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Spatial variation in the benthic community structure of coral reefs of Hsiaoliuchiu, Taiwan

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Abstract

Hsiaoliuchiu, a coral reef island located off southern Taiwan, was characterized by high coral cover in the 1970s but shifted from a coral- to an algal-dominated system 20 years ago. That being said, there is little information on the ecology of the coral reefs around Hsiaoliuchiu, nor do we know what drove this dramatic decline in live coral cover. In this study, comprehensive benthic community surveys were carried out at 36 sites around Hsiaoliuchiu between 2010 and 2012, and four of these sites were surveyed in greater detail to understand depth-related differences in benthic structure (to 30 m). Turf algae dominated the benthic communities at most sites around the island (% cover ranging from 35 to 81%). However, at Houshi fringing reef, which was located at the southeastern side of the island, hard coral cover was still 23.8 to 54.2%. At this site, encrusting *Montipora* spp. colonies dominated the shallows, while plating and massive corals were most common on the deeper reefs. Also, at Houshi fringing reef, coral cover increased with depth, while cover of macroalgae and turf algae were relatively rarer in deeper waters. Based on these data, we recommend that Houshi fringing reef be legally designated as a marine protected area in order to conserve these remaining coral communities of Hsiaoliuchiu.

Key words: algae, coral, coral reef ecology, marine protected area, phase shift, upwelling

Introduction

Coral reefs are amongst the most ecologically and economically important ecosystems in the world; unfortunately, they are also amongst the most threatened (Pandolfi et al., 2003; Wilkinson, 2008), and the costs to restore coral reefs are higher than for all other ecosystems (De Groot et al., 2013). Both natural and anthropogenic disturbances (Hughes, 1994; Hughes and Connell, 1999; Knowlton, 2001; Bellwood et al., 2004; Knowlton and Jackson, 2008), such as overfishing, eutrophication, and coastal development (associated with increased sediment loads, amongst other issues), are predominantly responsible for global declines in coral reef health.

Anthropogenic disturbances can cause phase shifts in which hard coral-dominated communities transition to algal-dominated ones (Done, 1992; Hughes, 1994; Connell, 1997; Gardner et al., 2003). For example, chronic overfishing of reef herbivores can lead to algal overgrowth, and these algae can then out-compete corals for reef substrate (Hughes, 1994). Concurrently, coastal development may also increase turbidity and nutrient levels in the surrounding waters, suffocating corals and limiting the ability of coral larvae to recruit to the reefs (Gilmour, 1999; Malcolm et al., 2003). The eutrophication associated with such development also causes accelerated algal growth, resulting in the reefs ultimately becoming dominated by turf or macroalgae (McCook, 1999). Furthermore, as a result of rising seawater temperature caused by global climate change, corals are currently disappearing at an alarming rate (Hughes et al., 2010), and coral disease prevalence is at an all-time high. At some locations, coral reef ecosystems are more prolific further offshore, as well as in deeper waters, due to the better water quality and cooler temperatures associated with such environments (Bak and Nieuwland, 1995; Bak et al., 2005; Menza et al., 2008; Sommer et al., 2011).

One means of mitigating the effects of anthropogenic disturbances on coral reefs is the formation of marine protected areas (MPA). In the course of establishing conservation areas, it is critical to identify the capacity for resistance and resilience of the existing coral reefs systems to environmental change (West and Salm, 2003). Additionally, determining the benthic community composition also provides a baseline against which future changes in the biota and habitat quality can be quantified (Kuo et al., 2012; Grizzle et al., 2015). This documentation of biodiversity is an important factor in the designation of MPAs since marine reserves are only useful when they can be proven to serve as spatial and temporal shelters for buffering the harmful effects of anthropogenic disturbance (Allison et al., 1998).

Hsiaoliuchiu, which is located about 14 km from the southwestern coast of mainland Taiwan, is the country's only coral reef island. Surveys carried out in 1970s (Yang et al., 1975; Randall and Cheng, 1977) revealed that coral cover ranged from 50-80%, with a high diversity of scleractinian corals and various, huge coral colonies (e.g., tabulate *Acropora* spp). Randall and Cheng (1977) indicated that the coral communities at Hsiaoliuchiu were diverse and thriving, and that the overall coral reef was more structurally developed and complex than elsewhere in Taiwan. Since then, there has been no detailed study of the coral reef ecology of Hsiaoliuchiu, nor do we know how/if these reefs have been affected by local activities and global climate change.

We do know that, for the past two decades, the reefs surrounding Hsiaoliuchiu have been adversely affected by various anthropogenic and natural factors. Over-fishing has caused a significant reduction in herbivorous fish and invertebrate biomass (T.-Y. Fan, personal observation). As there is no sewage system on the island, most domestic waste is discharged directly into the sea, which has resulted in eutrophication and numerous algal blooms. Due to these combined stressors, the hard coral cover around the island has reduced greatly. Results of a "Reef Check" conducted in 2009 found that hard coral cover at Hsiaoliuchiu was the lowest (15%) in Taiwan and indicated that these reefs have been severely damaged (Dai, 2010). However, data on coral reef ecosystems around Hsiaoliuchiu are still limited; only a small number of reefs were surveyed in 2009, and we have very limited knowledge on the benthic community structure of Hsiaoliuchiu's coral reefs (Fan, 2011). An updated, accurate, and complete report of community structure is the foundation of a suitable management plan needed for the conservation of coral reefs (Grizzle et al., 2015). As such, to provide information for guiding coral reef conservation and management at Hsiaoliuchiu, we sought to 1) document the current benthic community composition, 2) assess the overall health of existing coral reef ecosystem, and 3) determine the influence of depth and temperature on coral cover and composition around Hsiaoliuchiu. We hypothesized that reefs farther away from the island's main population center on the south coast would be characterized by higher hard coral cover. We also predicted that coral cover would be higher at greater depths due to the less anthropogenic disturbances.

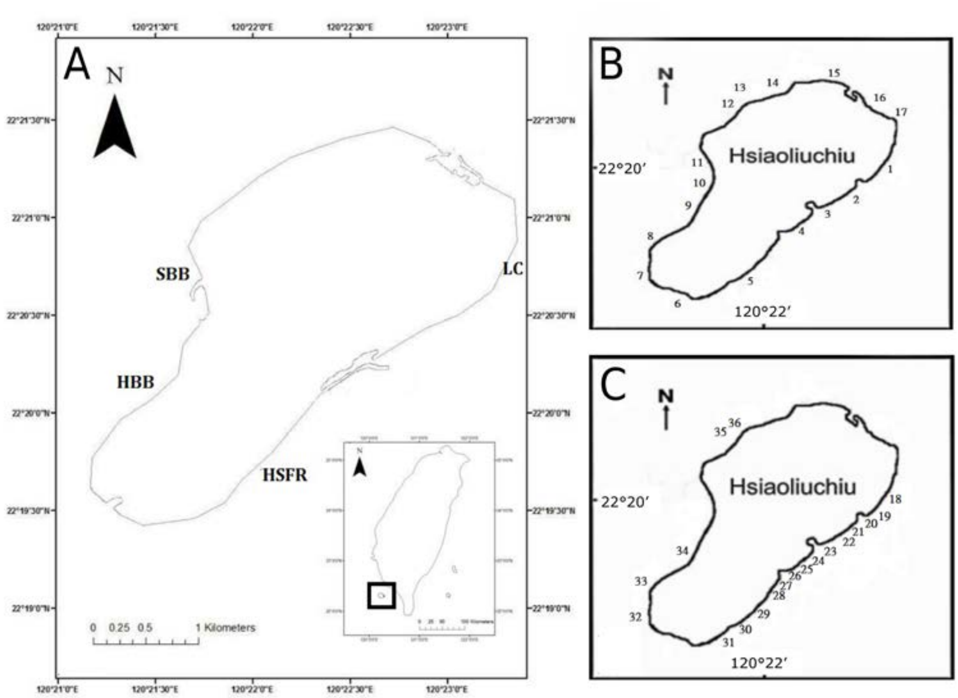

Fig. 1. Map of Hsiaoliuchiu featuring study sites. (A) Surveys were carried out at 36 sites around Hsiaoliuchiu. Additional surveys were carried out at four sites- Lobster Cave (LC), Houshi fringing reef (HSFR), Shanbay Bay (SBB), and Hanban Bay (HBB)- to determine benthic cover variation across depths. Map of the location of the 17 study sites surveyed between June and August 2011 (B). Map of the location of the 19 study sites surveyed between November 2011 and February 2012 (C).

Materials and Methods

Study sites

We surveyed 36 sites to characterize the benthic cover around Hsiaoliuchiu (22°20' N, 120°22' E, Figure 1). In addition, we also chose four locations amongst these survey sites to further investigate the impacts of depth and temperature on the benthic communities. Initial surveys were carried out across 17 study sites (June-August 2011) that were evenly distributed around the island, while the second set of surveys was carried out on 19 locations (November 2011-February 2012); the latter were mainly on the eastern and southern sides of Hsiaoliuchiu (Figure 1) since our preliminary surveys revealed that these sides featured much higher coral cover and diversity coral reef communities.

Based on results from our initial surveys, we further examined four locations with a distinct history of environmental and anthropogenic impacts. Located at the east of the island, Lobster Cave (LC; 22°20'891"N, 120°23'444"E) abuts a heavily populated area, with housing located right on the coast; sewage runoff is therefore a potential problem at this site. Houshi fringing reef (HSFR; 22°19'547"N, 120°22'137"E), the largest and deepest reef area (Yang et al., 1975), which is located in the south, is the farthest from major population areas. It was therefore hypothesized to be characterized by higher live hard coral cover. Hanban Bay (HBB; 22°19'730"N, 120°21'161"E), located off the west coast of the island, is a key tourist spot with a history of coral harvesting. Lastly, Shanban Bay (SBB; 22°21'048"N, 120°21'834"E) is located on the west coast near marine cage fish cultures (Jan et al., 2014).

Benthic cover and abiotic data acquisition

We deployed three, 10-m transects at each site. The transect tapes were positioned parallel to depth contours between 5-8 m. We used a Canon G15 camera to photograph the benthos within a 0.35 m x 0.35 m quadrat, resulting in a total of 30 images per transect. We constructed the quadrats according to Tkachenko et al. (2007). The base frame (0.35 m x 0.35 m) of the quadrat had 0.4-m rods that were attached at each of the four corners, which joined to a smaller square frame above the base transect to fit the camera lens. This set-up ensured that each quadrat was the same size and that the camera was the same distance from the quadrat (0.4 m).

We investigated the impact of depth and temperature on the benthic community of four locations: LC, HSFR, HBB, and SBB. Due to unforeseen circumstances (namely typhoons and unstable surf conditions), surveys were conducted at different times. We conducted photo surveys for LC and SBB in November 2010, while surveys for

HBB and HSFR were performed in April and August 2011, respectively. At the four locations, five 10-m transects were deployed 10-m apart and parallel to the shoreline at each depth. A total of 30 photos were taken along each transect to compare the benthic community at different depths. We started the survey started at 5 m depth and deployed 10-m transects at 5-m intervals (ensuring that there were at least 10 m separation between transects) until 30 m (5, 10, 15, 20, 25, and 30 m). If the reefs did not extend to 30 m, surveys were instead conducted until the deepest 5-m increment. Seawater temperature was recorded at 10-min intervals using HOBO temperature recorders (Onset® MA, USA) at 5 m at each of the four locations from October 2010-May 2012. In addition, temperatures were recorded at 12, 20 and 30 m at HSFR from March-September 2012. The HOBO recorders were set to monitor and record the surrounding water temperature every 10 mins.

Data analysis

We used Coral Point Count with Excel extensions (Kohler and Gill, 2006) to analyze all survey images by randomly selecting fifty points within the quadrat and matching the points to a code that indicated the coral morphology, coral genus, and substrate type. The benthos was categorized as hard corals, soft corals, macroalgae, turf algae or other. In terms of hard corals, it was further subdivided into several different growth forms and genera as described in Table 1: 1) branching *Acropora* spp., 2) branching *Pocillopora* spp., 3) massive and encrusting species, 4) foliaceous and plating species, 5) encrusting *Montipora* spp., and 6) "other." We used one-way-ANOVA (Minitab ver. 14) on normalized and transformed data, followed by *post-hoc* Tukey's honestly significant difference (HSD) tests to determine the effect of depth on the benthic composition for each of four locations (LC, HSFR, HBB, and SBB; $p<0.05$).

Results

Benthic cover

Turf algae dominated the benthos around Hsiaoliuchiu (35-81%; Figure 2), with site 21 having the highest turf algal cover (>80%). The cover of macroalgae (<23%) was lower than that of turf algae at all sites. Hard coral cover was higher (21-45%) along the eastern and southern coasts (sites 1-4 and 20-31), with highest cover at sites 3 (45%) and 25 (44%). The lowest hard coral cover was documented along the western and northern coasts (Figure 2). Sites 17 and 18, which were located on the east coast, had the highest soft coral cover (up to 42%; Figure 2). The cover of hard corals was higher than soft corals at most of the sites (excepting 17 and 18).

Table 1. Classifications of hard corals at the four locations at which depth variation in the benthic community structure was examined. Br= branching, M=massive, EC= encrusting, and F=foliaceous.

Morphology	Description
Br. *Acropora*	Branching *Acropora* spp.
Br. *Pocillopora*	Branching *Pocillopora* spp.
M and EC	Massive, encrusting *Astreopora* spp., *Symphyllia* spp., *Pavona* spp., *Leptastrea* spp., *Platygyra* spp., *Montastrea* spp., *Porites* spp., *Montipora* spp., *Goniastrea* spp., *Favia* spp., *Favites* spp., *Galaxea* spp., *Leptoria* spp., *Lithophyllon* spp., *Hydnophora* spp., *Lobophyllia* spp., *Goniopora* spp., *Euphyllia* spp.
F or Plate	Foliaceous or plating *Acropora* spp., *Pavona* spp., *Merulina* spp., *Porites* spp., *Montipora* spp., *Turbinaria* spp., *Echinophyllia* spp., *Echinopora* spp., *Leptoseris* spp., *Pachyseris* spp., *Mycedium* spp.
EC. *Montipora*	Encrusting *Montipora* spp.
Other	Free-living corals, columnar corals, or other branching corals

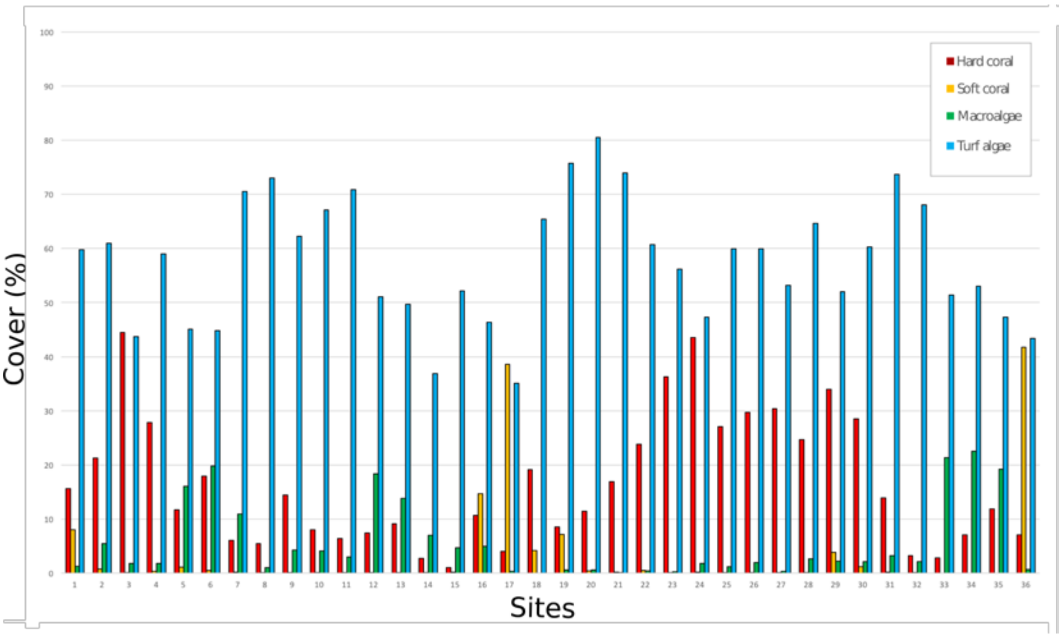

Fig. 2. Benthic cover data from Hsiaoliuchiu. Benthic cover data from the 17 Hsiaoliuchiu sites surveyed between June and August 2011 (sites 1-17) and the 19 sites surveyed between November 2011 and February 2012 (sites 18-36). N=3/site.

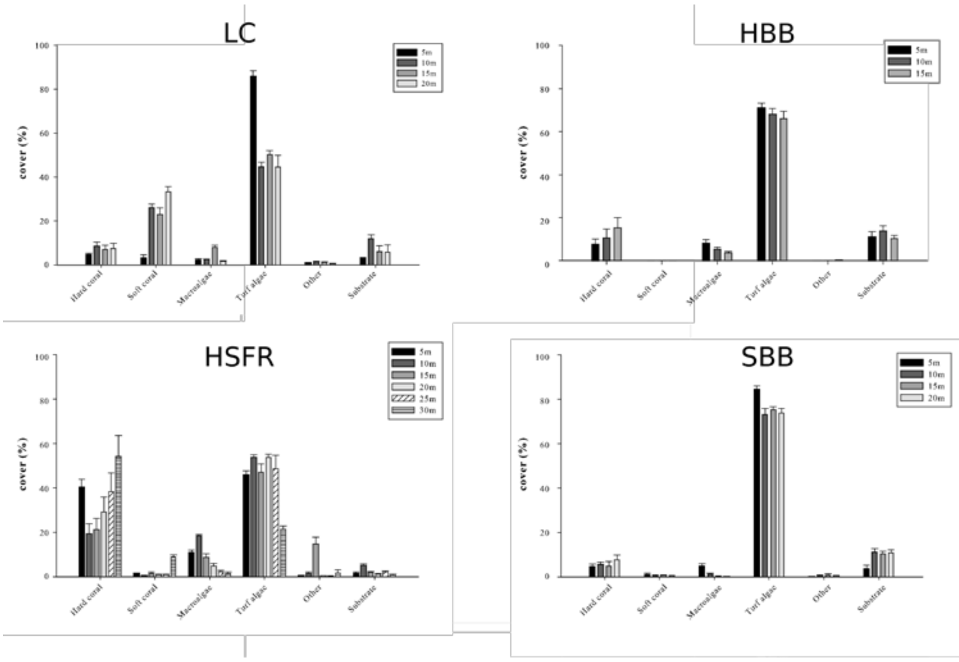

Fig. 3. Depth effects on benthic community structure. Variation (mean± standard error [SE]) in benthic community structure at 3-6 depths at four locations: Lobster Cave (LC), Houshi fringing reef (HSFR), Hanban Bay (HBB), and Sanban Bay (SBB). Error bars represent standard deviation. N=5/depth.

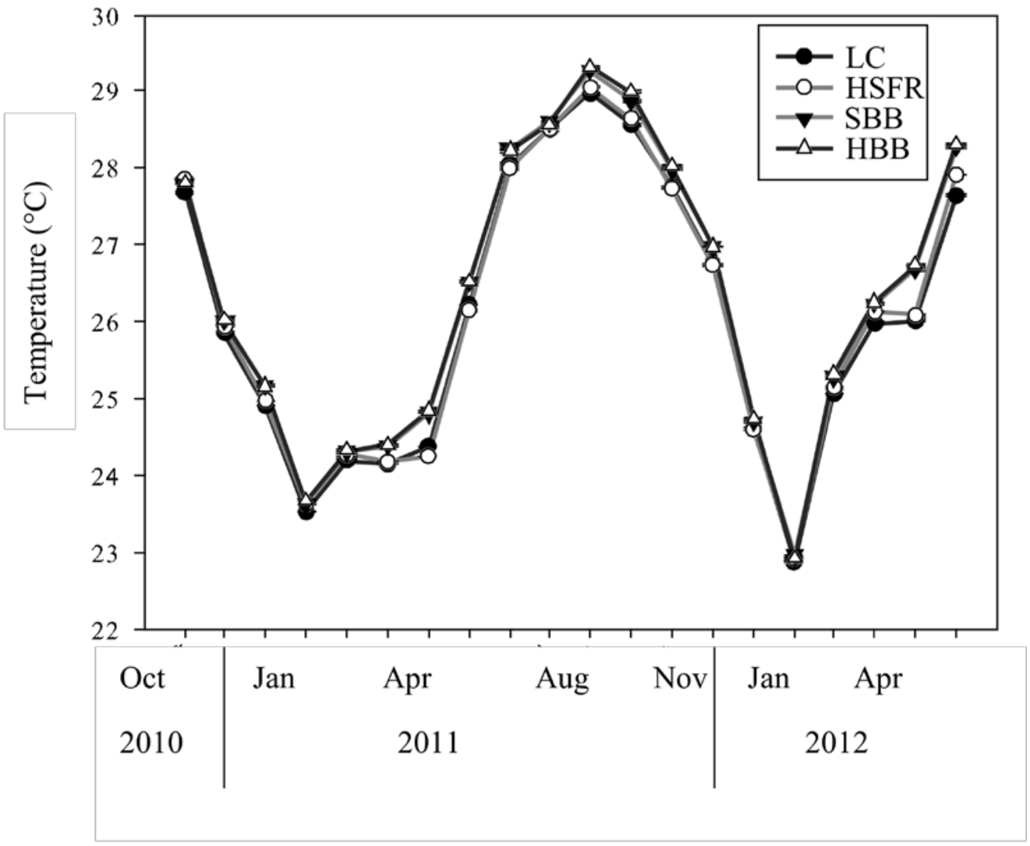

Fig. 4. Seasonal variation in monthly mean seawater temperature at four study sites around Hsiaoliuchiu, Taiwan: Lobster Cave=LC, Houshi fringing reef=HSFR, Sanban Bay=SBB, and Hanban Bay=HBB. Error bars represent standard deviation.

Benthic cover variation across depths

Turf algae was prevalent at LC, HSFR, HBB, and SBB, with cover of 50% or higher at all depths; the exception was HSFR at 30 m (Figure 3). At LC, the cover of turf algae at 5 m depth was the highest (86%), and it was almost double that of the other depths (Table 2). There was also a significant difference in macroalgal and soft coral cover across depths at LC (Table 2). Less than 10% of this site was covered by macroalgae, and while the soft coral cover was low (3%) at 5 m, there was an increase from 10 m and deeper (30-40%; Figure 3). Hard coral cover was low at all depths (4-8%) and did not vary between them (Table 2).

At HSFR there was a significant difference in all functional groupings of taxa across depths (Table 2). Hard coral cover was lowest (19%) at 10 m but increased with depth (Figure 3). Highest hard coral cover was documented at 30 m (54%), followed by 5 m (40%). Although soft coral cover was low (0.4-9%; Figure 3), it did vary across depths (Table 2). Finally, the cover of macroalgae decreased significantly as the water depth increased from 10 m (18%; the maximum) to 30 m (1%; Figure 3 and Table 2).

Depth had no significant effect on the benthic cover at HBB (Table 2). At all depths, hard coral, macroalgal, and turf algal cover were 8-15%, 4-8%, and 6-7%, respectively (Figure 3). At SBB the cover of macroalgae (5%) and turf algae (84%) was significantly higher at 5 m than at other depths (Table 2 and Figure 3). The cover of hard corals (4-8%) and soft corals (<1%) was low.

Encrusting montiporids, such as *Montipora aequituberculata*, were significantly more dominant at 5 m at HSFR (Table 3). The plating coral growth form (e.g., *Montipora* spp., *Turbinaria* spp., *Echinophyllia* spp., *Merulina* spp., *Mycedium* spp., and *Pachyseris* spp.) dominated the coral cover at 30 m (Table 3). We observed an approximately 2-fold increase in the cover of massive and encrusting coral growth forms at depths between 20-30 m as compared to the shallower waters (<20 m; Table 3).

Seawater temperature

The seasonal variation of seawater temperature at 5 m was similar over both space (across the four sites) and time (across different seasons; Figure 4). However, the monthly mean seawater temperature at LC and HSFR was lower than at SBB and HBB between March-September 2011 and April-May 2012. We observed a high temperature fluctuation, especially during the summer, at HSFR at various depths (Figure 5), with a higher fluctuation in deeper waters (e.g. 26.1-28.0°C at 12 m, 23.7-27.8°C at 20 m, and 21.8-27.5°C at 30m during 1 to 7 AM on 25 June 2012).

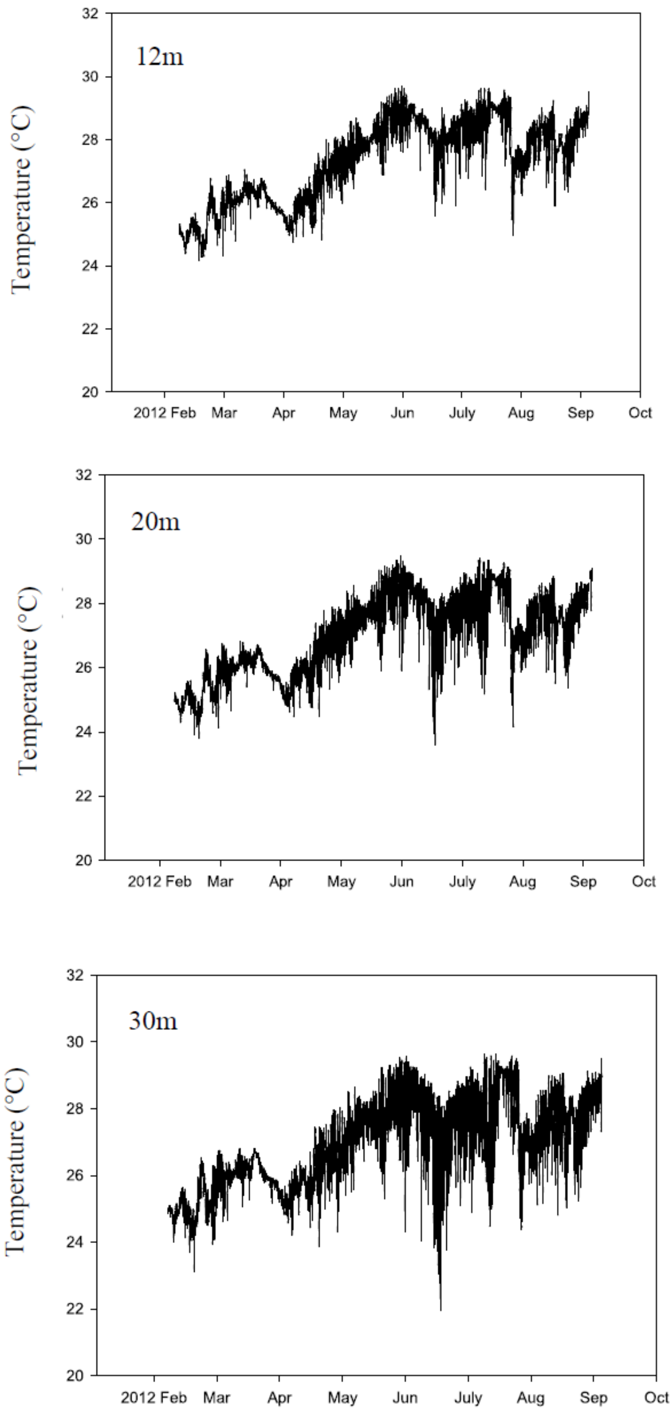

Fig. 5. Temperature variation at different depths – 12m, 20m and 30m at Houshi Fringing Reef (HSFR).

Table 2. Summary table of 1-way ANOVA and Tukey's honestly significant difference (HSD) tests comparing the benthic cover of various functional groups between depths at four locations: Lobster Cave (LC), Houshi fringing reef (HSFR), Hanban Bay (HBB), and Shanbay Bay (SBB). Lower-case letters (a, b, c) indicate Tukey's HSD differences between depths (p<0.05).

Site		df	MS	F	p	5m	10m	15m	20m	25m	30m
LC	Hard coral	3, 16	0.00583	2.56	0.091						
	Soft coral	3, 16	0.20274	39.75	<0.001	3%^{a}	26%^{b}	23%^{b}	33%^{b}		
	Macroalgae	3, 16	0.0296	18.08	<0.001	2%^{a}	2%^{a}	8%^{b}	2%^{a}		
	Turf algae	3, 16	0.24814	39.65	<0.001	86%^{a}	45%^{b}	50%^{b}	45%^{b}		
HSFR	Hard coral	5, 24	0.10191	13.77	<0.001	40%^{c}	19%^{ab}	21%^{ab}	29%^{bc}	38%^{c}	54%^{c}
	Soft coral	5, 24	0.04161	14.69	<0.001	1%^{a}	0%^{a}	1%^{a}	1%^{a}	1%^{a}	9%^{b}
	Macroalgae	5, 24	0.08246	25.56	<0.001	11%^{a}	18%^{a}	8%^{b}	5%^{b}	2%^{bc}	1%^{c}
	Turf algae	5, 24	0.08164	14.87	<0.001	46%^{a}	54%^{a}	47%^{a}	54%^{a}	49%^{a}	21%^{b}
HBB	Hard coral	2, 12	0.0206	1.56	0.249						
	Soft coral	2, 12	0.000215	0.67	0.529						
	Macroalgae	2, 12	0.01136	3.12	0.081						
	Turf algae	2, 12	0.0036	0.72	0.508						
SBB	Hard coral	3, 16	0.0039	1.76	0.195						
	Soft coral	3, 16	0.00142	0.52	0.672						
	Macroalgae	3, 16	0.0395	16.12	<0.001	5%^{a}	1%^{b}	0%^{b}	0%^{b}		
	Turf algae	3, 16	0.02111	6.78	0.004	84%^{a}	73%^{b}	75%^{b}	73%^{b}		

Table 3. Summary table of 1-way ANOVA and Tukey's honestly significant difference (HSD) tests comparing the cover of various hard coral morphotypes between depths at four locations: Lobster Cave (LC), Houshi fringing reef (HSFR), Hanban Bay (HBB), and Shanbay Bay (SBB). M=massive, EC=encrusting, and F=foliaceous. Lowercase letters reflect Tukey's HSD *post-hoc* differences between depths (p<0.05).

Site	Morphotype	df	MS	*F*	*p*	5m	10m	15m	20m	25m	30m
LC	M and EC	3, 16	16.25	4.08	0.025	$3\%^{a}$	$7\%^{a}$	$6\%^{ab}$	$6\%^{ab}$		
HSFR	M and EC	5, 24	447.7	8.69	<0.001	$36\%^{a}$	$16\%^{b}$	$15\%^{b}$	$23\%^{ab}$	$33\%^{a}$	$34\%^{a}$
HSFR	F or Plate	5, 24	204.1	9.64	<0.001	$3\%^{b}$	$2\%^{b}$	$5\%^{b}$	$5\%^{b}$	$6\%^{b}$	$19\%^{a}$
HSFR	EC *Montipora*	5, 24	627.1	52.71	<0.001	$33\%^{a}$	$9\%^{b}$	$5\%^{bc}$	$2\%^{c}$	$6\%^{bc}$	$10\%^{b}$
HBB	M and EC	2, 12	52.2	1.93	0.187						
SBB	M and EC	3, 16	8.1	3.03	0.06						

Discussion

Our survey revealed spatial differences in the benthic community structure of reefs of the coral reef island of Hsiaoliuchiu. Of note, the coral reefs around the northern and western sides of the island were seriously degraded and mostly overgrown by turf algae. Soft corals were abundant in eastern Hsiaoliuchiu, whereas some sites in the southeastern region maintained relatively high coral cover. The coral community varied across depths at these higher coral cover sites.

Phase shift

The coral cover around Hsiaoliuchiu was typically < 20%, and turf algae dominated all surveyed sites. Yang et al. (1975) noted that the coral community along the west coast of Hsiaoliuchiu was more developed than that of the east coast, while Randall and Cheng (1977) reported that coral cover was between 50 and 80% in the shallow reef and 20-40% in the deeper reef. However, we could not find the high coral cover described in these older works; instead, an algal-dominated system was documented. The possible reasons for this coral-to-algae phase shift are coral harvesting, overfishing, eutrophication, and sedimentation, as now discussed in further detail.

The excessive collection of corals has clearly played a role in the rapid decline in the coral reef ecosystems around the island, especially in the shallow areas. The local islanders have historically collected coral colonies, especially around the northern and western sides of the island (i.e., SBB and HBB) to supply to tourist gift shops (Yang et al., 1975). Another key factor in the hard coral decline is over-harvesting of herbivorous fish and invertebrates (Dai, 2010). In a top-down controlled ecosystem (Hughes, 1987; Bellwood et al., 2004), without these herbivorous fishes and invertebrates to remove fast-growing algae on the reefs, the algae can dominate; this increase in algal biomass can then limit the growth of existing corals and inhibit coral larvae settlement (Sammarco, 1980; Wilkinson, 2008).

Increased eutrophication and sedimentation might be another reason for the reefs' decline. Hsiaoliuchiu lacks a sewage treatment system, and wastewater from both the locals and tourists is discharged directly into coastal waters (Dai, 2010). Recently, tourism has increased on the island, and more than 1 million people are visiting the island every year at current estimates; as only 12,000 people currently live on Hsiaoliuchiu, new hotels and other buildings will likely be required to accommodate this rising influx of tourists. These tourists are likely to contribute to elevated seawater pollution levels, as well (Fan, 2011). Furthermore, land-derived nutrients and sedimentation are washed directly into the surrounding waters during heavy rainfall events.

Exacerbating the issue of eutrophication, a commercial fish farm was developed near the inshore coral reefs off the northern coast of Hsiaoliuchiu since 1994. Fish farms can release large quantities of excessive feed and fecal material, mostly as dissolved nutrients and organic particles, into the surrounding marine environment, and this may lead to algal blooms and coral reef degradation (Huang et al., 2011, 2012). At Hsiaoliuchiu, it has been shown that the particulate organic matter released by the farm may have entered the coral reef ecosystem through the pelagic food chain (Jan et al., 2014). The phase shift from coral-dominated to turf algal- or macroalgal-dominated ecosystems at Hsiaoliuchiu may, then, be the result of not only overfishing, but also increased eutrophication from terrestrial wastewater and sediment runoff.

Houshi fringing reef

The higher coral cover (24-44%) off the southeastern coast of Hsiaoliuchiu may be partly due to 1) lower human population density and human activity in general (Fan, 2011) and 2) upwelling. Regarding the former hypothesis, deeper waters are likely to be less affected by land-based anthropogenic factors, and such shallow-deep gradients in coral cover as a result of dampening of anthropogenic impact have been documented elsewhere (Bak and Nieuwland, 1995; Bak et al., 2005; Menza et al., 2008). Regarding the second hypothesis, hard coral cover may, alternatively, have increased with depth at HSFR because of the differential influence of upwelling on deep reefs relative to shallow ones. Shih (2006) documented spring tide upwelling in southeastern Hsiaoliuchiu in which deep ocean seawater characterized by low temperature, high salinity, high oxygen concentration, and low chlorophyll-a concentration was brought to the shallow water. Our temperature data shown the deeper water more influenced by the cold water (Figure 5). Such deep ocean seawater is likely to be more amenable to coral growth than the relatively polluted seawater coming from the island (Fabricius, 2005; Fabricius et al., 2012), though whether the cooler temperature or the lower pollutant levels associated with this upwelled water is more important in promoting coral growth over the shallow areas should be investigated more thoroughly in future works (Schmidt et al., 2012).

Encrusting *Montipora* species, such as *M. aequituberculata*, were the dominant hard corals at 5 m at HSFR. Encrusting *Montipora* spp. are well adapted to turbulent conditions in Hawaii (Jokiel et al., 2004), and this relatively wave-resistant morphotype appear to have adapted to the strong waves and swell characteristic of HSFR, a reef that also experiences boreal summer typhoons (Fan, 2011). On the other hand, the coral community in the deeper waters at HSFR was dominated by massive, encrusting, and plating (foliaceous) growth forms and featured corals such as *Turbinaria* spp. (plating form), *Echinophyllia* spp. (plating form), *Merulina* spp. (plating form), *Mycedium* spp. (plating form), and *Pachyseris* spp. (plating form). These species are also common on reef slopes in southern Taiwan (Dai, 1993), and, like other encrusting, massive, and plating corals, have a relatively greater surface area for capturing light compared to branching corals; this allows them to thrive in low-light areas (Goh et al., 1994; Dikou and van Woesik, 2006; Erftemeijer et al., 2012).

Management implications

The southeastern regions of Hsiaoliuchiu, including HSFR, should be prioritized for coral reef protection because they are characterized by the largest and deepest reefs (Yang et al., 1975), the highest coral cover (This study), and, presumably, the lowest human level of human and land-based impact. Given the aforementioned increase in tourism at Hsiaoliuchiu, it will be critical to establish a MPA around HSFR and then track changes in the benthic community to determine its efficacy as a conservation tool by comparison to the baseline dataset presented herein (Connell, 1997; Tkachenko and Soong, 2010; Kuo et al., 2012). Establishment of no-take MPAs could promote the repopulation of herbivorous fishes, which could consequently control algal densities and facilitate coral re-population (Lester et al., 2009). Houbihu in Nanwan Bay represents a successful MPA in Southern Taiwan; the closing of the area to fishing has resulted in relative higher coral cover and fish densities than non-protected areas in the near vicinity (Tkachenko and Soong, 2010). The formation and effective management of an MPA at Hsiaoliuchiu will ideally benefit its coral reefs in a similar manner.

Acknowledgments

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References

Allison, G.W., J. Lubchenco & M.H. Carr M.H. 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications, 8:S79-S92.

Bak, R.P.M. & G. Nieuwland. 1995. Long-term change in coral communities along depth gradients over leeward reefs in the Netherlands Antilles. Bulletin of Marine Science, 56:609-619.

Bak, R.P.M., G. Nieuwland & E.H. Meesters. 2005. Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs of Curacao and Bonaire.

Coral Reefs, 24:475-479.
Bellwood, D.R., T.P. Hughes, C. Folke & M. Nystrom. 2004. Confronting the coral reef crisis. Nature, 429:827-833.
Carilli, J., S.D. Donner & A.C. Hartmann. 2012. Historical temperature variability affects coral response to heat stress. PLoS ONE, 7(3):e34418.
Connell, J.H. 1997. Disturbance and recovery of coral communities. Coral Reefs, 16:S101-S113.
Dai, C.F. 1993. Patterns of coral distribution and benthic space partitioning on the fringing reefs of southern Taiwan. Marine Ecology, 42:185-204.
Dai, C.F., 2010, Status of Coral Reefs in Taiwan. In: Kimura T (ed.) Status of Coral Reefs in East Asian Sea Region: 2010, pp. 79-87. Ministry of Environment, Japan.
De Groot, R.S., J. Blignaut J, A. Van Der Ploeg, J. Aronson, T. Elmqvist & J. Farley. 2013. Benefits of investing in ecosystem restoration. Conservation Biology, 27:1286-1293.
Dikou, A. & R. van Woesik. 2006. Partial colony mortality reflects coral community dynamics: a fringing reef study near a small river in Okinawa, Japan. Marine Pollution Bulletin, 52:269-280.
Done, T.J. 1992, Phase shifts in coral communities and their ecological significance. Hydrobiologia, 247:121-132.
Erftemeijer, P.L.A., B. Riegl, B.W. Hoeksema & P.A. Todd. 2012. Environmental impacts of dredging and other sediment disturbances on corals: a review. Marine Pollution Bulletin, 64:1737-1765.
Fabricius, K. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine Pollution Bulletin, 50:125-146.
Fabricius, K., T.F. Cooper, C. Humphrey, S. Uthicke, G. De'ath, J. Davidson, H. LeGrand, A. Thompson A & B. Schaffelke. 2012. A bioindicator system for water quality on inshore coral reefs of the Great Barrier Reef. Marine Pollution Bulletin, 65:320-332.
Fan, T.Y. 2011. Ecology and conservation of Hsiaoliuchiu coral reefs. Pingtung County Government. Chinese with English abstract.
Gardner, T.A., I.M. Cote, J. A. Gill, A. Grant A & A.R. Watkinson A. 2003. Long-term region-wide declines in Caribbean corals. Science, 301:958-960.Gilmour, J. 1999. Experimental investigation into the effects of suspended sediment on fertilization, larval survival and settlement in a scleractinian coral. Marine Biology, 135:451-462.
Goh, N.K.C., C.Y.Y. Chua & L.M. Chou L. 1994. Depth-related morphology of scleractinian corals on Singapore reefs. In: Proceedings of the Third ASEAN-Australia Symposium on Living Coastal Resources, vol. 2, pp. 61-67.
Graham, N.A.J., D.R. Bellwood, J.E. Cinner, T.P. Hughes, A.V. Norström & M. Nyström M. 2013. Managing resilience to reverse phase shifts in coral reefs. Frontier in Ecology and the Environment, 11:541-548.
Grizzle, R.E., K.M. Ward, R.M.S. AlShihi & J.A. Burt. 2016. Current status of coral reefs in the United Arab Emirates: distribution, extent, and community structure with implications for management. Marine Pollution Bulletin, 105:515-523.
Huang, Y.A., S.C. Huang, P.J. Meng, H.J. Hsieh & C.A. Chen. 2012. Influence of seasonal monsoon winds on the water quality around a marine cage-culture zone in a semi-closed embayment in Taiwan. Marine Pollution Bulletin, 64:851-860.
Huang, Y.A., H.J. Hsieh, S.C. Huang, P.J. Meng, Y.S. Chen, S. Kevashavamurthy, Y. Nozawa & C.A. Chen. 2011. Nutrient enrichment caused by marine cage culture and its influence on subtropical coral communities in turbid waters.

Marine Ecology Progress Series, 423:83-93.
Hughes, T.P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science, 265:1547-1551.
Hughes, T.P. & J.H. Connell. 1999. Multiple stressors on coral reefs: a long-term perspective. Limnology and Oceanography, 44(3 II):932-940.
Hughes, T.P., D.C. Reed & M.J. Boyle. 1987. Herbivory on coral reefs: community structure following mass mortalities of sea urchins. Journal of Experimental Marine Biology and Ecology, 113:39-59.
Hughes, T.P., N.A.J. Graham, J.B.C. Jackson, P.J. Mumby & R.S. Steneck. 2010. Rising to the challenge of sustaining coral reef resilience. Trends in Ecology and Evolution, 25:633-642.
Jan, R.Q., S.J. Kao, C.F. Dai & C.T. Ho. 2014. Assessment of the effects of cage fish-farming on damselfish-associated food chains using stable-isotope analyses. Marine Pollution Bulletin, 86:111-121.
Jokiel, P.L., E.K. Brown, A. Friedlander, S.K. Rodgers & W.R. Smith. 2004. Hawaii coral reef assessment and monitoring program: Spatial patterns and temporal dynamics in reef coral communities. Pacific Science, 58:159-174.
Jouffray, J.B., M. Nystrom, A.V. Norstrom, I.D. Williams, L.M. Wedding, J.N. Kittinger, & G.J. Williams. 2015. Identifying multiple coral reef regimes and their drivers across the Hawaiian archipelago. Philosophical Transactions of Royal Society, 370B:20130268.
Knowlton, N. 1992. Thresholds and multiple stable states in coral reef community dynamics. American Zoologist, 32:674-682.
Knowlton, N. 2001. The future of coral reefs. Proceedings of the National Academy of Sciences of the United States of American, 98:5419-5425.
Knowlton, N. & J.B.C. Jackson. 2008. Shifting baselines, local impacts, and global change on coral reefs. PLoS Biology, 6(2):e54.
Kohler, K.E. & S.M. Gill. 2006. Coral point count with Excel extension (CPCe): a visual basic program for determination of coral and substrate coverage using random point count methodology. Computers and Geosciences, 32;1259-1269.
Kuo, C.Y., P.J. Meng, P.H. Ho, J.T. Wang, J.P. Chen, Y.W. Chiu, H.J. Lin, Y.C. Chang, T.Y. Fan, A.H. Baird & C.A. Chen. 2012. Recurrent disturbances and the degradation of hard coral communities in Taiwan. PLoS One, 7(8):e44364.
Lester, S.E., B.S. Halpern, K. Grorud-Colvert, J Lubchenco, B.I. Ruttenberg, S.D. Gaines, S. Airamé & R.R. Warner. 2009. Biological effects within no-take marine reserves: a global synthesis. Marine Ecology Progress Series, 384:33-46.
Malcolm, M., F. Stewart, W. Timothy, H. Erica H, L. Janice L & B. David. 2003. Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. Nature, 421:727-730.
Maynard, J.A., P.A. Marshall, J.E. Johnson & S. Harman. 2010. Building resilience into practical conservation: identifying local management responses to global climate change in the southern Great Barrier Reef. Coral Reefs, 29:381-391.
McCook L.J. 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. Coral Reefs, 18:357-367.
Menza, C., M. Kendall & S. Hile. 2008. The deeper we go the less we know. Revista de Biologia Tropical, 56:11-24.
Pandolfi, J.M., R.H. Bradbury, E. Sala, T.P. Hughes, K.A. Bjorndal, R.G. Cooke, D. McArdle, L. McClenachan, M.J.H. Newman, G. Paredes, R.R. Warner, J.B.C. Jackson. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science, 301:955-958.
Randall, R.H. & Y.M. Cheng. 1977. Recent

corals of Taiwan. Part I. Description of reefs and coral environments. Acta Geologica Taiwanica 19:79-102.

Sammarco, P.W. 1980. *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. Journal of Experimental Marine Biology and Ecology, 45:245-272.

Schmidt, G.M., N. Phongsuwan, C. Jantzen, C. Roder, S. Khokiattiwong & C. Richter. 2012. Coral community composition and reef development at the Similan Islands, Andaman Sea, in response to strong environmental variations. Marine Ecology Progress Series, 456:113-126.

Shih, H.E. 2006. Investigation of flow pattern and upwelling characteristics near the wakes of Liu-Chiu-Yu Island. Master's thesis, Department of Marine Biotechnology and Resources, National Sun Yat-Sen University.

Sommer, B., P.L. Harrison, L. Brooks L & S.R. Scheffers. 2011. Coral community decline at Bonaire, Southern Caribbean. Bulletin of Marine Science, 87:541-565.

Tkachenko, K.S. & K. Soong. 2010. Protection of habitat types: a case study of the effectiveness of a small marine reserve and impacts of different habitats on the diversity and abundance of coral reef fishes. Zoological Studies, 49:195-210.

Tkachenko, K.S., B.J. Wu, L.S. Fang L.S. & T.Y. Fan. 2007. Dynamics of a coral reef community after mass mortality of branching *Acropora* corals and an outbreak of anemones. Marine Biology, 151:185-194.

West, J.M. & R.V. Salm. 2003. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. Conservation Biology, 17:956-967.

Wilkinson, C.R. 2008. Status of the coral reefs of the world: Global Coral Reef Monitoring Network and Australian Institute of Marine Science, Townsville.

Yang, R.T., K.S. Chi, S.C. Hu & H.T. Chen. 1975. Corals, fishes and benthic biota of Hsiao-Liuchiu. Spec Publication No 7, Institute of Oceanography, National Taiwan University.