs. broadcasting coral communities). We therefore conclude by providing some hypotheses to explain the recruitment patterns and coral community structures at Koh Tao.

2. Methods

2.1. Data collection

2.1.1. Coral communities

Surveys were carried out between January 2018 and June 2019 at eight fringing nearshore reef sites and four offshore pinnacle sites. All 12 sites (Fig. 1) were predominantly comprised of aragonite skeleton/rubble (reefs) and granite boulders (pinnacles) and were thus classed as natural substrate sites. Surveys were also carried out at eight cubic frame (henceforth CF) sites and at the *HTMS Sattakut* shipwreck (henceforth 'Wreck'), together being classed as artificial substrate sites (Fig. 2). All artificial-substrate sites were adjacent (mean nearest distance <75 m) to at least one of the natural-substrate sites. Time since deployment was calculated for each artificial substrate immediately after surveys and were grouped into three classes, recent (<40 months), medium (40–90 months) and old (>90 months). All survey data was collected *in situ* using SCUBA, with distance measurements being taken using measuring reels and depth data collected via dive computers.

Surveys were carried out at natural substrate sites to collect data on the reef communities. Point-intercept transects (PITs) were carried out at two depth ranges, 3–5 m and 6–8 m, with a final total survey distance of 2.88 km. A 100-m measuring line was laid out across the natural reef at both depth ranges, divided into four 20-m replications being surveyed

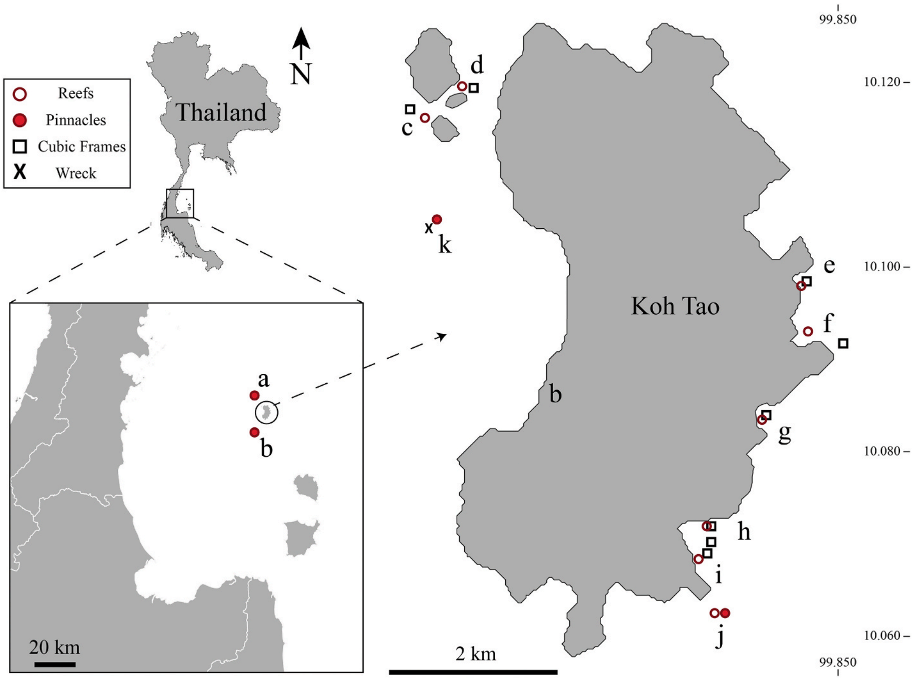

Fig. 1. A map of surveyed sites in the vicinity of Koh Tao. Sites: a) Chumphon Pinnacle, b) Southwest Pinnacle, c) Twins, d) Japanese Gardens, e) Mao Bay, f) Laem Thien, g) Tanote Bay, h) Leuk Bay, i) Hin Ngam, j) Shark Island, k) *HTMS Sattakut* wreck and Hin Pee Wee.

with a 5-m interval in between each following the protocol by Scott (2012). Surveys involved categorising the genus, health, and growth-form of every scleractinian coral at 50-cm intervals within each 20-m replicate resulting in 40 'points' surveyed per replicate. Non-coral substrates were categorised independently based on their nature (sponge, rock, sand etc.). Reef sites for PIT surveys were chosen based on the shortest distance to artificial substrate sites (see supplementary data). This was to best assess the hypothesis that artificial substrates nearest to natural reefs would share the greatest similarities in community structure. All suitable artificial substrate sites at Koh Tao were chosen and thus the maximum number of fringing reef sites were surveyed in an attempt to provide the best representation of natural reef community structures at the island. Surveys at pinnacle sites were carried out at four depth ranges, 9–11 m, 14–16 m, 19–21 m, and 24–26 m following the same methodology. Pinnacle survey depths were constrained by site-specific topography with a minimum of two depth ranges surveyed per site based on substrate available, and a mean of 2.7 PIT surveys per depth range per site, with a total survey distance of 0.54 km. Identifications followed Hoeksema (1989) for Fungiidae and Veron (2000) for other corals, with their taxonomy updated according to the WoRMS standard (Hoeksema and Cairns, 2021). At each site, data was collected on the community structure of hard coral cover (HCC) (i.e. abundance and diversity to a genus level) and structural complexity (based on coral growth forms). The community structure assessed presently includes the proportional representation of different coral groups (based on taxonomy, biological traits, structural complexity etc.) to provide a more holistic overview and provide inferences on possible successional pathways.

Surveys at artificial substrate sites collected data on coral recruits growing on the substrates. At CF sites, a minimum of 10 individual frames were surveyed per site. At each frame, the total abundance, diversity and community structure of recruits was assessed on the upper surface (surface area of approximately 0.9 m^2). Recruits were broadly identified *in situ* as corals were the result of sexual reproduction. Visually they were identified as corals that bore features indicative of early life-stage scleractinian corals such as being recognised as not being the result of asexual propagation of a parent colony, lacking growth form as is typical in later colony development etc. Across all sites, a total of 121 cubic frames (109.43 m^2) were surveyed. Estimates of diversity and community structure of recruits were identified to genus level, however for Fungiidae corals, recruits were only identified to family due to challenges of non-invasive identification methods of many recruits. These were therefore divided into monostomatous and polystomatous Fungiidae corals (Hoeksema, 1989, 1991; Gittenberger et al., 2011) and were compared as such across all surveys. In addition to a total recruit assessment, five randomly placed quadrats of 20 × 20 cm^2 were deployed at each frame, within which the maximum diameter of each recruit was measured using callipers. Quadrats were only placed on the upper horizontal surface as initial investigations of coral growth on external vertical surfaces revealed very few recruits. The depth of each frame was assessed based on the upper surface and categorised into one of three depth ranges, <10 m ($n = 24$), 10–15 m ($n = 72$) and >15 m ($n = 25$). Surveys at the wreck instead utilised five 100 × 100 cm^2 quadrats placed on the main deck (the most exposed upper surface) across the depth range of 24–26 m. At each quadrat, the total number of recruits were counted, with the maximum diameter of each recruit being measured with callipers or rulers. The diversity and community structure were assessed in the same way and following the same criteria as carried out at CF sites.

2.1.2. Coral reproduction

Information on the reproductive strategies of the different coral groups were assessed to investigate the role of spawning mode on the recruitment on artificial substrates. This information was gathered via visual identification of the most prevalent species per recorded genus on natural substrates and cross referencing each with available literature. For each species two parameters were investigated, reproduction mode (gonochoric or hermaphroditic) and spawning mode (brooding or broadcasting). In addition, data was collected independently on reproduction strategy of corals. Annually during the years 2016–2019, roving diver surveys (Hoeksema and Koh, 2009) using snorkelling and SCUBA were conducted in the months of March and April. Surveys were carried out daily between 2 and 6 days after the full moon, between 6 and 10 p. m., with data being supplemented with incidental observations outside

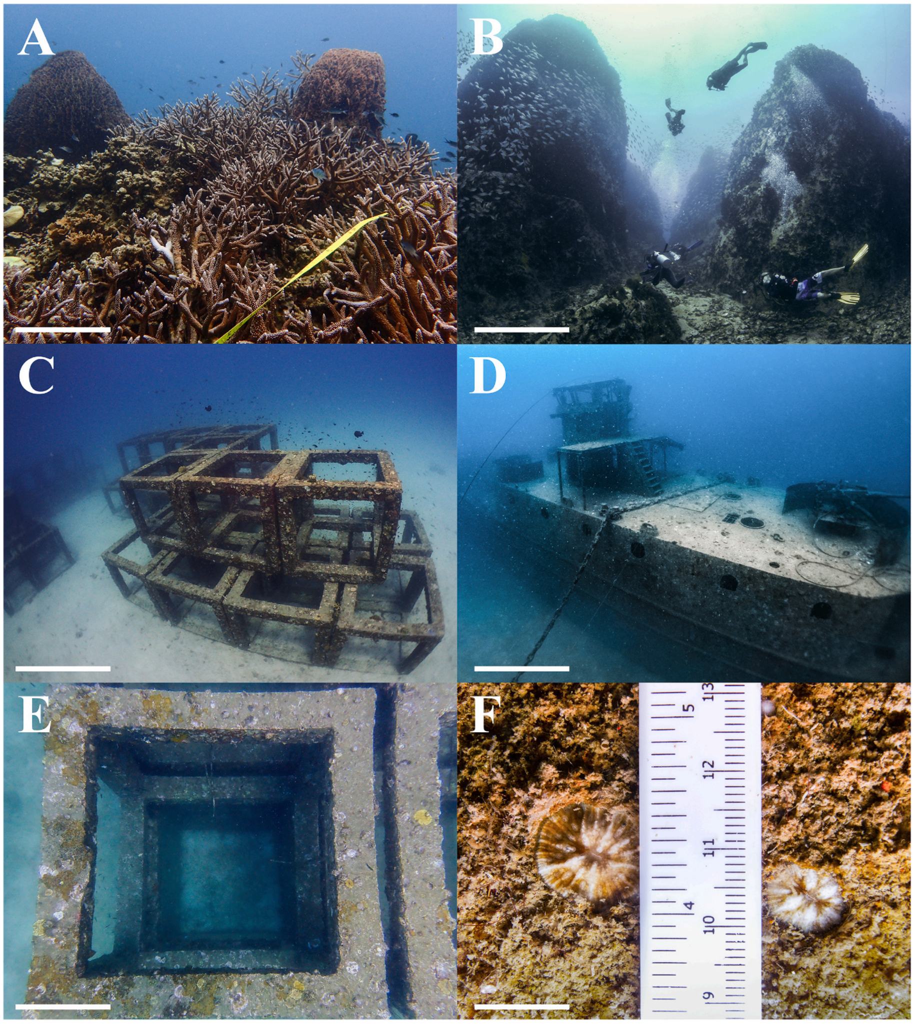

Fig. 2. The four substrate categories assessed around Koh Tao with scale bars (SB). A) Fringing reef SB 30 cm, B) Granite pinnacles SB 150 cm (photo by Wendy van Goethem), C) Cubic frames SB 100 cm, D) *HTMS Sattakut* wreck SB 120 cm (photo by Alexandra Vautin), E) Cubic frames from above SB 30 cm, F) Small Fungiidae recruits SB 1 cm.

dedicated surveys. Surveys were focused on documenting spawning method and times of different corals during the annual mass spawning events. Corals were identified to genus and to species level where possible. For simplicity in the present analysis, all species data were assumed as binary (either brooding or broadcasting, or either gonochoric or hermaphroditic), despite some evidence to the contrary (Harris, 1970; Guest et al., 2012). Once data for all species were reviewed (see supplementary data), reproduction data was generalised to genus level based on the modes and methods of the majority of species within each genus. The majority of prevalent species across all genera were found to be broadcast spawners therefore spawning mode was not included as a variable in further analyses, and only reproduction mode was tested.

2.2. Data treatment

To allow for comprehensive analyses, data were standardised where appropriate. Across all sites, community structure was assessed by calculating heterogeneity (Pielou's evenness index of abundance, PEI) based on abundance per group (per genus and both categories of Fungiidae recruits). This was supplemented by mean proportional abundance (%) per group per site for group-specific analyses. For artificial substrates, number of recruits were standardised to abundance.m^{-}2 and mean recruit size per CF or wreck quadrat was calculated based on individual recruits measured in each quadrat.

The growth form of all corals encountered during PIT surveys was assessed, resulting in a sample size of 2064 corals. The relative proportion of each growth form of each genus from natural substrate sites was calculated. All monostomatous Fungiidae corals were found to be detached, although they were originally attached directly after settlement, as in mushroom coral studies at other localities (Hoeksema and Gittenberger, 2010; Hoeksema and Yeemin, 2011; Hoeksema and Benzoni, 2013). Growth forms were categorised into three criteria: low structural complexity (encrusting, laminar, solitary), moderate complexity (massive, submassive, tabulate), and high complexity (branching, corymbose, digitate, foliose). The relative proportion of each type of complexity per genus was extrapolated to recruits on artificial substrates to investigate the near-future structural complexity of coral communities recruiting to artificial substrate sites.

2.3. Statistical analyses

All statistical analyses were performed in RStudio 1.1.463 (RStudio Team, 2015).

2.3.1. Environmental parameters

To evaluate the effect of environmental parameters on the coral community structure (abundance, diversity, evenness and diameter of

Table 1
Abundance, diversity and Pielou's evenness index (PEI) of coral communities at natural substrate sites at Koh Tao, based on PIT surveys. Values shown with ±standard error.

Natural Substrates and their depths	Abundance (HCC%)	Diversity (genera)	PEI
Fringing Reefs			
Shallow (3–5 m)	46.35 ± 2.29	5.36 ± 0.29	0.76 ± 0.02
Deep (6–8 m)	25.9 ± 1.81	4.23 ± 0.25	0.84 ± 0.02
All reefs	37.00 ± 1.72	4.84 ± 0.20	0.80 ± 0.02
Pinnacles			
10 m	10.00 ± 5.00	1.50 ± 0.50	1.00 ± 0
15 m	28.12 ± 4.53	4.50 ± 0.76	0.79 ± 0.02
20 m	18.96 ± 3.32	3.92 ± 0.57	0.87 ± 0.03
25 m	16.88 ± 6.24	3.50 ± 1.50	0.82 ± 0.06
All pinnacles	20.77 ± 2.44	3.85 ± 0.42	0.84 ± 0.02

the recruits), General Linear Models (GLM) (package lme4; Bates et al., 2015) were conducted with sites set as random factors to test the influence of depth on coral abundance, diversity and Pielou's evenness index (henceforth PEI) on natural substrates. The same GLMs were used to test the influence of depth, time and distance to the reef on recruit abundance, diversity, evenness and diameter.

Similarity of coral communities was examined using PERMANOVA (Adonis function, package vegan; Oksanen et al., 2019). The analysis was based on a resemblance matrix constructed from Bray-Curtis distances (based on the mean relative abundance per site of (1) genus; (2) family; (3) structural complexity class; (4) reproductive mode) and 9999 permutations. The environmental parameters were included as fixed factors in the PERMANOVA to test the influence of depth, time since deployment and distance to the closest reef for each artificial substrate site. To determine which coral genera primarily contributed to any demonstrated species differences, we conducted a SIMPER (Similarity Percentages Test) analysis, which provides the contribution of each individual variable to the overall Bray-Curtis dissimilarity. The test displays variables that contribute at least to 70% of the differences observed. SIMPER procedure was followed by Kruskal-Wallis test and Dunn test (package FSA; Ogle et al., 2019) for pairwise comparisons.

2.3.2. *Community comparisons*

Data were split and analysed separately, following the procedure described below, to: (1) compare the community between natural habitats (reefs vs. pinnacles); (2) compare the community between artificial habitats (wreck vs. CF); (3) compare the community present in artificial and natural habitats (CF and wreck vs. fringing reefs and off-shore pinnacles).

The differences in coral abundance, genus diversity and evenness of abundance were investigated using generalised linear mixed models (GLM) with the type of habitat or category as a fixed effect, and site identity as random factor. For inter-category comparisons, models were followed by a post-hoc pairwise comparison including a Bonferroni correction (package multcomp; Hothorn et al., 2008). Using similar models, the abundance and size of recruits on the two artificial substrate types were compared.

To visualize differences in coral communities, PERMANOVA and non-metric multidimensional scaling (nMDS) analyses were run. Hypothetical habitat definitions based on the ecological conditions of the sampling sites (reefs, pinnacles as natural condition, cubic frames, wreck as artificial condition) were used to overlay the samples in the generated ordination plots with 95% confidence ellipses to aid in understanding the differences in coral community structure. When PERMANOVA showed composition differences, SIMPER and Kruskal-Wallis tests were carried out as described above.

3. Results

3.1. *Abundance and diversity*

Across natural substrate sites, evenness was found to be fairly consistent with the lowest mean PEI values being at the shallowest fringing reefs surveyed (Table 1), suggesting relatively heterogenous coral communities throughout with no significant differences across depth gradients (Table 2). In contrast, considerable variation was found in terms of HCC at both fringing reefs and pinnacle sites. A continuous significant drop in coral cover was recorded with increasing depth across sites (GLM -2.265 ± 0.358, $p < 0.001$) with fringing reef sites overall hosting significantly higher coral cover than pinnacle sites (GLM 9.744 ± 2.663, $p = 0.001$) and reefs at 3–5 m with greater HCC than those at 6–8 m (GLM -5.024 ± 0.761, $p < 0.001$). Diversity of genera per transect was also found to be significantly reduced with depth (GLM -0.151 ± 0.044, $p < 0.001$) with reefs at 6–8 m hosting fewer genera than those at 3–5 m (GLM -0.437 ± 0.080, $p < 0.001$). However, no significant differences were found in the number of genera per transect between fringing reef and pinnacle sites (GLM 0.271 ± 0.385, $p = 0.485$) nor across different depths at pinnacle sites alone (GLM 0.074 ± 0.113, $p = 0.523$).

The relative proportion of coral groups did not vary significantly with depth, at either the higher taxonomic resolution (individual genera

Table 2
Statistical assessment on the influence of depth, time since deployment and distance from reef of coral communities at Koh Tao. Hard coral cover (HCC), diversity, Pielou's evenness index (PEI), abundance and size of recruits and tested using General Linear Models, remaining variables tested using PERMANOVA. Significant results in bold.

	Depth	Deployment	Distance from reef
Natural habitat			
HCC	−2.265 ± 0.358, **p < 0.001**	–	–
Diversity	−0.151 ± 0.044, **p < 0.001**	–	–
PEI	0.021 ± 0.021, p = 0.320	–	–
Genera	Pseudo-F = 1.091, p = 0.356	–	–
Families	Pseudo-F = 1.113, p = 0.351	–	–
Structural complexity	Pseudo-F = 3.848, **p=0.011**	–	–
Reproductive mode	Pseudo-F = 0.022, p = 0.880	–	–
Artificial habitat			
Recruit abundance	9.040 ± 1.022, **p < 0.001**	1.674 ± 0.444, **p=0.003**	−0.066 ± 0.171, p = 0.708
Diversity	0.231 ± 0.097, **p=0.034**	0.029 ± 0.026, p = 0.285	0.008 ± 0.006, p = 0.200
Recruit size	−0.015 ± 0.760, p = 0.985	−0.165 ± 0.184, p = 0.389	−0.004 ± 0.047, p = 0.938
PEI	−0.024 ± 0.041, p = 0.565	0.002 ± 0.011, p = 0.880	0.002 ± 0.002, p = 0.288
Genera	Pseudo-F = 6.440, **p < 0.001**	Pseudo-F = 2.855, p = 0.069	Pseudo-F = 0.766, p = 0.535
Families	Pseudo-F = 7.126, p = 0.053	Pseudo-F = 3.140, p = 0.073	Pseudo-F = 0.363, p = 0.670
Structural complexity	Pseudo-F = 9.300, p = 0.053	Pseudo-F = 3.834, p = 0.057	Pseudo-F = 0.249, p = 0.693
Reproductive mode	Pseudo-F = 10.101, p = 0.063	Pseudo-F = 3.385, p = 0.073	Pseudo-F = 0.326, p = 0.604

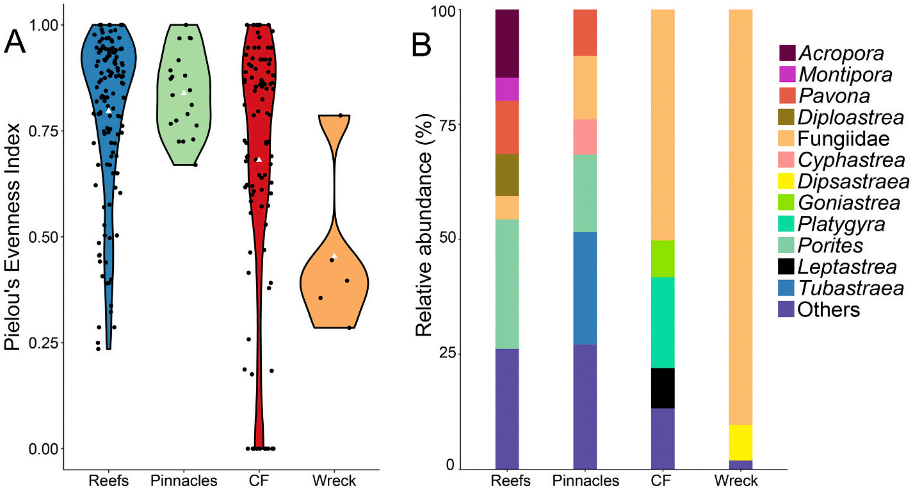

Fig. 3. Evenness (A) and proportional representation of coral groups (B) at surveyed substrates. 'Others' include corals with <5% representation at any substrate type. Cubic frames abbreviated to CF.

and Fungiidae categories) or lower resolution (coral families). There were, however, significant differences between fringing reefs and pinnacle sites (PERMANOVA Pseudo-F = 3.306, $p < 0.001$) with the genera *Acropora* (Kruskal-Wallis H = 9.758, df = 1, p = 0.002) and *Diploastrea* (Kruskal-Wallis H = 9.442, df = 1, p = 0.002) being represented at significantly greater proportions at reefs over pinnacles (see Supplementary data). In contrast, the Dendrophylliidae (Kruskal-Wallis H = 8.626, df = 1, p = 0.003) and in particular the genus *Tubastraea* (Kruskal-Wallis H = 6.821, df = 1, p = 0.009) were significantly more abundant at pinnacle sites over reefs (Fig. 3B).

A total of 2677 coral recruits were counted and identified across all artificial substrate sites, 733 of which the diameter was measured. In contrast with natural substrates, the abundance of corals at artificial substrate sites was found to increase with depth (GLM 9.040 ± 1.022, $p < 0.001$) (Table 3). While recruit abundance was found to increase significantly with deeper cubic frames (GLM 0.365 ± 0.072, $p < 0.001$), no significant difference was found between CF sites and the wreck (GLM 2.315 ± 1.148, p = 0.069), nor across the narrow depth range at the wreck (LM 47.25 ± 40.86, p = 0.331). Similarly, diversity of corals increased significantly with depth across artificial substrates (GLM 0.231 ± 0.097, p = 0.034) with significant differences across CF sites (GLM 0.430 ± 1.308, p = 0.015) but none between CF sites and the wreck (GLM 0.598 ± 1.718, p = 0.734). The mean size of recruits did not vary considerably and was not significantly different across the different parameters tested.

Recruit abundance varied significantly (GLM 1.674 ± 0.444, p = 0.003) across artificial substrates deployed years apart, ranging from 17.52 ± 2.36 to 140.8 ± 41.69 over the three time periods (Table 3). However, no significant difference was found in recruit diversity or PEI values between the three time periods (Table 2). Depth did not appear to influence heterogeneity across artificial substrate sites, with PEI varying considerably, ranging from 0.40 ± 0.04 to 0.76 ± 0.04 (Table 3). The proportion of monostomatous fungiids in the attached anthocaulus phase was found to be significantly greater at artificial substrate sites >15 m than those at the 10–15 m depth range (Kruskal-Wallis H = 9.867, df = 1, p = 0.031). This contributed to a disproportionate increase in abundance with depth when compared to other corals at the genus level but not to family (Table 2). This was largely driven by a 3.4 times greater proportion of these recruits at the wreck than across all CF sites.

Coral communities overall differed significantly between natural and artificial substrate sites (Fig. 4). Natural sites hosted more heterogeneous coral communities (GLM 0.183 ± 0.035, $p < 0.001$) with a higher mean PEI value of 0.80 ± 0.01 compared to 0.67 ± 0.03 at artificial substrate sites (Fig. 3A). Differences in diversity were driven by attached monostomatous and polystomatous Fungiidae corals being significantly more abundant (Kruskal-Wallis H = 8.866, df = 1, p = 0.003 and H = 19.274, df = 1, $p < 0.001$, respectively) at artificial substrate sites and *Pavona* and *Porites* corals being more abundant (H = 20.609, df = 1, $p < 0.001$ and H = 8.696, df = 1, p = 0.003 respectively) at natural substrate

Table 3
Abundance, diversity, size and Pielou's evenness index (PEI) of coral communities at artificial substrate sites at Koh Tao, based on quadrats. Values shown with ±standard error.

Artificial substrates	Abundance (m^{-2})	Diversity (genera.m^{-2})	Diameter (mm)	PEI
Depth range				
<10 m	6.45 ± 1.66	1.83 ± 0.33	31.76 ± 4.23	0.54 ± 0.10
10–15 m	11.21 ± 1.61	2.94 ± 0.23	35.13 ± 2.23	0.76 ± 0.04
>15 m	64.12 ± 9.71	4.47 ± 0.30	29.55 ± 2.59	0.57 ± 0.04
Time since deployment				
<40 months	17.52 ± 2.36	2.86 ± 0.22	36.59 ± 2.24	0.66 ± 0.04
40–90 months	18.80 ± 3.5	3.33 ± 0.33	27.26 ± 2.34	0.71 ± 0.05
>90 months	140.8 ± 41.69	4.20 ± 0.49	33.43 ± 1.63	0.45 ± 0.19
Distance from reef				
<70 m	15.53 ± 4.63	2.24 ± 0.20	33.42 ± 2.22	0.63 ± 0.05
70–140 m	38.23 ± 4.20	4.30 ± 0.29	31.70 ± 2.282	0.68 ± 0.04
>140 m	17.58 ± 1.92	4.80 ± 0.39	35.07 ± 2.63	0.86 ± 0.02
Wreck only				
24 m	103 ± 26.58	3 ± 0.67	33.90 ± 2.8	0.49 ± 0.15
26 m	197.5 ± 99.5	5.00 ± 0	32.73 ± 1.48	0.40 ± 0.04

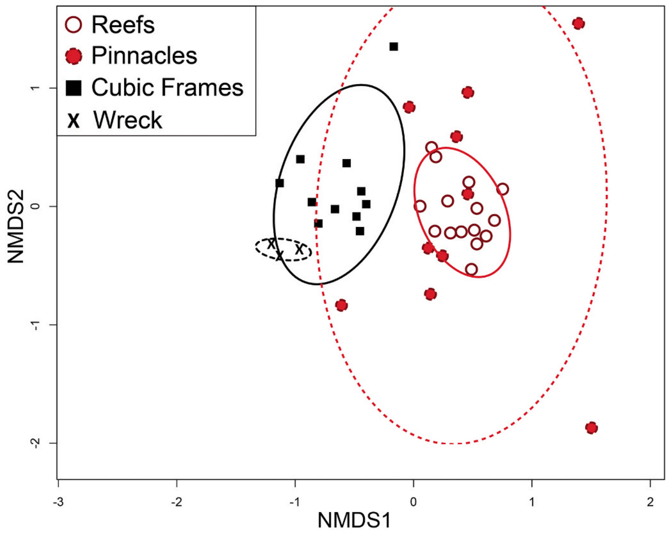

Fig. 4. Non-metric MDS ordination (stress 0.11) of coral community variation among surveyed sites. Ellipses represent the 95% confidence interval.

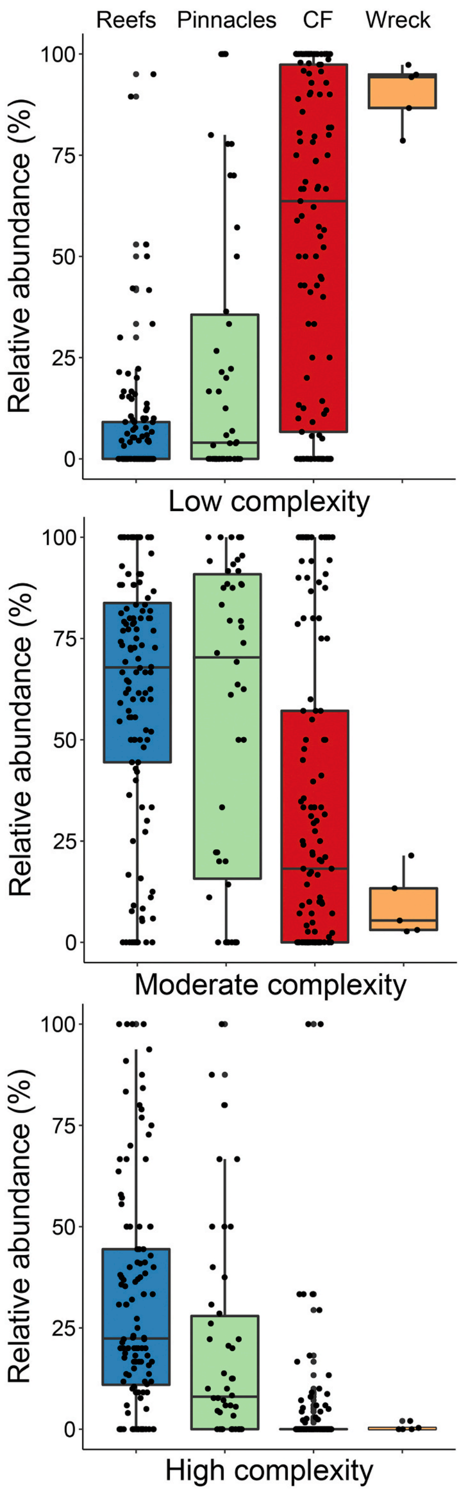

Fig. 5. Proportional representation of coral communities at different substrate types around Koh Tao based on structural complexity.

sites (Fig. 3B).

3.2. *Growth and reproduction*

Assessments of structural complexity across natural substrate sites revealed depth to be an influencing factor (Fig. 5, Tables 2 and 4), with the abundance of low-complexity corals increasing with depth (GLM 0.126 ± 0.032, $p < 0.001$). Conversely, moderate and high complexity corals decreased with depth (GLM -0.067 ± 0.035, $p = 0.050$ and -0.043 ± 0.025, $p = 0.083$ respectively). While depth was not found to influence complexity across fringing reef sites (PERMANOVA Pseudo-F = 0.369, $p = 0.862$), it was found to be an influencing factor across offshore pinnacle sites (PERMANOVA Pseudo-F = 4.062, $p = 0.022$). In particular, the relative abundance of low complexity corals was found to drastically increase with depth (GLM 0.175 ± 0.068, $p = 0.010$). An inverse trend between depth and relative abundances of high-complexity corals was also observed, however this was not found to be significant (GLM -0.057 ± 0.037, $p = 0.130$). Structural complexity was found to differ significantly between fringing reef sites and offshore pinnacles (PERMANOVA Pseudo-F = 6.750, $p = 0.004$) driven by pinnacle sites hosting greater proportions of low complexity corals (Kruskal-Wallis: $H = 5.691$, $df = 1$, $p = 0.017$) and reef sites hosting greater proportions of moderate complexity corals (Kruskal-Wallis $H = 5.436$, $df = 1$, $p = 0.020$). In contrast, neither depth nor time since deployment were found to influence structural complexity across CF sites, the wreck or all artificial substrates combined. Overall, artificial substrates sites appeared to be significantly enriched in low-complexity corals (Kruskal-Wallis $H = 14.941$, $df = 1$, $p < 0.001$) and natural substrate sites appeared to host relatively greater proportions of moderate complexity corals (Kruskal-Wallis $H = 4.568$, $df = 1$, $p = 0.033$). Natural substrate sites also hosted proportionally higher abundances of high complexity corals (Kruskal-Wallis $H = 15.739$, $df = 1$, $p < 0.001$) with only the deepest pinnacles hosting <10% of high complexity corals and only the shallowest artificial substrates hosting >10% (Table 4).

Night-time field surveys resulted in the documentation of repeated synchronous spawning by corals belonging to 18 coral genera at Koh Tao between 2016 and 2019 (see Table 5). In conjunction with available literature, the assigned generalised genus-specific reproduction modes yielded no significant difference in coral community structure as defined by their reproductive biology. The relative proportion of either reproductive mode varied considerably across depth ranges and substrate types. Neither natural nor artificial substrate sites varied significantly in their proportion of gonochoric or hermaphroditic corals across any of the tested parameters (Tables 2 and 5). The majority of assessed corals were broadcast spawners, the relative proportion of which did not vary considerably by depth or between natural and artificial substrate sites. Assessments of the distance between artificial substrate sites and their nearest pinnacle or reef found no significant effect on any tested variable.

The diversity and abundance of corals were both found to decline with depth significantly across the natural substrate sites of Koh Tao.

Table 4

Proportional representation of coral communities at different substrate types around Koh Tao based on structural complexity and reproductive mode. Values shown with ±standard error.

Substrate depths	Low (%)	Moderate (%)	High (%)	Gonochoric (%)	Hermaphroditic (%)
Fringing reefs					
Shallow (3–5 m)	7.64 ± 1.92	68.58 ± 2.96	28.78 ± 2.30	64.22 ± 2.89	35.78 ± 2.89
Deep (6–8 m)	7.61 ± 1.69	54.82 ± 4.36	37.56 ± 3.85	51.49 ± 3.55	48.51 ± 3.55
All reefs	7.63 ± 1.28	61.79 ± 2.67	30.58 ± 2.29	58.4 ± 2.31	41.6 ± 2.31
Pinnacles					
10 m	0 ± 0	25.00 ± 25.00	75.00 ± 25.00	0 ± 0	100 ± 0
15 m	24.17 ± 5.16	36.33 ± 10.41	39.5 ± 9.91	49.01 ± 11.24	50.99 ± 11.24
20 m	44.53 ± 11.6	36.35 ± 11.78	19.12 ± 8.53	45.46 ± 9.56	54.54 ± 9.56
25 m	87.50 ± 7.5	5.0 ± 5.0	7.5 ± 4.79	88.89 ± 7.86	11.11 ± 7.86
All pinnacles	41.45 ± 7.27	30.65 ± 6.71	27.90 ± 6.17	49.73 ± 6.93	50.27 ± 6.93
Cubic Frames					
<10 m	15.98 ± 3.17	73.67 ± 6.14	10.35 ± 6.70	19.10 ± 6.35	80.90 ± 6.35
10–15 m	66.86 ± 3.65	29.78 ± 3.46	3.37 ± 1.00	55.91 ± 4.70	44.09 ± 4.70
>15 m	85.92 ± 2.74	13.82 ± 2.69	1.27 ± 0.44	79.87 ± 4.01	20.13 ± 4.01
All	62.22 ± 3.16	33.69 ± 3.02	4.09 ± 1.31	54.95 ± 3.64	45.05 ± 3.64
Wreck					
24 m	90.61 ± 3.94	9.34 ± 3.93	0.05 ± 0.05	88.28 ± 6.54	11.72 ± 6.54
26 m	96.27 ± 0.53	3.05 ± 0.86	1.68 ± 0.34	94.68 ± 0.32	5.32 ± 0.32
All wreck	92.87 ± 2.57	6.82 ± 2.66	0.31 ± 0.19	90.84 ± 3.91	9.16 ± 3.91

Table 5

Summary of *in situ* spawning observations at Koh Tao (2016–2019, complete table available as supplement). Observations where reproduction mode was unclear were recorded as 'Unknown'. *Observations of *Diploastrea* corals appeared gonochoric *in situ* however verification is needed based on conflicting literature.

Family	Coral	Years observed	Rep. Mode
Acroporidae	*Acropora* spp.	2017–019	Hermaphroditic
Acroporidae	*Montipora* spp.	2016, 2018, 2019	Hermaphroditic
Agariciidae	*Pavona explanulata*	2016	Gonochoric
Diploastraeidae	*Diploastrea heliopora*	2016–2019	Gonochoric?*
Euphylliidae	*Galaxea fascicularis*	2016–2019	Hermaphroditic
Fungiidae	*Danafungia scruposa*	2019	Gonochoric
Fungiidae	*Fungia fungites*	2019	Gonochoric
Fungiidae	Misc. Fungiidae spp.	2016–2019	Unknown
Fungiidae	*Polyphyllia talpina*	2019	Gonochoric
Lobophylliidae	*Lobophyllia* spp.	2016–2019	Hermaphroditic
Merulinidae	*Cyphastrea* sp.	2019	Hermaphroditic
Merulinidae	*Dipsastraea* spp.	2018, 2019	Hermaphroditic
Merulinidae	*Favites* spp.	2016, 2018, 2019	Hermaphroditic
Merulinidae	*Goniastrea edwardsi*	2016–2019	Hermaphroditic
Merulinidae	*Goniastrea* sp.	2019	Hermaphroditic
Merulinidae	*Merulina ampliata*	2018, 2019	Hermaphroditic
Merulinidae	*Paragoniastrea australensis*	2019	Hermaphroditic
Merulinidae	*Platygyra* spp.	2016–2019	Hermaphroditic
Poritidae	*Goniopora* sp.	2018	Unknown
Poritidae	*Porites* spp.	2016, 2017, 2019	Gonochoric

Meanwhile, both diversity and abundance of coral recruits on artificial substrates increased significantly with depth, in direct contrast to patterns on natural substrates. Depth was found to be a more influential factor of all assessed variables of recruitment on artificial substrate sites than time since deployment of each substrate site, and distance from nearest natural reef (Table 2). The observation that most recruitment occurred on exposed upper surfaces is also common in other studies investigating the influence of depth on recruitment (Fisk and Harriott, 1990; Gleason, 1996; Kramer et al., 2019). Natural substrate sites were however, not found to vary significantly in their compositional evenness (Fig. 3A), with PEI values ranging from 0.80 (±0.02) across fringing reefs to 0.84 (±0.02) at pinnacle sites, indicating relatively heterogeneous reefs across all depths. Additionally, no significant differences were found in the representation of any surveyed coral taxon across natural substrate sites. These trends lend themselves to the crude assumption that the coral communities at natural substrate sites are, at present, relatively stable (but see Scott et al. (2017b)), and are influenced by similar factors across the surveyed sites. In contrast, the present findings indicate significant differences in the evenness and representation of corals across artificial substrate sites. Specifically, artificial substrates had a mean PEI ranging from 0.68 (±0.03) across CF sites to 0.45 (±0.19) at the wreck. The coral community structure on artificial substrates was also significantly more homogenous, with certain coral groups being far better represented than others, and more variable than those on natural substrate sites (Tables 1–3; Fig. 3). While other organisms such as macroalgae (specifically *Lobophora* sp.), sponges, and bivalves were observed utilising the substrates at various levels, observed cases of direct competition were few (<1%) and abundance of these organisms was not quantified. Similarly, while crustose coralline algae (CCA), an important facilitator of coral recruitment, was found to be present on some surveyed CFs and entirely absent on others, this was not quantified in the present study.

4. Discussion

4.1. Variation in coral recruitment

In the literature, there is conflicting evidence to suggest that specific artificial reefs and substrate types both do and do not appear to alter recruitment dynamics of some invertebrates when compared to some non-synthetic substrates. Calumpong et al. (2003) showed that concrete tiles offered no significant difference to larval recruitment of the reef-dwelling giant clam *Tridacna squamosa*, when compared to that of dead coral or shells of dead adult *T. squamosa*. Similar treatments have been applied to *in situ* coral recruitment such as by Fitzhardinge and Bailey-Brock (1989) who found similar community development of coral recruits on both concrete and dead coral skeleton substrates over a 12-month period, however noting significantly higher recruitment on painted steel. Creed and De Paula (2007) and Burt et al. (2009a) found no significant difference in coral recruitment between synthetic and natural mineralogical substrates that are widely used in recruitment studies (terracotta, granite, concrete etc.) Instead, variability in recruitment was greater across study sites than across substrate types, further suggesting a non-significant influence of these substrates on recruitment studies (Burt et al., 2009a). In the latter case however, the same authors also highlight significant differences in community structure between well-established artificial reefs (<25 years) made of the same substrates, and those of nearby natural reef sites (Burt et al., 2009b).

Similarly, other studies (Perkol-Finkel and Benayahu, 2004; Blakeway et al., 2013; Hill et al., 2021) were able to compare coral communities between natural reefs and recruits on artificial substrates, finding dramatic differences in their composition with several groups being better represented on one substrate type over the other. Coral recruitment on reefs at Koh Tao has recently been assessed (Hein et al., 2020) where juvenile coral counts were carried out at restored sites (i.e. those with active transplantation of coral onto artificial substrates) and compared to control natural reefs. High variability in juvenile abundance was found across the three surveyed sites, possibly linked to structure and substrate types assessed, however compositional differences were not assessed. Few comparisons can be made between Hein et al. (2020) and the present findings, as recruitment on natural substrates, and on artificial substrates influenced by active transplantation, was not within the scope of this study. Divergences in coral communities on artificial substrates in the present study were largely driven by disproportionately low abundances or complete absences of corals that are abundant on fringing reef (i.e. *Porites*, *Acropora*, *Pavona* and *Diploastrea*) or pinnacle (i.e. *Tubastraea*, *Porites* and *Pavona*) sites (see supplementary material). Instead, certain coral groups were found to be exceptionally well represented (i.e. *Dipsastraea* and *Platygyra*), often playing dominant roles on artificial substrates that were less abundant on natural substrates. In particular, the representation of two coral groups were most notable, these being corals of the Fungiidae, and of *Leptastrea*.

Fungiid corals are well represented at Koh Tao (Hoeksema et al. 2012, 2013; Mehrotra et al., 2019) with the present findings indicating a proportional abundance of 5.08% (±1.23) at fringing reefs and 13.85% (±5.61) at pinnacle sites. However, the relative proportion at CF sites were at least four times greater (23.55 ± 2.81%) than at reefs, and at the wreck was approximately 13 times greater (80.56 ± 3.96%) than that of fringing reefs (Fig. 3B). The higher relative abundances of fungiid corals at pinnacle sites over fringing reefs, and at the wreck over shallower CF sites, further indicates a possible depth-based influence, therefore supporting our first hypothesis. It should be noted that the wreck was the only site at which sufficient time had passed to allow many fungiid recruits to reach a size whereby identification to species level was possible *in situ*. Species identified include *Cycloseris costulata*, *C. mokai*, *Fungia fungites*, *Pleuractis moluccensis*, and *P. paumotensis*. However, as identification to such a level was not possible for all recruits at all sites, analyses remained restricted to monostomatous and polystomatous recruits, though it was observed that a substantial proportion of small polystomatous fungiids were *C. mokai*, an encrusting species that always remains attached (Benzoni et al., 2012; Hoeksema, 2012a). Unattached species at the wreck were able to mature sufficiently to allow for many to break free of their stalks and gain access to mobility and dispersal over the seafloor (see Hoeksema, 1988; Mondal and Raghunathan, 2015; Ohara et al., 2021). This allowed for the observation that both, encrusting and free-living Fungiidae were well represented at the wreck and around it.

The absence of *Tubastraea* corals on the shipwreck (since 2011) and the cubic frames (since 2013) is remarkable. In many localities, *Tubstraea* spp. have been observed to grow on all kinds of artificial substrate, such as concrete (Ho et al., 2017) and plastics (Hoeksema and Hermanto, 2018; Valderrama Ballesteros et al., 2018; Faria and Kitahara, 2020), and in particular as invasive species on metal structures, such as ship hulls (Boschma, 1953), shipwrecks (Hoeksema et al., 2019b; Soares et al., 2020), pontoons (López et al., 2019; Tanasovici et al., 2020), and oil platforms (Brito et al., 2017; Creed et al., 2017). At Koh Tao, high abundances of *Tubastraea micranthus* were only found on the pinnacles, where they showed high abundances during the present study and earlier (Fig. 3; Valderrama Ballesteros et al., 2018), whereas the same species has been recorded as an invasive on oil rigs in the Gulf of Mexico (Sammarco et al., 2010, 2014). The absence of *Tubastraea* on the artificial substrates around Koh Tao, cannot be explained by isolation because they are situated close to natural reefs and they have been in the water for many years. *Tubastraea* corals have been observed to have rapid range expansions (Santos et al., 2019) and the larvae of *T. coccinea*, for example, have been observed to survive in the water for 2–3 months (Luz et al., 2020). Also, there is no reason to believe that the artificial substrate was unsuitable for settlement because fungiids were sufficiently abundant. Furthermore, *Tubastraea* corals are azooxanthellate and therefore they have not undergone coral bleaching and mortality like most other assessed genera at the island. The absence of *Tubastraea* species on the artificial substrates of Koh Tao and their abundant presence on natural substrates therefore certainly deserves further study.

The genus *Leptastrea* (specifically *L. purpurea*) was found to be uncommon throughout the surveyed reefs, comprising less than 1% of the coral communities at either fringing reef or pinnacle sites, and was entirely absent from the surveyed areas of the wreck. In previous studies (2014), *Leptastrea* corals were reported as relatively rare or absent (Moerland et al., 2016; Scott et al., 2017a). However, recruits of the genus comprised 8.77% (±1.89) of corals at CF sites, being at their highest abundance at structures in the 10–15-m range (10.94 ± 2.77%). Furthermore, *Leptastrea* recruits were recorded at all CF sites with no indication that any particular site hosted a disproportionate abundance of the coral, with no statistical support for differences based on depth, time since deployment nor distance from the reef, weakening support for hypotheses i-iii). Therefore, at present its abundance at CF sites across the island cannot be explained by the results in this investigation. The prevalence of both these corals and the remarkable differences in their abundances across the different substrate types strongly suggests that coral recruitment is determined fundamentally by life-history traits of specific coral groups. Indeed, this has been suggested and observed for a number of years within natural reefs. Edmunds (2000) surveyed juvenile corals within reefs at the US Virgin Islands finding that neither diversity, abundance nor reproductive mode correlated with those of the natural reef. The sparsity of information in this regard was highlighted by Bridge et al. (2020) who showed little correlation between the IUCN Red List conservation status of corals and their life-history traits. They further argue that most assessed corals should instead be classified as ‘Data deficient’ due to the lack of data for most species. Recent efforts have begun to focus on these aspects when investigating *in situ* recruitment (Doropoulos et al., 2017) however no work has yet been carried out to thoroughly compare coral recruitment within natural and artificial reefs with a focus on life-history traits.

In an effort to bridge this gap, we investigated one such aspect on recruitment and resulting community structure. Overall, it was found that 60% of coral genera surveyed at Koh Tao for which data was available in the literature were hermaphroditic, with the remaining being gonochoric or probably gonochoric (see Guest et al. (2012) regarding *Diploastrea*). When analysed, the proportions of corals employing either reproductive mode were not found to vary significantly across the tested parameters. Additionally, it was noteworthy that the higher abundance of coral recruits at ‘older’ artificial structures (those deployed earlier) combined with the lack of difference in the mean size of recruits are indicative of continued and regular settlement of coral larvae. Sporadic or halted colonisation of substrate by larvae would likely allow for resolved differences in mean recruit size as older recruits continued to grow. This assumes however that growth rate is uniform across substrates, among other factors, some of which have been investigated here.

Similar comparisons of reproductive mode were not carried out for the more relevant aspect of spawning mode due to an insufficient representation of, or available data on, brooding corals at Koh Tao (see supplementary material). The reproductive biology of corals has nonetheless been investigated as a possible contributing trait to recruitment patterns, with the most extensive work being carried out at the Great Barrier Reef (GBR). Hughes et al. (2002) identified spatial variability in the proportions of brooding versus broadcasting corals across multiple locations within the GBR, highlighting strong latitudinally driven trends in corals carrying out either spawning mode. The same authors had however also shown earlier (Hughes et al., 1999) that reefs across the GBR showed profound differences in their reproductive turnover (with regards to the spawning mode of corals) despite similarity across parent reefs. These studies show that while successional patterns may be observed over large spatial scales, reef colonisation at local scales need not be a linear process and may in fact be determined by factors yet unknown.

4.2. Possible explanations

In the present study, we aimed to test the following hypotheses: i) there is a direct relationship between depth and the community structure of corals on artificial reefs and natural reefs; ii) distance between artificial reefs and their nearest natural reef has a significant influence on the community of coral recruits on artificial reefs; iii) the time since deployment of artificial substrates has a significant influence on coral community structure; iv) there is a direct relationship in the community structure between artificial and natural reefs, which can be explained by the influence of depth, distance and time as mentioned in i-iii). Our data indicates that while hypothesis i) appears to be valid with depth significantly influencing community structure across artificial and natural reefs, hypotheses ii) and iii) are not supported by our findings. By almost all measured attributes, no direct relationship can be found between the community structure on artificial and natural substrates at Koh Tao and surrounding sites, further disproving hypothesis iv). Therefore, we briefly discuss three possible hypotheses to explain these findings, as a guide for further investigations.

4.2.1. Local barriers to settlement

Hypothesis: ‘The recruitment patterns of corals at Koh Tao are primarily determined by the influence of disturbance events, which act as a barrier to survival of less resilient larvae’. The reefs of Koh Tao have been subject to multiple disturbance events in recent years such as predator outbreaks, adverse weather events and mass coral bleaching driven by elevated sea surface temperatures (Scott et al., 2017a, 2017b). Several such events have been attributed to play a role in shifting coral communities across the reefs of Koh Tao (Scott et al., 2017a), with the frequency of such events being found to be increasing in recent years. Both factors (elevated sea surface temperatures and high rates of precipitation) have been linked to a changing global climate (Baker et al., 2008; Trenberth, 2011; Cai et al., 2015). The influence of such events during optimal spawning and settlement periods for corals at Koh Tao may act as a barrier to larval survival and settlement, in particular to less resilient corals. Testing this hypothesis would require a comprehensive assessment of natural recruitment within reefs, as well as investigations into rates of survival of coral larvae at Koh Tao.

Nonetheless, comparisons may be made between the community structure documented here and those on the reefs of Koh Tao between 2006 and 2014 (Scott et al., 2017a). Overall, there is general agreement in the compositional structure of reefs between 2014 and 2018–2019, with *Porites*, *Pavona* and *Acropora* corals being the most abundant overall (comprising 51.9% in 2014 and 54.5% in 2018–2019), and fungiids on a few localities (Hoeksema and Matthews, 2011; Hoeksema et al., 2012, 2013). It should be noted that the recent findings represent only a subset of sites surveyed in 2014. The proportion of corals attributed as ‘resilient’ (i.e. *Porites*, *Pavona*, Fungiidae) and those of less resilience (*Acropora*, *Montipora* and *Diploastrea*) do vary considerably in their representation. A dramatic increase in the representation of *Porites* corals is documented, from 16.6% (±1.9) in 2014 to 28.2% (±2.55) in 2018–2019, in agreement with the trends observed by Scott et al. (2017a). However, less resilient corals were remarkably similar in their representation with a 0.1% increase, 1.2% decrease and 2.8% increase for *Acropora*, *Montipora* and *Diploastrea,* respectively. In contrast, *Pavona* and Fungiidae corals were found to be represented at 9.1% and 8.7% less than in 2014. Crucially, while the representation of fungiid corals is dominant across artificial substrates in 2018–2019, other corals that have been found to be resilient to environmental stressors in Thailand (Sutthacheep et al., 2018, 2019) are almost entirely absent from artificial substrates, thus not supporting the hypothesis.

4.2.2. External drivers to settlement

Hypothesis: ‘The recruitment patterns of corals at Koh Tao are driven primarily by non-local parent populations which act as a source for resulting communities on artificial substrates’. The discrepancy between proportional representation of corals on natural substrates and those on artificial substrates (hypothesis iv) may be explained by considering the hydrodynamic conditions during peak spawning periods at Koh Tao. Assessments of sea surface currents for the Gulf of Thailand during peak spawning and settlement periods at Koh Tao (March–May) indicate a flow from the mainland in the North and West towards Koh Tao (Sojisuporn et al., 2010; Saramul, 2017). This may play a significant role in larval transport, potentially driving recruitment of corals better represented nearer to the mainland than at offshore islands and pinnacles. This is possibly supported by the recent findings of Sutthacheep et al. (2019) who found a relatively high representation of juvenile fungiid and *Leptastrea* corals at nearby mainland reefs, both of which are well represented at artificial substrates at Koh Tao (Fig. 3B). However, high representation was also found of *Pocillopora*, *Porites* and *Pavona* corals, which are less well represented or entirely absent from the same structures at Koh Tao though *Porites* and *Pavona* are well represented at both fringing reefs and offshore pinnacles near Koh Tao. The same hydrodynamic constraints may further explain the divergence in community structure between reefs at Koh Tao and the nearby artificial substrates, if the majority of local larvae are transported elsewhere rather than being retained nearby. A comprehensive assessment into the population genetics of corals along the western Gulf of Thailand may help test this hypothesis.

4.2.3. Competitive advantages

Hypothesis: ‘The recruitment patterns of corals at Koh Tao are primarily determined by life-history traits providing competitive advantages to specific coral groups over others’. Common selective pressures may vary considerably in their limiting capabilities on successful coral recruitment, and successful recruitment of a given group may be reinforced by specific life-history traits. The artificial substrates tested differ from the natural substrates in multiple ways, such as substrate type, distance from sexually active corals, length of time in which to support colonisers etc. The findings presented here were unable to test possible influences of substrate type as a limiting or reinforcing factor on specific coral types. Of the three core parameters tested (depth, time since deployment and distance from reef), the role of depth (hypothesis i) was most significant in its possible influence on coral communities, on both natural and artificial substrates. Therefore, we will use depth as an example to explore the possible mechanisms that lead to a coral community resulting from a scenario driven by competitive advantages.

The primary constraint of depth in most photoautotrophic reefs systems is the availability of light. Certain corals may have developed traits to be better suited to low-light conditions, thus giving them a competitive advantage over other colonising corals. For example, there is evidence to suggest that multiple groups of zooxanthellae may be found in corals predominantly in deeper waters, possibly facilitating improved autotrophic gains to host corals under low-light conditions (Frade et al., 2008; Bongaerts et al., 2010; Lesser et al., 2010). Additionally, there is growing evidence that different zooxanthellate corals likely rely on their symbionts to different degrees, with some adapted to favouring heterotrophic energy acquisition over autotrophic means (Slattery et al., 2011; Conti-Jerpe et al., 2020). Various free-living fungiid corals for example have been found to be able to ingest and consume a wide range of relatively large prey, an ability that has been attributed to their large gape size (Alamaru et al., 2009; Hoeksema and Waheed, 2012; Mehrotra et al., 2019). Similarly, the soft sediment associated coral *Heteropsammia cochlea* has also been shown to be able to ingest large prey due to its gape size (Mehrotra et al., 2016) and is believed to be apozooxanthellate based on its facultative relationship with algal symbionts (Hoeksema and Matthews, 2015). Such adaptations are likely to provide a competitive advantage to corals in deeper waters where prey availability is able to support metabolic needs of corals to a greater degree than products limited by light availability. This in turn may drive the development of highly divergent coral communities, a trend that is increasingly apparent in mesophotic coral ecosystems (Slattery et al., 2011; Rocha et al., 2018), with certain groups such as fungiid corals being better represented at depth (Kramer et al., 2019) in certain areas.

While the gape size of coral groups recruiting onto the artificial substrates at Koh Tao was not measured, it may be observed that some disproportionately well-represented corals (i.e. Fungiidae, *Dipsastraea* and *Platygyra*) typically have gape sizes far larger than underrepresented groups (i.e. *Acropora*, *Pavona* and *Porites*). This, however, may not explain all significant divergences (i.e. *Leptastrea* and *Diploastrea*). Instead, primary succession of these substrates may be driven by inherent competitive advantages irrespective of depth as a constraint. For example, some fungiid corals have been found to possess multiple strategies that are likely to give them a competitive advantage over other corals when colonising an area. They are known to tolerate the close proximity and presence of other fungiid corals in reefs but aggressively defend against non-fungiid corals (Chadwick-Furman and Loya, 1992). The coral *Lobactis scutaria* has been found to exude large amounts of nematocyst-enriched mucus when in contact with neighbouring corals (Chadwick, 1988), and to begin producing and releasing gametes as early as 1.5 years old and as small as 25 mm (Goffredo and Chadwick-Furman, 2003). In conjunction with the mobility of free-living species and their capacity to shed sediments (Bongaerts et al., 2012; Hoeksema and Bongaerts, 2016), fungiid corals have been shown to be highly plastic in their reproductive methods (Eyal-Shaham et al., 2020) and be well-suited to thrive in various reef environments (Hoeksema and Moka, 1989; Chadwick-Furman and Loya, 1992; Hoeksema, 2012b; Hoeksema, 2012a).

In contrast to the Fungiidae, corals of the genus *Leptastrea* have been found to be particularly susceptible to inter-colony defensive strategies, exhibiting higher levels of damage to the sweeper tentacles of *Platygyra* in the Red Sea (Lapid et al., 2004). This is in general agreement with the conclusion of Dai (1990) who found *Leptastrea purpurea* to be 'moderately subordinate' during interspecies competition. Darling et al. (2013) provided a comprehensive analysis based on the life-history traits (such as corallite diameter, fecundity, growth form among others) of multiple coral species, including *L. purpurea*. In their analysis, *L. purpurea* was designated a 'weedy' species, and Fungiidae were classified as 'stress tolerant' on the reefs of Kenya and was generally considered relatively tolerant to stress from thermal bleaching but sensitive to fishing pressure. When assessed in terms of recruitment between natural and artificial substrates, *L. purpurea* was found to be among the fastest growing species in artificial substrates in Western Australia (Blakeway et al., 2013), while not being prevalent on natural substrates. However, *L. purpurea* was found to be equally abundant on natural and artificial substrates in assessments in the Red Sea (Perkol-Finkel and Benayahu, 2004; Kramer et al., 2019). Despite conflicting evidence regarding the possible advantages or disadvantages in *Leptastrea* recruits, it should also be noted that life-history strategies may vary considerably over larger spatial areas. These will be based on the spatial variability in selective pressures (Darling et al., 2013) and thus assessment of strategies based on such traits need to be assessed at a local level.

Additionally, while not included in the scope of this study, it should be noted that influence from coral competitors, particularly those that are well-established prior to a coral spawning event and subsequent settlement of larvae, may further influence the resultant coral community due to direct competition for substrate, or allelopathy (Glassom et al., 2004; Ritson-Williams et al., 2016; Roth et al., 2018). Alternatively, the presence of other benthic colonisers such as serpulid tubes or other substrate-creating organisms may improve or otherwise influence settlement success of some corals (Glassom et al., 2004). Again, assessment of these was not included within our study and may reinforce competitive differences between corals.

4.3. Succession

Investigations into coral reef successional dynamics prove challenging due to various factors. These include, but are not limited to, the relatively slow increments of measurable change in reef community structure, paucity of historical baseline data from many regions, and rapid, dramatic contemporary changes across reefs such as those driven by climate change. Hence the value in providing defined, testable hypotheses to explain successional change. The successional implications of the coral communities on the artificial substrates of Koh Tao can be explored in relation not only to the above three hypotheses, but also in regard to the three broad models of succession developed by Connell and Slatyer (1977). Namely these are 'facilitation' (the environment is steadily altered by a sequence of successional species with earlier species promoting success of later ones); 'tolerance' (earlier species are constrained by their tolerance to external environmental modifications); and 'inhibition' (early colonisers are those that have the competitive advantage by preventing colonisation of other species until displaced).

The present status of coral communities at artificial substrates at Koh Tao are largely represented by monostomatous and polystomatous Fungiidae and various merulinids. If they have achieved a stable state and do not change considerably in coming years, the resulting coral composition will be determined by the biological and structural traits offered by these colonisers. This may already have important successional implications, as it is likely that many of the monostomatous fungiid recruits are likely free-living as adults (as observed around the wreck). Free-living fungiid corals are believed to contribute significantly to sandy or uncolonized substrates by creating patch reefs over time and bringing hard substrates to soft substrate areas (Sheppard, 1981; Goffredo and Chadwick-Furman, 2000; Hoeksema, 2012a; Hoeksema, 2012b). Their capacity to play this remarkably specialised ecological role could result in the colonisation of surrounding substrates among and around the artificial substrate sites surveyed. This in turn may lead to relatively rapid growth in available substrates for future recruitment, as well as offering aragonite skeletons as an increasingly viable substrate.

Distinct trends are also visible in the proportions of coral groups representing growth forms of varying complexity. Artificial substrate sites were found to host corals of generally lower structural complexity than natural reefs, regardless of depth. If the current community structure at these artificial sites is maintained, a proliferation of available substrate being colonised by encrusting, massive and submassive corals may be expected, which in turn may greatly constrain the diversity of organisms supported within. This would therefore result in reefs that are structurally and ecologically distinct from the nearby natural reefs. The implications of reefs dominated by such corals as those prevalent at these artificial substrate sites are that they may be considered more stress tolerant and less prone to partial mortality (Darling et al., 2013; Madin et al., 2020), while also being subject to slower recovery from disturbance (Graham et al., 2011).

5. Conclusions

Cubic frames and other artificial substrates are a commonly used tool for conservation efforts in Thai waters and beyond (Jankusol, 2004; Kheawwongjan and Kim, 2012; Kantavichai et al., 2019). Increasingly, coral community structures on artificial substrates are being recognised as ecologically and functionally distinct from natural reefs, and should not be considered as a replacement for natural reefs (Burt et al., 2009b; Hill et al., 2021). The mechanisms defining coral community structures and their resulting succession are in need of further exploration if conservation and restoration efforts are to be employed successfully (Bridge et al., 2020). The present findings highlight the need for a greater understanding of life-history traits in colonisation and succession of coral communities with a careful assessment of restoration techniques applied. Our results indicate that passive restoration efforts at Koh Tao result in communities destined for lower structural complexity than natural reefs, which in turn may host lower complexity than at actively restored sites (Hein et al., 2020). Utilising techniques such as population genetics, natural and artificial substrate recruitment tiles and long-term monitoring of communities will continue to shed light on the complex evolution of coral reefs. The hypotheses we have suggested to test our findings may be applicable to similar divergences in communities documented elsewhere, however data from greater spatial and temporal scales will be needed to identify successional mechanics within coral reefs.

CRediT authorship contribution statement

Coline Monchanin: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing. **Rahul Mehrotra:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Supervision, Project administration. **Elouise Haskin:** Methodology, Investigation, Writing – original draft, Writing – review & editing. **Chad M. Scott:** Investigation, Writing – original draft, Writing – review & editing. **Pau Urgell Plaza:** Investigation, Writing – original draft, Writing – review & editing. **Alyssa Allchurch:** Investigation, Writing – original draft, Writing – review & editing. **Spencer Arnold:** Investigation, Writing – original draft, Writing – review & editing. **Kirsty Magson:** Investigation, Writing – original draft, Writing – review & editing. **Bert W. Hoeksema:** Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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