

**Partitioning the effects of newly-implemented MPAs, benthic
structure, depth, and recreational activities on the fish assemblages of
Koh Tao Island, Thailand**

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Abstract

In coral reef ecosystems, overharvesting is the main cause of depletion of fish populations and assemblages. No-take marine reserves (MPAs) are advocated as a promising management tool for enhancing the resilience of coral reef ecosystems and sustaining fisheries. However, reef fish assemblages are also influenced by a multitude of natural and anthropogenic factors, including benthic structure, depth, and water-based human activities. Understanding the extent to which reef fish assemblages may be affected by habitat protection, physical factors, and anthropogenic activities is essential to develop more effective management plans for coral reef fish assemblages. The objectives of the present thesis were to assess the influence of newly implemented MPAs, benthic structure, depth, and recreational activities on the coral reef fish assemblages of Koh Tao, Thailand. Data were recorded before and one year after MPA establishment, for seven indicator reef fish families. No MPA effects were detected for density of targeted reef fish families (i.e. Serranidae, Lutjanidae, Scaridae) nor other reef fish species. Reef fish density and diversity were significantly higher in shallow reef slopes (<6m) than deeper slopes. Also, planktivores and corallivores were respectively 1.23 fold and 2 fold more abundant in shallow reef slopes. Although no significant differences in reef fish density and diversity were found between ‘hard coral’, ‘rock’, and ‘rubble’ dominated (>50%) habitats, *Dascyllus reticulatus* and *Chaetodon octofasciatus* densities were respectively found to be negatively ($R^2=0.655$, $p=0.049$) and positively correlated ($R^2=0.71$, $p=0.034$) with hard coral cover. A principal component analysis showed that Serranidae were associated with rocky habitats whereas *Cheilinus fasciatus* and *Stegastes obreptus* were associated with high hard coral cover. A BIO-ENV test revealed that 62.5% of the dissimilarities between reef fish assemblages were driven by the benthic structure (i.e. hard coral, rubble, rock). Altogether, this study supports the need to increase the representativeness of habitat types when implementing MPAs and MPA networks. Most importantly, this study provides an essential baseline to continue monitoring the effects of MPAs around Koh Tao.

Keywords: Marine protected areas, fisheries, coral reef fish, depth, recreational activities, benthos, hard coral cover

Introduction

The depletion of fish populations worldwide and its consequences on marine ecosystems has received considerable scientific attention recently (Hixon 2011, Watson et al 2102, Worm and Branch 2012). In 2012, 56.4% of the worldwide fish stocks were considered overexploited or depleted (WOR 2013). In tropical coral reef ecosystems, overharvesting is the main cause of depletion of fish populations and assemblages (Hixon 2011). Yet, coral reef fish assemblages are also threatened by the accelerating destruction of their habitats at both regional and national scales, through coral bleaching induced by climate change and ocean acidification (Hoegh-Gulberg et al. 2007, Cinner et al. 2009, Graham et al. 2011, Hixon 2011, Pandolfi et al. 2011), increasing prevalence of coral diseases (Ruiz-Diaz et al. 2013, Slattery et al. 2013), mechanical destruction (e.g. anchoring, *Acanthaster planci* outbreaks, typhoons) (Carpenter et al. 2008, Ruppert et al. 2013), and sedimentation and pollution induced by land-based human activities (e.g. dredging, deforestation) (Wilkinson 2008, Brewer et al. 2013). Other frequently cited factors for coral reef fish depletion are the introduction of non-indigenous species (Semmens et al. 2004) and the intensification of water-based human activities (Hixon 2011). Hundreds of species of coral reef fishes are currently listed on the IUCN (International Union for Conservation of Nature) red list (Hixon 2011). Facing this reality, a major shift of focus occurred in recent years toward conservation biology, and marine reserves (the no-take components of Marine Protected Areas (MPAs)) are today advocated as a promising management tool for enhancing the resilience of tropical coral reef ecosystems and sustaining fisheries (Russ and Alcala 2004, Hixon 2011).

Marine Protected Areas (MPAs) are defined by the IUCN as “any area of the intertidal or subtidal terrain, together with its overlying water and associated fauna, flora, historical, and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment” (Kelleher 1999). Although an ongoing debate rages between scientists about the utility of MPAs as conservation and fisheries management tools, numerous authors (Russ et al.

2004, Mascia et al. 2010, Aburto-Oropeza et al. 2011, Kerwath et al. 2013) consider MPAs as a viable management option to enhance the conservation of coral reef ecosystems and promote sustainable fisheries. There is an overwhelming body of evidence that the abundance, mean size, age and per-capita fecundity of exploited species increases within adequately located and protected MPAs (Barrett et al. 2007, Anderson et al. 2008, Harmelin-Vivien et al. 2008, Lester et al 2009, Molloy et al 2009). Evidence also exists that MPAs can boost fishery yields beyond their borders through the net export of adult individuals (i.e. spillover effect) and larvae (i.e. recruitment subsidy) (Russ et al. 2004, Harrison et al. 2012, Kerwath et al. 2013). The extent of productivity gains within MPAs can be driven by several ecological factors, including the natural state of benthic assemblages (e.g. highly complex habitats provide more shelter and support more individuals than degraded habitat), the size of a marine reserve (large MPAs are more likely to protect fish species that have large home ranges) (Aburto-Oropeza et al. 2011), and the inclusion of spawning areas within reserve boundaries (Sala et al. 2003). Adequate levels of compliance are also essential if targeted fish populations are to increase within MPA boundaries (Russ et al. 2004, Guidetti et al. 2008, Russ and Alcala 2010, Bergseth et al 2013).

The exact number of MPAs implemented in tropical coral reef areas is unknown (Mora et al. 2006). Thus, it is difficult to evaluate and quantify the potential fishery sustainability benefits of MPAs at regional and global scales. Most studies that have investigated MPA effectiveness have had a study period extending from 1 year to 10 years after MPA establishment. Several short-term (~ 1 year) studies have revealed a paucity of MPA effects (Edgar and Barrett 2012, Colleter et al. 2012). Yet, a recent study by Kerwath et al. (2013) showed that MPAs could begin benefiting fishery yields immediately after implementation. However, numerous studies (Eklof et al. 2009, Colleter et al. 2012, Frascetti et al. 2012) have showed that MPAs could only begin having beneficial effects on fish and benthic assemblages after at least 2 to 9 years of protection. Recent studies have concluded that significant changes in coral reef fish population structure (biomass and composition) could be observed from 5.1 (Babcock et al. 2010) to 9.5 years (Steward et al. 2009)

after MPA establishment, and that whole ecosystems may only stabilise after decades of protection (Russ and Alcala 2010, Claudet and Guidetti 2010).

Reef fish assemblages are also influenced by a multitude of biological and physical factors, including benthic structure and complexity (Chittaro et al. 2005, Pittman et al. 2011, Chong-Seng et al. 2012, Pinheiro et al. 2013), nutrient and light availability (Francini-Filho et al. 2010, Francini-Filho et al. 2013), predatory pressure and food availability (Floeter et al. 2007), larval dispersal (Hixon 2011), the nature of sessile benthic assemblages (Gonzalez-Sanson et al. 2009, Garcia-Sais 2010), size of reef patches (Hattori and Shibuno 2010), wave exposure and water motion (Floeter et al. 2007, Krajewski and Floeter 2011), depth (Brokovitch et al. 2010, Malcolm et al. 2011), and temperature (Mellin et al. 2010, Karnauskas et al. 2012). Macroalgal growth rate (Markager and Sand-Jensen 1992), richness and density (Gilmartin 1960), nutrient loads (Lesser et al. 2009), and light availability (Brokovitch et al. 2010) all directly depend on depth (Gonzalez-Sanson et al. 2009, Brokovitch et al. 2010, Garcia-Sais 2010, Pereira-Filho et al. 2011). Yet, most recent studies have investigated depth gradients ranging from 50m to 150m (Brokovitch et al. 2010, Bryan et al. 2013, Corell et al. 2012). Few studies have investigated the influence of depth on shallow coral reefs, but all concluded that depth should be considered as a key-structuring factor of coral reef fish assemblages (Gonzalez-Sanson et al. 2009, Page-Albins et al. 2012, Francini-Filho et al. 2013). For instance, Karnauskas et al. (2012) concluded that depth could be the primary discriminant factor driving the distribution patterns of herbivorous and planktivorous coral reef fishes. Specific fish species and trophic groups often favour particular depth zones and habitat types for feeding on plankton, foraging for turf algae or hunting prey (Fox and Bellwood 2007). Interestingly, Francini-Filho et al. (2013) showed that depth is the most critical factor determining benthic composition of shallow coral reefs, and had a bigger influence than latitude, distance offshore, and protection levels.

Numerous recent studies (Brokovitch et al. 2006, Krajewski and Floeter 2010, Chong-Seng et al. 2012) have demonstrated that benthic (i.e. habitat) structure is key factor shaping coral reef

fish assemblages. In tropical coral reef systems, a positive correlation often exists between fish assemblage richness/density and habitat diversity/complexity (Toller et al. 2010, Pereira-Filho et al. 2011, Pinheiro et al. 2013). Small-scale variations of reef fish assemblage composition, diversity, and density may simply result from differences in the cover of live hard coral or macroalgae (Garpe and Ohman 2003, Chong-Seng et al. 2012). Algal-dominated habitats generally support lower reef fish species richness and fewer functional groups than highly diverse coral reef patches (Chong-Seng et al. 2012, Franco et al. 2012). Chong-Seng et al. (2012) found a 5-fold increase in reef fish abundance between low complexity algal dominated reefs and highly complex coral dominated reefs.

The structure of coral reef fish assemblages may also be influenced by water-based anthropogenic activities (Zakai and Chadwick-Furman 2002, Claudet et al. 2010, Dearden et al. 2010). Although not considered as a key factor affecting fish assemblages within multiple-use MPAs, the effects of intensive SCUBA diving and snorkelling operations have recently received much attention. It is now accepted that snorkelers and divers can negatively impact fragile sessile coral reef assemblages by walking on reefs, trampling, contact with and breakage of coral, and re-suspension of sediments (Plathong et al. 2000, Zakai and Chadwick-Furman 2002, Claudet et al. 2010, Dearden et al. 2010). Yet, a study by Roupheal and Inglis (2001) did not reveal any strong correlations between diving/snorkelling activities and levels of benthic substrate degradation. Noise related to boat engines is another factor possibly affecting coral reef fish populations, but most literature today focuses on large marine organisms, such as dugongs (Marsh and Anderson 1983) and turtles (Hazel and Gyuris 2006). Some recent studies suggest that boat sounds could have a dramatic impact on coral reef fish assemblages, including changes in territorial behaviour (e.g. Gobiidae species) (Sebastianutto et al. 2011). Although a study by Jung and Swearer (2011) showed that boat sound may not have detrimental effects on recruitment patterns of coral reef fish, a recent study by Holles et al. (2013) showed that the orientation of cardinal fish larvae were significantly altered by boat noises. Understanding the impact of boat noise is critical, as many coral reef fish

species rely on underwater sounds for predator avoidance and prey detection (Simpson et al. 2011), habitat selection (Stanley et al. 2012), mating (Slabbekoorn et al. 2012), and territorial behaviours (Picciulin et al. 2010, Sebastianutto et al. 2011).

Thailand has approximately 2,130 km² of coral reefs, supporting upwards of 400 coral reef fish species (Satapoomin 2007). Damselfish (Pomacentridae), wrasses (Labridae), groupers (Serranidae), and butterflyfish (Chaetodontidae) are the most common species, as they altogether represent 77% of the families found in the Gulf of Thailand (GCRMN 2010, Scott 2012). In the Gulf of Thailand, about 4.4 million people rely on coral reef resources for subsistence fishing, livelihoods, and food (17.6% of all protein supply) (Panjarat 2007, Ping 2011). Following worldwide fisheries trends, the fish stocks declined dramatically in the Gulf of Thailand, with a 6.5 fold decrease in CPUE of trawl fishing between 1960 and the mid nineties (Pauly and Chuenpagdee 2003). Understanding the extent to which fish assemblages may be affected by physical factors and anthropogenic activities is thus critical, as the Gulf of Thailand appears at risk in terms of food security. Such understanding might also permit us to develop more effective management plans regarding coral reef fish assemblages. Apart from solely fisheries and conservation objectives, fish stocks are also regarded as major drivers of ecosystem resilience (Pauly and Christensen 1995) and evolutionary changes (Kuparinen and Merila 2007).

The objectives of the present paper were to assess the influence of newly implemented no-take marine reserves in MPAs, benthic structure, depth, and recreational activities on the coral reef fish assemblages of Koh Tao, Thailand. I tested the hypotheses that (1) a year post-MPA establishment is insufficient to observe significant changes in reef fish density and assemblage composition (2) there will be a significant increase in reef fish density/diversity in live hard coral dominated habitats (3) there will be a significant decrease in reef fish density/diversity and functional groups as depth increases, with more herbivores and planktivores in shallow reef slopes (4) SCUBA/snorkelling activities and boat traffic have negative impacts on reef fish density.

Material and Methods

Study Site and field sampling

The study was carried out in August and September 2013 in Koh Tao, a small (21 km²) island located about 70km off the western coastline of the Gulf of Thailand (10°5'44.2"N, 99°55'14.4"E). Koh Tao is one of the top tourist destinations in the country, receiving approximately 300,000 tourists annually, the vast majority of which are there for scuba diving and fishing (Chavanich et al. 2012, Terlouw 2012). Consequently, coral reefs around the island are exposed to high usage levels and a wide range of stressors, including mechanical damage (e.g. diver fin damage, anchor damage), sedimentation (e.g. terrestrial clearing), and nutrient enrichment (e.g. wastewater runoff, sewage disposal) (Scott 2012, Terlouw 2012). Additionally, a major bleaching event occurred in 2010 in the Gulf of Thailand, and coral reefs around Koh Tao were severely impacted, with subsequent coral mortality estimated at 72% in some sites (Chavanich et al. 2012).

Commercial and subsistence fishers operate around Koh Tao, however there are very limited records of fish harvests (Yeemin et al. 2006). Most of the reefs are harvested by small-scale traditional fishers, with fish traps, lines and small nets used for the collection of shells and ornamental fish (e.g. Parrotfish, Butterflyfish, and Damselfish) (Yeemin et al. 2006). Conversely, commercial and tourist fishers mainly target pelagic species, such as marlin, mackerel, snapper, and trevally. To counter overfishing and insure the sustainability of reef fish stocks around Koh Tao, a fish sanctuary zone (no-take marine reserve) was established in 1996 on the western side of the Island (Marine Conservation Koh Tao 2012). However, no formal surveillance or enforcement was in place between the creation of the reserve and June 2012 (Marine Conservation Koh Tao 2012, Scott 2012). In this context, the Marine Fisheries Department and the local government established a new zoning plan in July 2012, which included three new no-take marine protected areas (MPAs) in which all fishing and harvesting is now banned (Marine Conservation Koh Tao 2011).

Pre-Reserve baseline data

Pre-reserve baseline data were recorded between January 2006 and June 2012 by the ‘New Heaven Reef Conservation Program’ (NHRCP) (Scott 2012). NHRCP is a conservation program bringing together volunteers and researchers (Scott 2012). They are involved in a number of conservation initiatives around the island such as reef restoration projects, mooring line installations and maintenance, and protection of turtle nurseries (Scott 2012). They also take part in a monitoring program that was set up by the Save Koh Tao Group in 2006, and survey fish populations, as well as benthic and invertebrate assemblages around the island. Altogether, 6 sampling sites distributed all around the island were surveyed between 2006 and 2012: Had Sai Nuan, Hin Wong Bay, Ao Leuk, Sairee, Twins, and Shark Island (Figure 2). The six sites surveyed between 2006 and 2012 were the same study sites as the ones surveyed during the present study. From 2006 to 2012, the study was designed to follow the principles of a modified BACI sampling design (Underwood 1995). At each site, underwater visual census (UVC) of the fish community was carried out on SCUBA along the permanent transects that were established by the “New Heaven Reef Conservation Program” (NHRCP). The transect lines used by the NHRCP were 100m long and each was divided into four replicates transect of 20m each, with 5m gaps between replicates (Figure 1). For each 20m transect, the survey included a search area of 2.5m on each side of transect lines. In each site, four replicate 20m transects were conducted on reef slopes in both shallow (3 - 6 meters) and deep (6 - 13 meters) habitats.

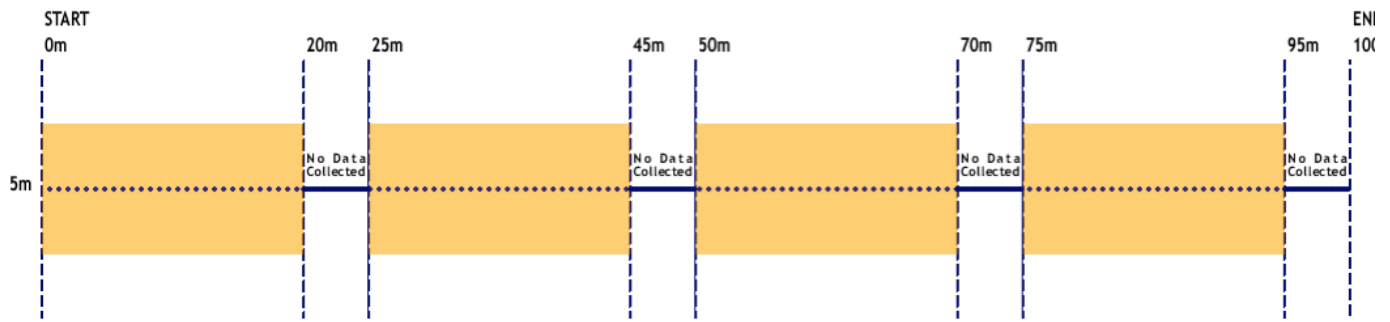


Figure 1. Sampling design used to collect baseline (pre-reserve) fish data at both shallow and deep habitats at each monitoring site. The 100m lines were divided into 4 transects of 20m each, and fish surveys were conducted on these (yellow parts).

Post-reserve data

The present study included three sites within the newly established MPAs (Twins, Sairee, and Shark Island) and three sites in areas that have remained open to fishing (Had Sai Nuan, Hin Wong Bay, and Ao Leuk) (Figure 2).

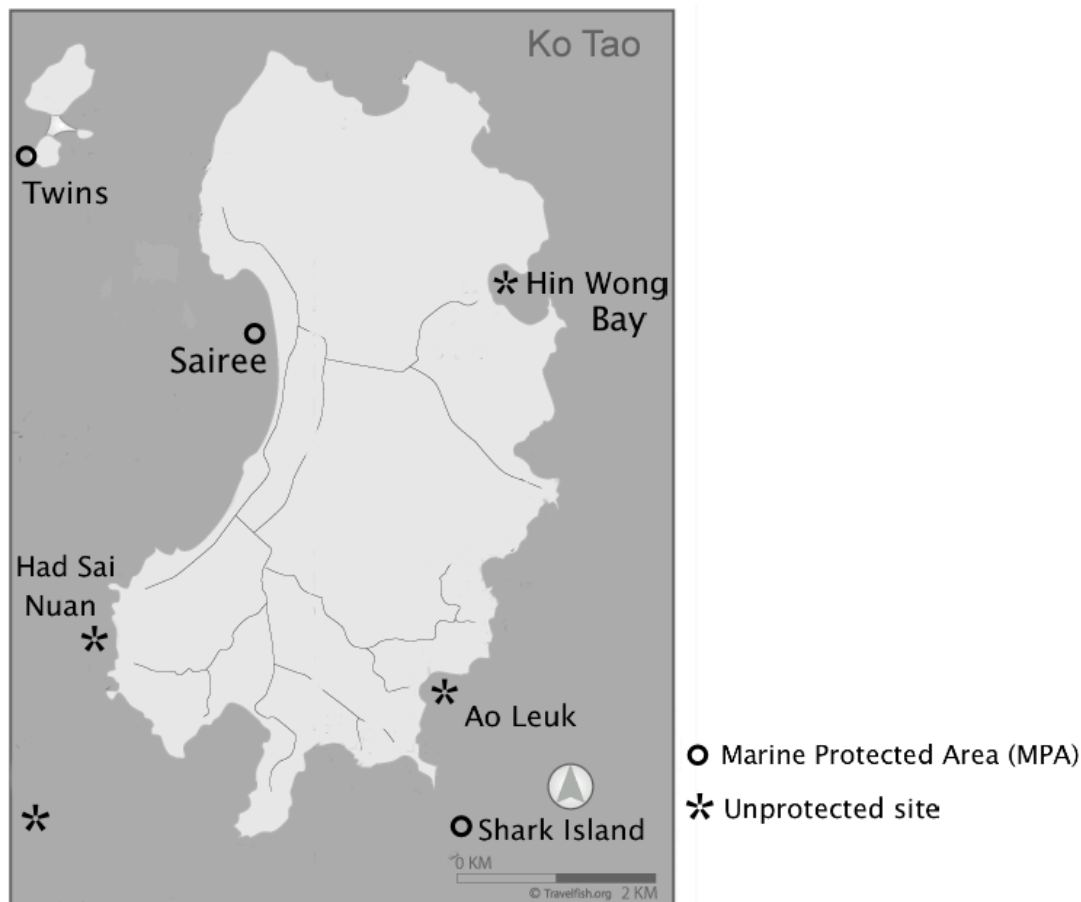


Figure 2. Location of the six study sites around Koh Tao Island. Sairee, Twins, and Shark Island are classified under no-take 'Marine Protected Area'. Hin Wong Bay, Had Sai Nuan, and Ao Leuk are unprotected sites.

In each of the 6 sites, four 50m transects were deployed in deep (> 6m) and shallow (< 6m) reef slope habitats (Figure 3), the same reef slope habitats sampled in the baseline study. The ‘shallow’ and ‘deep’ reef slope habitats were defined within the marine conservation program of the New Heaven Dive School (Chaalok Baan Kao). Each transect tape was laid parallel to the shoreline (dependent of the topography of the coast), and all transect tapes were separated by 5m.

The Underwater visual census (UVC) technique of Fowler (1987) was carried out to survey fish communities. Two observers on SCUBA counted a subset of fish species from 7 families within a 5m wide belt along each 50m transect tape (total survey area was 250m² per transect). To avoid biases associated with human disturbances, the first observer (front position) recorded all fish species except those in the family Pomacentridae. The second observer recorded the Pomacentridae, as they were considered as more territorial and less likely to be affected by the presence of divers underwater (Gonzalez-Sanson et al. 2009). Both observers recorded their data on underwater slates. In order to achieve more accurate depth estimates between ‘shallow’ and ‘deep’ reef slopes, the exact depth measures were recorded at the start and end of each transect. The average depth of each transect was then calculated and used to estimate the influence of depth on fish assemblages. Each site was sampled twice over two non-consecutive days (4 transects/depth/day).

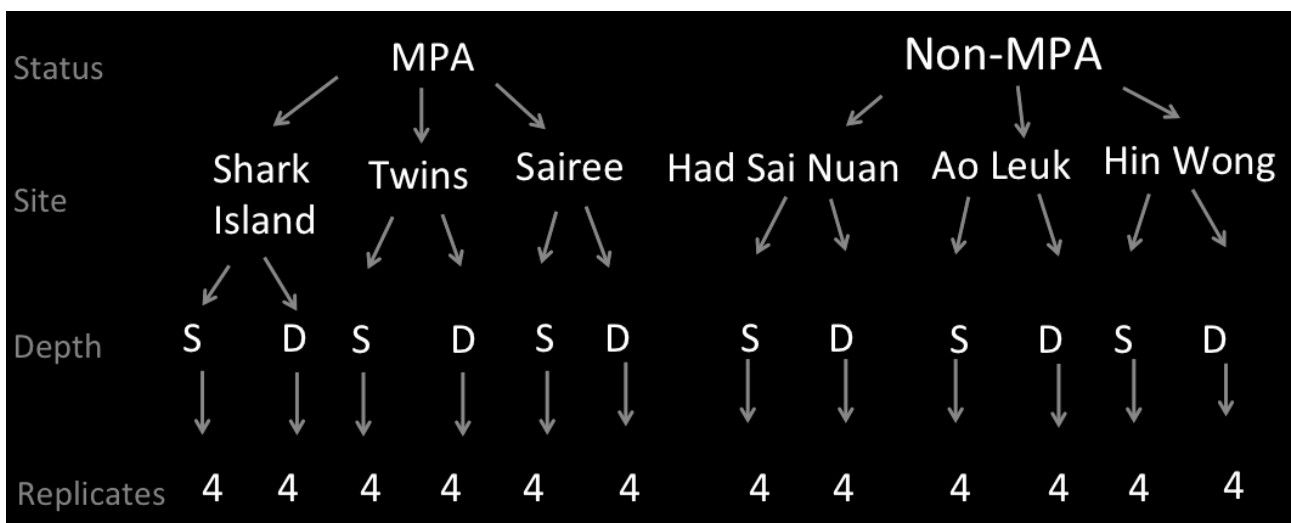


Figure 3. The sampling design used in this study. In each site, four 50m transect tapes were deployed on both shallow and deep reef slope habitats. Each sampling was replicated over two days, with 4 transects laid in shallow and deep reef slopes each day.

Study species

Altogether, 7 fish families were sampled as indicators of the fish assemblages (Table 1).

Table 1. Fish families/species surveyed at the six study sites.

Fish families	Species	Fish families	Characteristics
Chaetodontidae	<i>Chelmon rostratus</i>	Serranidae	Large (>30cm)
	<i>Chaetodon octofasciatus</i>		Small (<30cm)
	<i>Chaeton lineolatus</i>	Scaridae	Large (>20cm)
	<i>Heniochus acuminatus</i>		Small (<20cm)
	<i>Chaetodon wiebeli</i>	Siganidae	
Pomacentridae	Lutjanidae		
	<i>Dascyllus reticulatus</i>		
	<i>Amphiprion perideraion</i>		
	<i>Pomacentrus moluccensis</i>		
	<i>Stegastes obreptus</i>		
Labridae	<i>Cheilinus fasciatus</i>		

Boat traffic & diving/snorkelling usage patterns

For each site, boat surveys were done over two non-consecutive days. Observations were conducted from the shoreline with binoculars between 10:00AM and 02:00PM (boat traffic peak period). Observers recorded both the ‘diving pressure’ and the ‘boat traffic’. Sighted boats were classified as ‘dive and snorkelling boats’ or ‘passing boats’. For each diving/snorkelling boat, the arrival and departure times were recorded. The time of each passing boat within the spatial limits of the sampling sites was recorded. For each of the six study sites, eight hours of boat observation surveys were carried out.

Data handling and statistical analysis

In order to meet all the assumptions of the following statistical tests, square root (sqrt) or $\log(x+1)$ transformations were applied to all fish density data. All fish densities were standardised to 100m² by dividing raw (i.e. transect) counts by 2.5. In terms of univariate analysis, a three-way Analysis of Variance (ANOVA) was computed for the three factors ‘MPA status’ (two levels: MPA/non MPA), ‘depth’ (two levels: shallow/deep), and ‘sites’ (six sites) nested in MPA status (Underwood 1995) (Table 2). ‘Reef fish density’ and ‘Reef fish diversity’ were computed as the variates. ‘MPA status’ and ‘Depth’ were considered as fixed factors, whereas ‘Sites’ was

considered as a random, nested factor. This three-way factor ANOVA was computed using the statistical software SPSS (version 20). Similar univariate analyses were computed for the variates ‘fisheries targeted species’ and ‘functional groups’. When necessary, reef fish density and diversity were compared using the Tukey-Kramer HSD (Honest statistical difference) post-hoc test (Quinn and Keough 2002).

All graphical outputs were computed with the software package Excel (version 20).

1) The effects of newly implemented MPAs

- On fisheries targeted species

The effects of newly implemented MPAs were investigated on the fish species targeted by local commercial fisheries around Koh Tao: Lutjanidae, Scaridae, and Serranidae (Yeemin et al. 2006). Scaridae and Serranidae were divided into large (Scaridae (>20cm), Serranidae: (>20cm)) and small (Scaridae (<20cm, Serranidae: (20cm)) individuals. The ‘before MPA establishment’ data were the pre-reserve baseline data collected by the NHRCP between 2006 and 2012. The six years of data were pooled together for each fisheries targeted reef fish species and expressed in average density (number/100 m²). The ‘after MPA establishment’ data were recorded as part of the present study, a year after MPAs were established around Koh Tao.

- By site

The effects of newly implemented MPAs were also investigated for fisheries targeted species within the three new MPAs: Twins, Shark Island, and Sairee.

2) The influence of depth

- Density/diversity and trophic groups

For each transect, depth was averaged between the starting and ending point of each transect. Each transect with a mean depth lower than 6 meters was considered as ‘shallow’, while each transect with a mean depth greater than 6 meters was considered as ‘deep’. Regarding functional

groups, all fish families/species were assigned to one of four functional groups: carnivores, herbivores, corallivores, and planktivores.

3) The influence of benthic structure

- Live hard coral cover

Linear regressions of fish density against live hard coral cover were computed for all fish species/families using the statistical software PRIMER (Primer-E version 6; Clarke and Goley 2006). R-squared (R^2) and p -values were also computed.

- Benthic Assemblage compositions

The James Cook University Master student Margaux Hein recorded all data on benthic composition. The transects used for the benthic assemblages were not the same as the ones used for fish surveys. The benthic assemblages were also surveyed in August and September 2013, and surveys were done along 3 transects of 15m laid between 2 and 5 meters deep. The benthic transects were located approximately 100 m to 300 m from the transects used to survey reef fish assemblages.

For each site, the mean percentage cover was computed for five substrate types: hard coral, rock, rubble, soft coral, and sand. After all data were normalised, a principal component analysis (PCA) was computed for the three major substrate types 'Hard coral', 'Rock', and 'Rubble'. For each site, the dominant benthic component (>50%) was then recorded, and each site was then 'assigned' with its dominant benthic component. In order to understand which fish species/families drove dissimilarities in fish composition between benthic habitats, non-metric Multi-Dimensional Scaling (MDS) plots of the square root or log transformed raw data were projected onto the Bray Curtis resemblance matrix and dissimilarities was plotted (Primer-E version 6; Clarke and Gorley 2006). An associated analysis of similarity (ANOSIM) was performed to provide a measure (R) of the similarities among the different habitat types (Primer-E version 6; Clarke and Gorley 2006). A

SIMPER analysis was also run to identify which individual fish families/species accounted for the majority of the dissimilarities in fish assemblage structure among the three habitat types (Primer-E version 6; Clarke and Gorley 2006).

Multi-Dimensional Scaling (MDS) was also used to examine broad differences in fish assemblage composition between the six study sites. To investigate the relationship between fish assemblage structure and physical variables, a BIO-ENV test was carried out using PRIMER (Primer-E version 6; Clarke and Gorley 2006). Six physical variables were considered: hard coral cover, rubble, rock, soft corals, sand, and depth. In order to describe the similarities between sites and habitat types, sequences of SIMPROF tests were computed for both MDS analyses (Clarke et al. 2008).

3) The influence of recreational activities

For each site, the number of passing/diving/snorkelling boats was computed for the eight hours of observation, and averaged over one hour to give a number N (number of boats/hour). When the number N was lower than 10 boats per hour, the site was classified as being under low recreational pressure. When N was between 10 and 20 boats per hour, the site was classified as being under medium recreational pressure. When N was higher than 20 boats per hour, the site was classified as being under high recreational pressure.

A one-way ANOVA (fixed factor: recreational pressure) was computed to test for the effects of recreational pressure on density of each fish family. Here, each fish family/species was analysed as independent groups.

Results

Sixteen fish groups (species/families) were recorded and analysed in the present study. All species/family groups were recorded at least once, except the copper-banded Butterflyfish (*Chelmon rostratus*) that was not recorded at any site in 2013 (Table 2).

Table 2. Total number (N) counted and frequency of occurrence in samples (S) of the 16 coral reef fish family/species included in the 2013 study. %N and %S represent the percentage of the total. The symbol * indicates if fish family/species is targeted by fishing.

Fish families/species	N	% N	S	% S
Serranidae *				
Large, >30cm	38	<0.5	26	27.1
Small, <30cm	348	3.6	76	79.2
Scaridae *				
Large, >20cm	301	3.1	67	69.8
Small, <20cm	382	3.96	52	54.2
Lutjanidae *	20	<0.5	13	13.5
Siganidae	358	3.7	66	68.7
Labridae				
<i>Cheilinus fasciatus</i>	102	1.1	57	59.4
Chaetodontidae				
<i>Chelmon rostratus</i>	0	0	0	0
<i>Chaetodon wiebeli</i>	146	1.5	54	56.2
<i>Chaetodon octofasciatus</i>	209	2.2	68	70.8
<i>Heniochus acuminatus</i>	28	<0.5	17	17.7
<i>Chaetodon lineolatus</i>	5	<0.1	4	4.2
Pomacentridae				
<i>Dascyllus reticulatus</i>	1931	20.1	60	62.5
<i>Pomacentrus moluccensis</i>	4489	46.6	89	92.7
<i>Stegastes obreptus</i>	1079	11.2	77	80.2
<i>Amphiprion perideraion</i>	197	2.04	25	26

No significant differences were found in reef fish density and diversity before and after MPA establishment (Table 3AB). Conversely, significant differences in density (ANOVA, $p < 0.0001$) and diversity ($p = 0.001$) were found between the six sites of study (Table 3AB). The study site ‘Twins’ supported the highest density (67 individuals per 100m²), whereas ‘Shark Island’ supported the lowest density (21 individuals per 100m²) of reef fish (Figure 4). The associated post-hoc Tukey-Kramer HSD test revealed that ‘Twins’ and ‘Shark Island’ were significantly different from other study sites and from each other in terms of reef fish density ($q^* = 4.267$, Alpha=0.05).

The study sites ‘Twins’, ‘Hin Wong’, and ‘Ao Leuk’ exhibited the highest reef fish diversity, with values ranging from 3 to 3.5 species/100m². This pattern was confirmed by the Tukey-Kramer HSD test ($q^*=4.267$, $\text{Alpha}=0.05$) that showed that those three study sites could be considered significantly different from the study sites ‘Shark Island’ and ‘Had Sai Nuan’, but not from each other.

Table 3. Three-way ANOVA of the variates ‘density’ (A) and ‘diversity’ (B) of all reef fish species/families for the three factors ‘MPA status’ (fixed), ‘Depth’ (fixed), and ‘Sites’ (random, nested).

(A)

	Df	Sum of Squares	Mean Squares	F value	Pr(F)
Status	1	4.3104	4.3104	0.0173281	0.9036042
Depth	1	139.0351	139.0351	8.483006	0.0333004
Status*Depth	3	0.5958	0.5958	0.03635	0.8562936
Sites (Status)	3	746.2473	248.7491	15.328	< 0.0001
Depth*Site (Status)	5	81.9492	16.3898	13.052	0.000
Residuals	82	673.1352	8.208966		

(B)

	Df	Sum of Squares	Mean Squares	F value	Pr(F)
Status	1	5.04167	5.04167	0.2467474	0.653494
Depth	1	6.97676	6.976758	2.39641	0.032
Status*Depth	3	0.20166	0.201658	0.069267	0.802909
Sites (Status)	3	61.29751	20.4325	4.171	0.001
Depth*Site (Status)	5	14.55669	2.911338	0.943	0.334
Residuals	82	224.3899	2.736462		

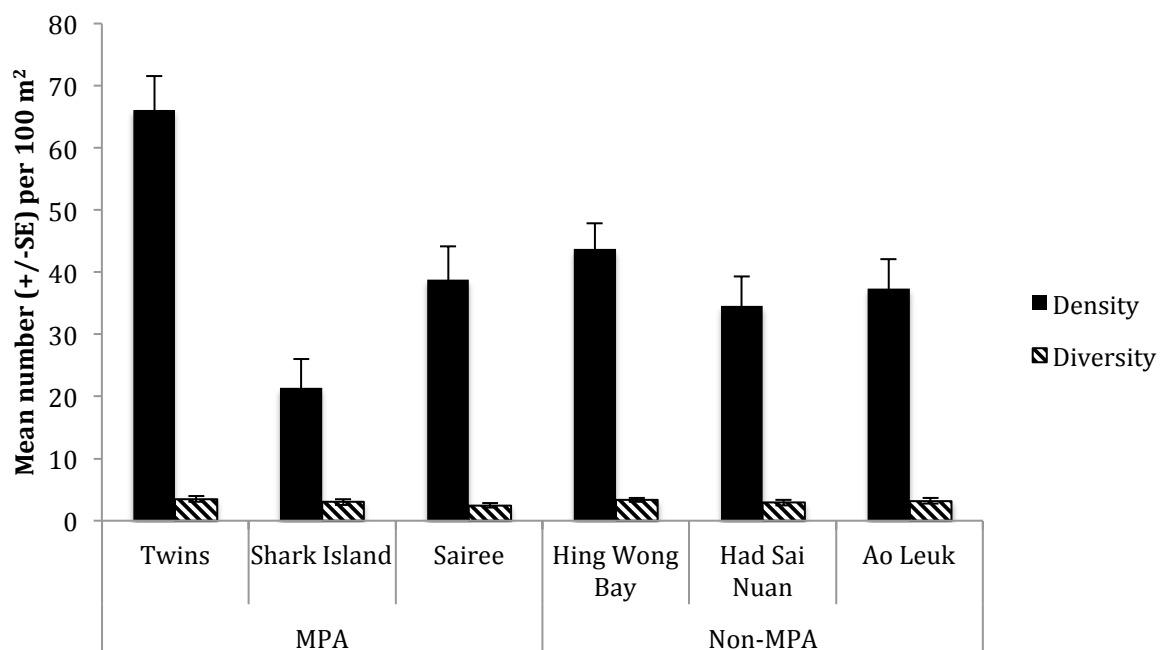


Figure 4. Mean density and diversity (number/100m² +/-SE) of reef fish families/species in the six study sites.

- *The effects of newly-implemented MPAs on fisheries targeted species*

No significant differences in density of any fisheries targeted fish families were detected before and after MPA establishment (Figure 5). Lutjanidae and large Serranidae were much less abundant overall than Scaridae and small Serranidae (Figure 5).

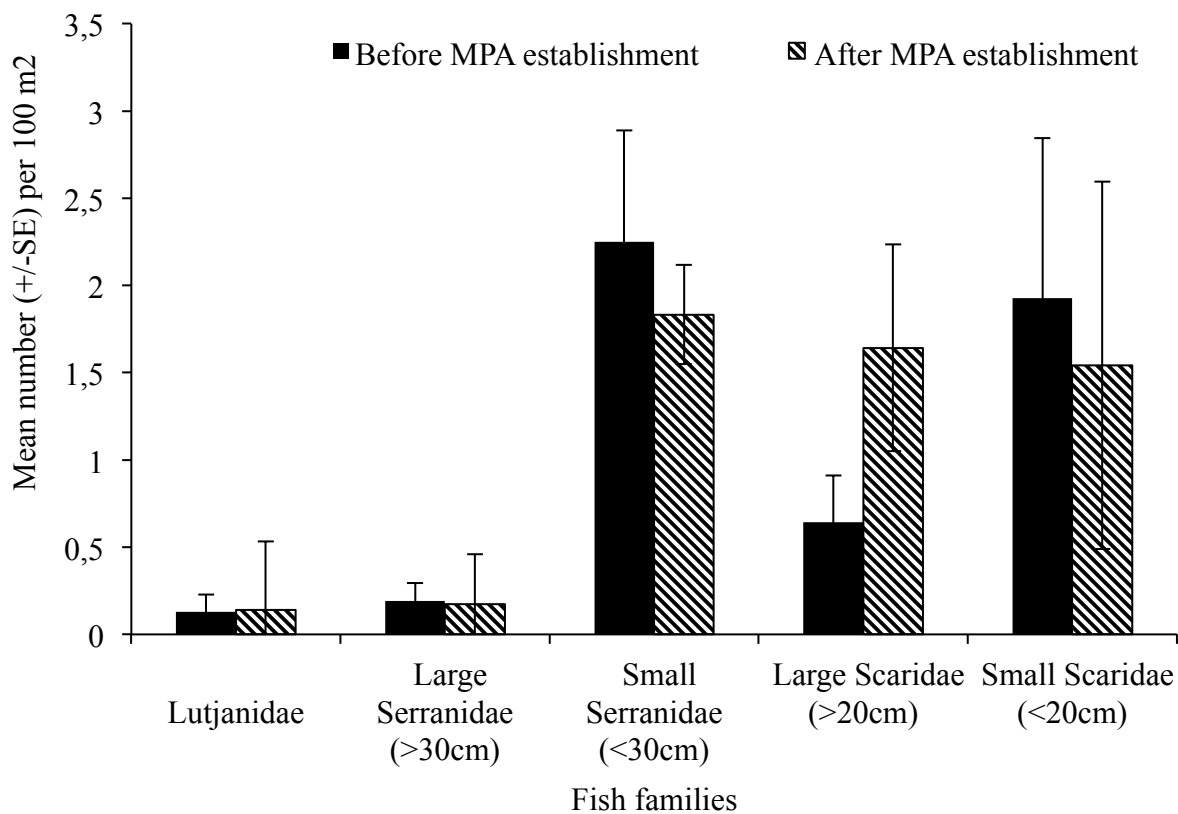


Figure 5. Mean density (number/100m² +/-SE) of fisheries targeted reef fish families before (2006-2012) and after (2013) MPA establishment.

There was a significantly lower density (ANOVA, $p=0.007$) of small Scaridae after reserve establishment at ‘Twins’ (Figure 6A). The density was 3.5 fold higher before than after MPA establishment. Large Scaridae were 5 fold higher in density after than before MPA establishment at “Shark Island” (Figure 4B, ANOVA, $p = 0.037$). No significant differences were detected in the densities of fishery targeted groups before and after MPA establishment at Sairee (Figure 6C).

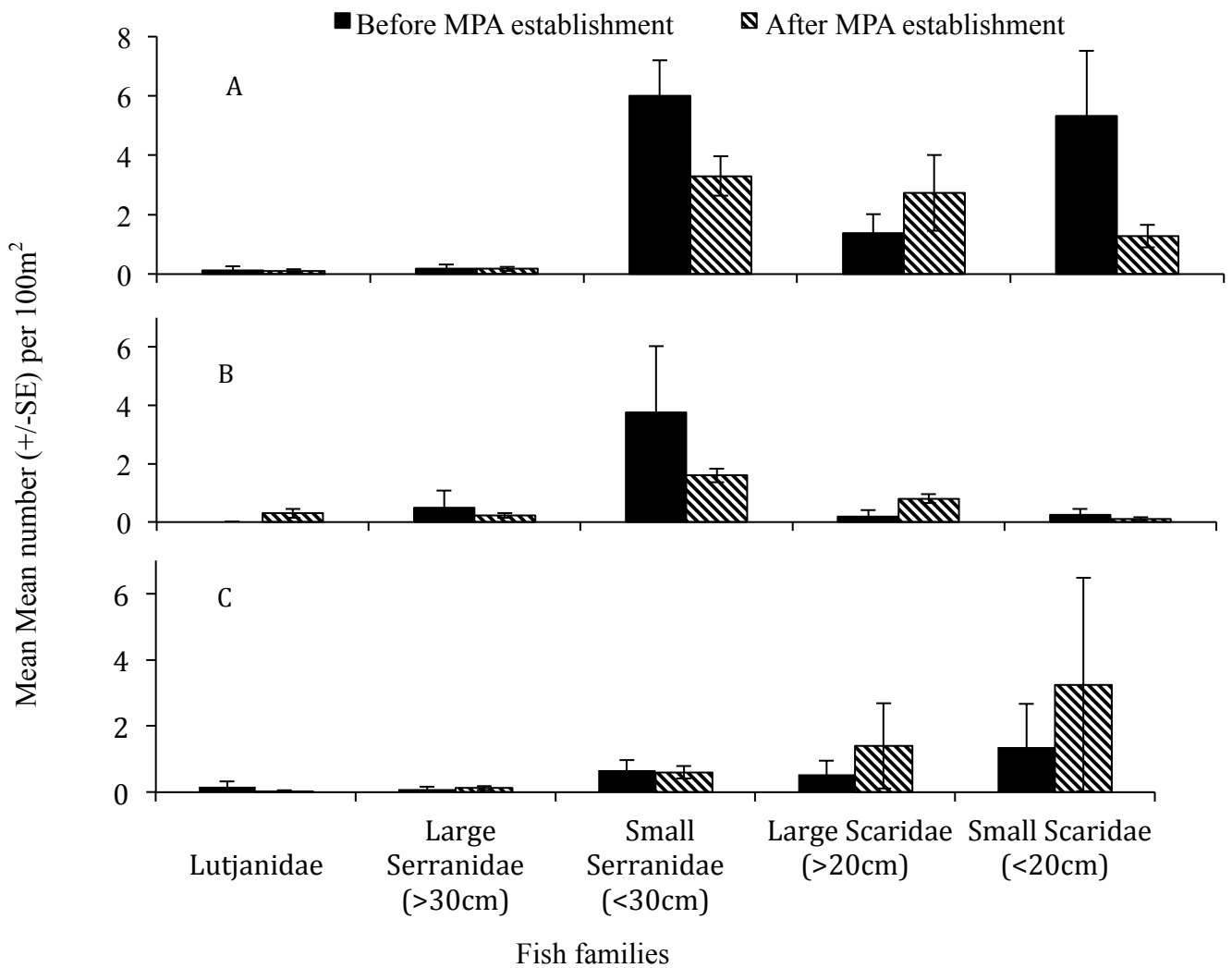


Figure 6. Mean density (number/100m² +/-SE) of fisheries targeted fish families before and after MPA establishment in the three MPA sites of the study: Twins (A), Shark Island (B), and Sairee (C).

- ***The influence of depth***

Significant differences were found in the density (ANOVA, $p=0.036$) and diversity (ANOVA, $p=0.032$) of the fish families/species of the study between shallow (<6m) and deep (>6m) reef slope habitats (Table 3AB). The mean density was 1.27 fold higher in shallow than in deep reef slope habitats (+27%) (Figure 7).

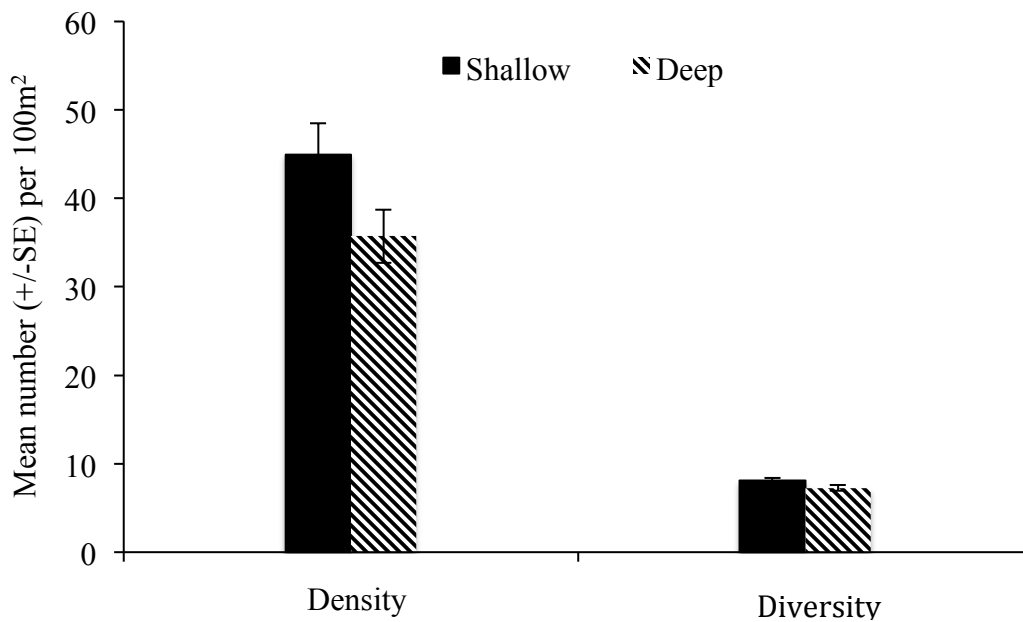


Figure 7. Mean density (number/100m² +/-SE) and diversity (number of families/100m² +/-SE) of coral reef fish in shallow (<6m) and deep (>6m) reef habitat strata.

There were no significant differences in carnivore (ANOVA, $p=0.124$) and herbivore (ANOVA, $p=0.165$) densities between the shallow (<6m) and deep (>6m) reef habitats at any of the study sites. Conversely, significant differences were found in planktivore (ANOVA, $p=0.001$) and corallivore (ANOVA, $p=0.003$) densities between shallow and deep reef slopes. The mean density of planktivores was 1.23 fold higher in shallow than in deep habitats (+21.1%) (Figure 8). Similarly, the mean density of corallivores was 2 fold higher in shallow than in deep reef slope habitats (Figure 8). Interestingly, herbivores, planktivores, and corallivores were all at higher abundances in shallow habitats than in deep habitats, whereas carnivores tended to follow the inverse pattern (Figure 8).

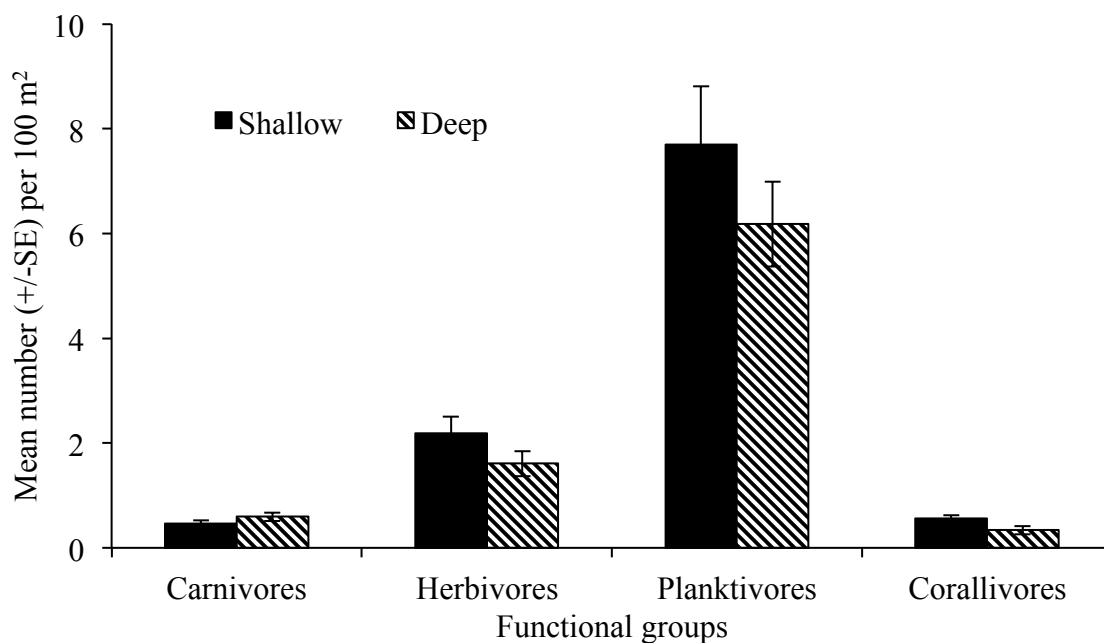


Figure 8. Mean density (number/100m² +/-SE) of functional groups between shallow (<6m) and deep (>6m) reef habitat strata.

- *The influence of benthic structure*

No significant differences were found in either fish density or diversity among the three types of habitats hard-coral, rock, and rubble. Yet, visual observations indicated that higher reef fish densities occurred in hard coral/rubble habitats than in rocky habitats (Figure 9).

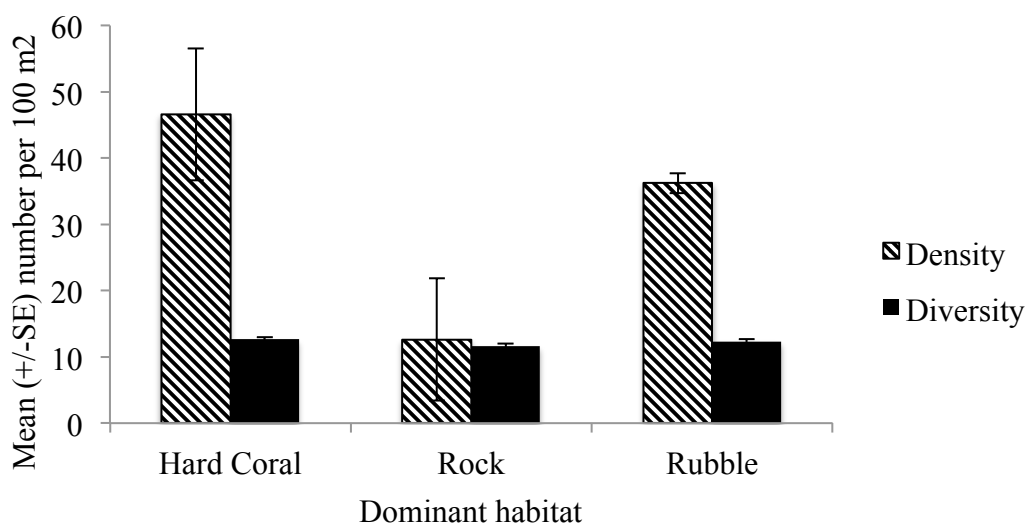


Figure 9. Mean density and diversity (number/100m² +/-SE) of reef fish between hard coral, rock, and rubble dominated habitats.

Linear regression analyses indicated that the densities of only two species of fish were significantly correlated with the cover of live hard coral: *Dascyllus reticulatus* (Regression, $R^2=0.655$, $p=0.049$) (Figure 10A) and *Chaetodon octofasciatus* (Regression, $R^2=0.71$, $p=0.034$) (Figure 9B). The density of *Dascyllus reticulatus* was inversely correlated with the percentage of hard coral cover (Figure 10A). Conversely, the density of *Chaetodon octofasciatus* was positively correlated with the percentage of hard coral cover (Figure 10B).

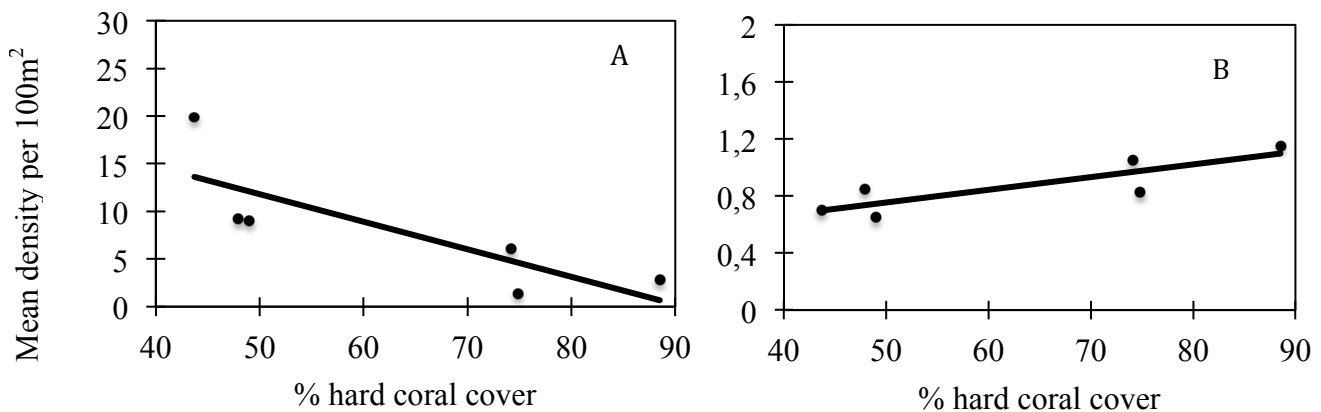
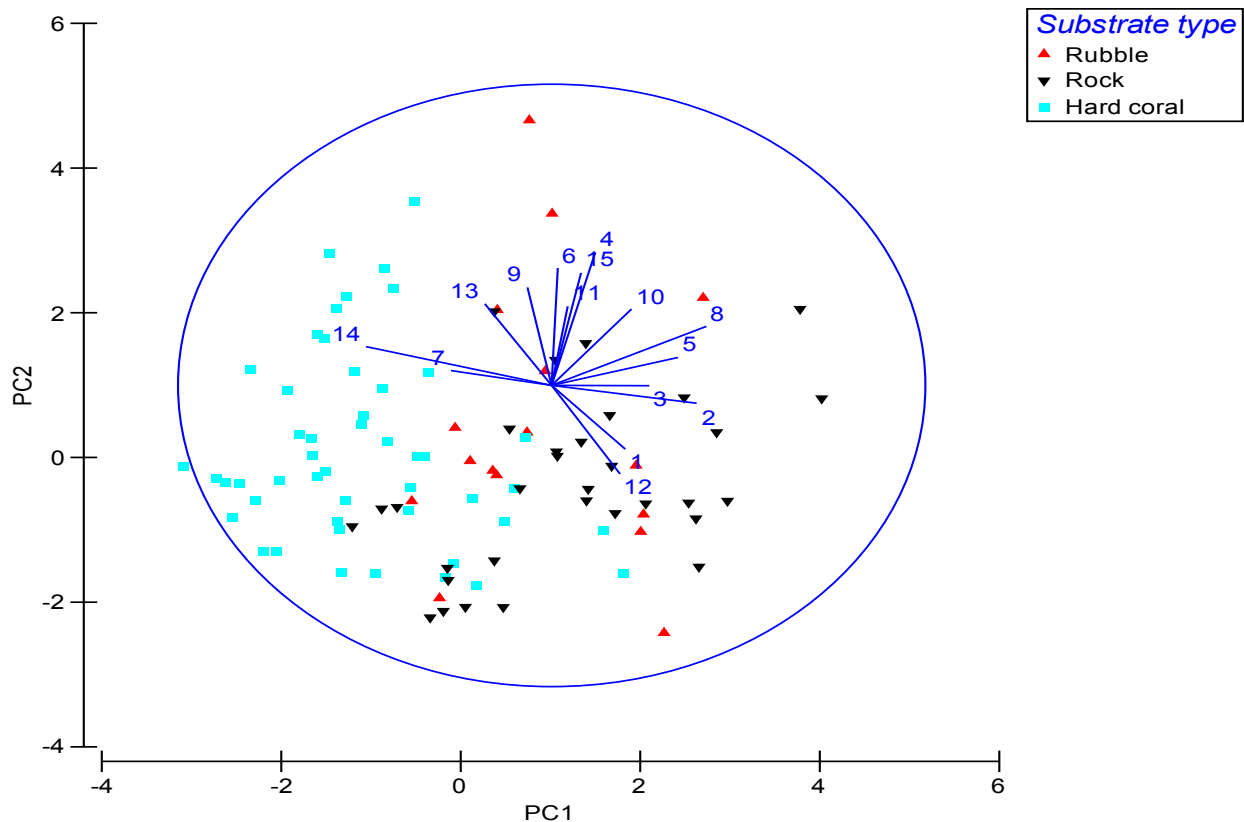


Figure 10. Linear regressions of the density (number/100m²) of *Dascyllus reticulatus* (A) and *Chaetodon octofasciatus* (B) as a function of the % hard coral cover.

Principal components analysis revealed strong relationships between substrate types and the density of fish families/species (Figure 11). The mean density of Labridae (14) and the Pomacentridae *S. obreptus* (7) appeared to be positively correlated with percentage of hard coral cover (Figure 10). Conversely, the density of large Serranidae (1), small Serranidae (2), and *C. lineolatus* (12) appeared positively correlated with the presence of rocky substrates (Figure 10). Finally, the presence small Scaridae (4), Siganidae (15), and *H. acuminatus* (11) appeared to be highly correlated, and possibly associated with rubble substrates (Figure 11).



1. Serranidae (large) 2. Serranidae (small) 3. Scaridae (large) 4. Scaridae (small) 5. *Dascyllus reticulatus*
 6. *Pomacentrus moluccensis* 7. *Stegastes obreptus* 8. *Amphiprion perideraion* 9. *Chaetodon wiebeli*
 10. *Chaetodon octofasciatus* 11. *Heniochus acuminatus* 12. *Chaetodon lineolatus* 13. Lutjanidae 14. Labridae
 15. Siganidae

Figure 11. Principal Component Analysis of benthisc and fish data. Plot shows the projection of the 15 fish species/families (blue vectors) in relation to the three benthic variables ‘Rock’, ‘Rubble’, and ‘Hard coral’.

Multi-Dimensional Scaling (MDS) revealed that habitats dominated by hard coral showed less variability in reef fish assemblage composition than habitats dominated by rock (Figure 12). This is supported by the ANOSIM analysis, which showed that hard coral-dominated and rock-dominated habitats were significantly dissimilar in terms of fish assemblage compositions (ANOSIM, $R=0.568$) (Clarke and Warwick 2001). The SIMPER analysis indicated that Pomacentridae drove approximately 57% of the dissimilarities in the reef fish assemblage between hard coral and rock habitat types (contribution of *Pomacentrus moluccensis* (40.99%), *Dascyllus reticulatus* (8.4%), and *Stegastes obreptus* (7.74%)). Also, *Chaetodon octofasciatus* contributed

9.6% towards the fish assemblage dissimilarities between hard coral-dominated and rock-dominated habitats.

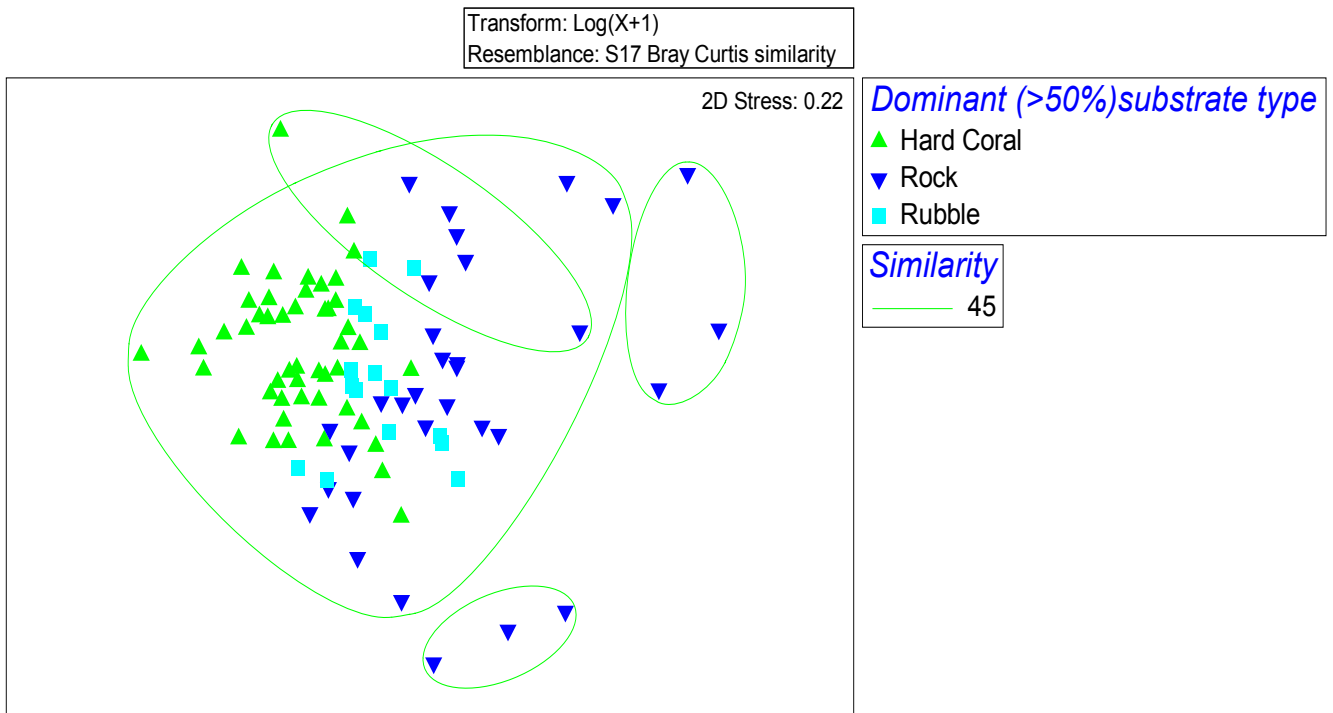


Figure 11. Non-metric Multi-Dimensional Scaling (MDS) plot of the $\log(x+1)$ and square root-transformed Bray-Curtis similarities of fish species/families recorded in relation to habitats dominated (>50%) by the three benthic components ‘Rubble’, ‘Rock’, and ‘Hard Coral’. The similarity level between substrate types illustrates the resemblance measures (SIMPROF test) of the Bray Curtis similarities.

Multi-Dimensional scaling (MDS) analyses also revealed obvious clustering among sites (Figure 13). Shark Island showed the highest variability in fish assemblage compositions, whereas Sairee and Hin Wong Bay were more clustered (Figure 13). The BIO-ENV analysis revealed that 3 physical variables are responsible for 62.5% of the dissimilarities in reef fish assemblage structure among sites: hard coral cover, rubble, and rock.

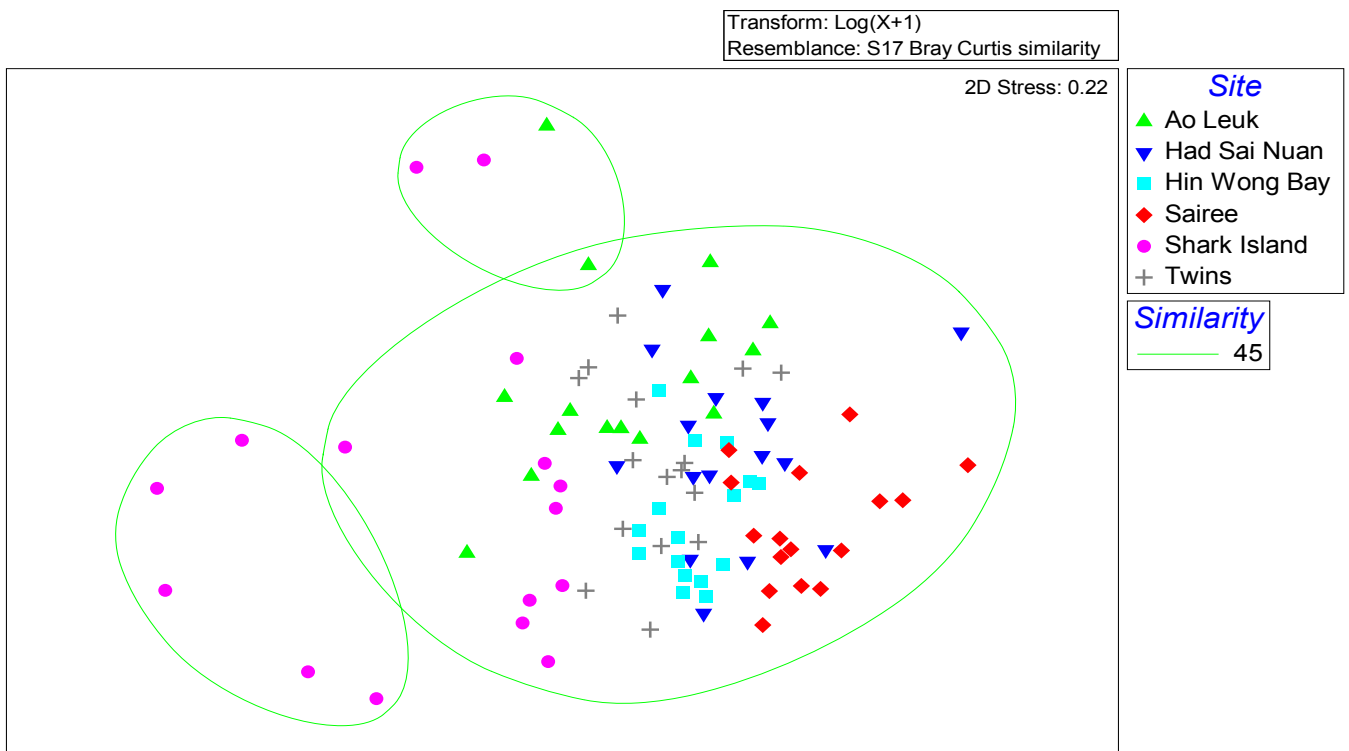


Figure 13. Non-metric Multi-Dimensional Scaling (MDS) plot of the $\log(x+1)$ transformed Bray-Curtis similarities of fish species/families recorded at the six study sites. The similarity level between substrate types illustrates the resemblance measures (SIMPROF test) of the Bray Curtis similarities.

The influence of recreational activities

Table 4. Mean number of Dive Boats (mDB) and Boats passing (mBP) at the six study sites. Shark Island, Twins, and Ao Leuk are under low recreational pressure (<10boats/hour). Had Sai Nuan and Hin Wong Bay are under medium recreational pressure (between 10 and 20 boats/hour). Sairee is under high recreational pressure (>20 boats/hour)

	mDB	mBP	DB+BP	Recreational pressure
Shark Island	2.5	5.5	8	low
Twins	2.17	2.83	5	low
Had Sai Nuan	0	10.67	10.67	medium
Hin Wong Bay	8.5	8.83	17,33	medium
Sairee	0	36.5	36.5	high
Ao Leuk	5.33	1.17	6.50	low

On deep reef slopes, significant differences (ANOVA, $p= 0.011$) were found in density of Labridae between sites with low and high recreational pressure. Labridae density was 1.15 fold higher under high recreational pressure than under low recreational pressure (Figure 14A). No other significant differences were found for density of other fish family under the three different

recreational pressures. Serranidae and Chaetodontidae were both generally less abundant with increasing recreational pressure (Figure 14A). Also, Scaridae appeared more abundant in sites with high recreational pressure (Figure 14A).

On shallow reef slopes, significant differences in density were found in Serranidae (ANOVA, $p=0.006$) and Chaetodontidae (ANOVA, $p<0.001$) between sites under low and medium recreational pressures. Both families were less abundant as recreational pressure increased (Figure 14B). For instance, the density of Serranidae was found 2.1 fold higher in density under low recreational pressure than under high recreational pressure. Siganidae were more abundant under medium recreational pressure in both shallow and deep reef slopes (Figure 14AB).

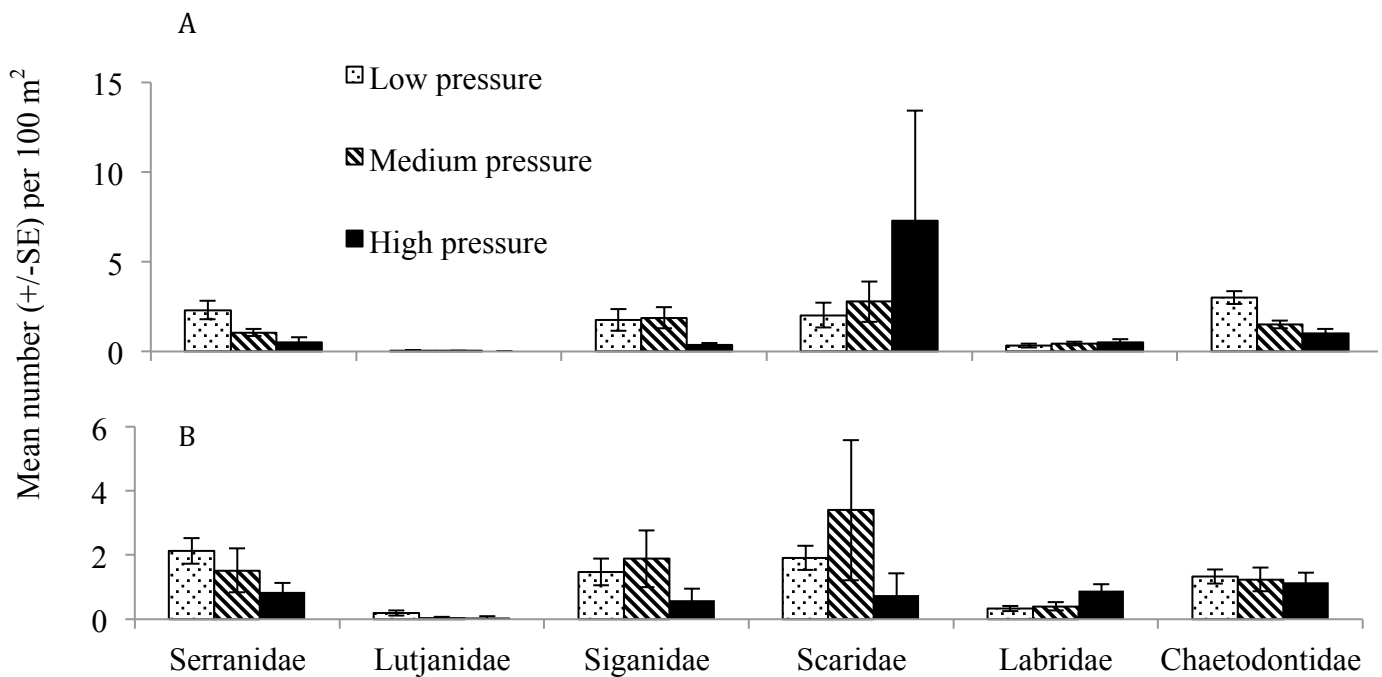


Figure 14. Mean density (number/100m² +/-SE) of the six fish families Serranidae, Lutjanidae, Siganidae, Scaridae, Labridae, and Chaetodontidae under high (N>20 boats/hours), medium (10 boats/hour<N<20 boats/hours), and low (N<10 boats/hour) recreational pressure in deep (A) and shallow (B) reef slope habitats.

No significant differences were found in densities of Pomacentridae between sites under different recreational pressure in either shallow or deep reef slope habitats. In deep reef slopes, Pomacentridae density decreased under increasing recreational pressure (Figure 15).

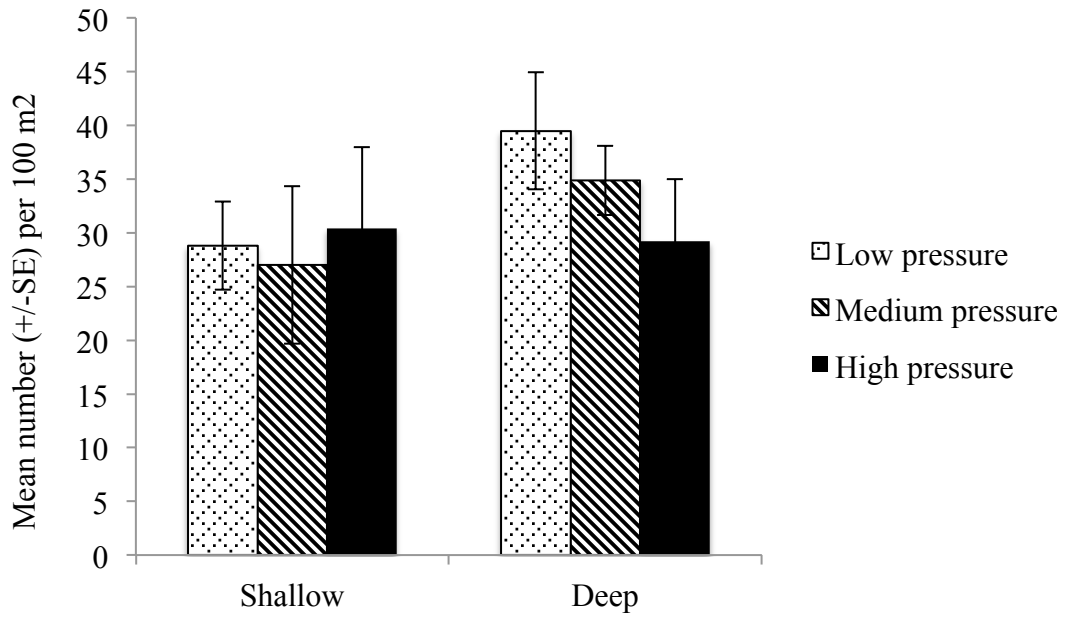


Figure 15. Mean density (number/100m² +/-SE) of the fish family Pomacentridae under high (N>20 boats/hours), medium (10 boats/hour<N<20 boats/hours), and low (N<10 boats/hour) recreational pressure.

Discussion

MPA effects

No significant short-term changes in density of fishery targeted reef fish families occurred after the implementation of the MPAs in Twins, Shark Island, and Sairee in June 2012. This conclusion is consistent with recent literature (Halpern and Warner 2002, Eklof et al. 2009, Colleter et al. 2012, Frascchetti et al. 2012) showing that MPAs could only become beneficial for fisheries targeted fish species after 2 to 9 years of protection. Serranidae and Lutjanidae are all long-lived fishes and have life history characteristics consistent with K-strategists, including slow growth and late sexual maturity (Musick 1999, Sale et al. 2005, Seyboth et al. 2011), large size (Choat et al. 1996, Coleman et al. 2000), short spawning season (Coleman et al. 1999), high site fidelity (Mason and Lowe 2010, Meyer et al. 2010), and migratory behaviour during the spawning season (Coleman et al. 1999). Given the life-history characteristics of these fishes, it is likely that significant MPA effects in the form of stock recoveries would generally only be observed after juveniles eventually recruit into adult populations and then grow (Aburto-Oropeza et al. 2007).

McClanahan and Humphries (2012) recently showed that the longer the time since fishing disturbances, the greater the average adult body size. Such knowledge could provide insights about growth, size of the spawning stock, mortality, and recruitment of fish stocks within no-take zones, allowing establishment of realistic minimum legal size at first capture and harvesting quotas beyond MPA borders (Lou et al. 2005, Watson et al. 2009). According to McClanahan and Humphries (2012), life-history characteristics of fisheries targeted reef fish species may evolve differently depending on the degree of protection. In all cases, potential benefits of MPAs for fish populations and fisheries yields could only be realistic if life-history changes of targeted reef fish species are taken into account (Conover and Munch 2002, McClanahan and Humphries 2012).

At this stage, the absence of MPA effects observed at Koh Tao could also be caused by a lack of active enforcement and poor compliance with the new MPAs. For instance, relatively small

boats using lines to fish may have a dramatic impact on Serranidae, Lutjanidae populations, as those reef fish families are big enough to outcompete most smaller reef fish species for bait (Gilmore and Jones 1992). MPA effects could only be expected if adequate MPA enforcement and compliance is in place (Agardy et al. 2011, Bergseth et al 2013). No information is currently available on MPA compliance on Koh Tao, however during the boat surveys in this study, no incidences of illegal fishing within MPA boundaries were recorded. Moreover, it is also critical to consider the potential biases associated with the Underwater Visual Census technique used in this study. Kulbicki et al. (2010) showed that the detection of reef fish species during UVC was highly affected by transect width, fish behaviour (e.g. swimming speed, inquisitiveness towards divers), adult size, position in the water column, and rarity. Interestingly, Lutjanidae and Labridae are often attracted by divers, and can be overestimated in fish surveys (Samoilys and Carlos 2000, Colvocoresses and Acosta 2007, Kulbicki et al. 2010). Finally, there is a need to consider baseline data and the reasons for selection of MPA sites when investigating MPA effectiveness (Edgar et al. 2004, Pinnegar and Engelhard 2008). Except for the study site ‘Twins’, the selection of the ‘no-take’ zones ‘Shark Island’ and ‘Sairee’ were not random. For instance, a parallel study recently showed that Shark Island had the lowest live hard cover among the six study sites, whereas Sairee exhibited a poor coral genetic diversity (Hein, unpublished data). Our results thus may simply reflect initial selection of ‘poor-resource’ sites, whereby local fishers may minimize the impacts of prohibition of fishing on their livelihoods (Edgar et al. 2004).

The influence of depth

The study revealed that coral reef fish density and diversity was higher above 6 meters than in deeper reef slope habitats. This conclusion is in line with previous literature (Meekan et al; 1995, Chong-Seng et al. 2002, Srinivasan 2003, Garcia-Sais et al. 2010). It is likely that the high density of coral reef fish species in shallow depths is partly determined by biological factors, including the vertical distribution of fish larvae (Srinivasan 2003, Correl et al. 2012), the absence/presence of

conspecifics/heterospecific reef fish species (Ohman et al. 1998, Jones et al. 1987), or simply the choice of settlement in shallow waters (Leis and Carson-Ewart 2000). Yet, changes in coral reef fish distribution with depth could be also attributed to changes in physical conditions (Srinivasan 2003, Garcia-Sais 2010). Light penetration into the water column diminishes as depth increases, and both coral and macro-algal assemblages rely on light for photosynthetic processes, growth, and productivity (Dubinski and Falkowski 2011). Consequently, shallow coral reefs are known to support a higher diversity and density of benthic components, and are thus often associated with a high diversity of relatively specialised coral reef fish species (Chong-Seng et al. 2002). For instance, few tropical coral species are physiologically adapted to live under diminished light levels, and the loss of coral on deep reef slopes directly reduces habitat complexity (Alvarez-Filip et al. 2009). Deep coral reef slopes are thus more likely to support fewer and more generalist fish species (Chong-Seng et al. 2002).

My study revealed that corallivores and planktivores were more abundant above 6m than in the deeper reef slopes. This conclusion is in line with previous literature (Chong-Seng et al. 2002). Again, the depth-dependent light attenuation and the loss of corals at depth may be a factor affecting distribution of corallivores and planktivores (Colvard and Edmunds 2012). The three major planktivore species in this study were *Amphiprion perideraion* (Coughlin 1994), *Dascyllus reticulatus* (Richardson 1846), and *Pomacentrus moluccensis* (Bleeker 1983). Although *Dascyllus reticulatus* and *Pomacentrus moluccensis* are not restricted to a specific diet, the planktonic component constitutes the major part of their diets (Randall and Allen 1977, Allen 1991). Both species are considered as highly specialised coral reef fish species associated with live hard corals (Bonin 2011, Pratchett et al. 2012). *Pomacentrus moluccensis* is closely related to live hard coral cover throughout all benthic life stages, and uses a very narrow selection of only four branching coral species (mainly *Acropora nasuta* and *Acropora microclados*) as primary habitats (Bonin 2012), whereas *Dascyllus reticulatus* is associated with eight coral species (mainly *Pocillopora damicomis* and *Stylophora pistillata*) (Pratchett et al. 2012). In all cases, the high density of those

species at shallow depths is likely to be associated with the light needed by the coral species upon which they depend. On the other hand, all *Amphiprion perideraion* individuals were found among the tentacles of the anemone species *Heteractis magnifica* and *Heteractis crispa* (Bridge et al. 2012). *Amphiprion perideraion* often reside within large anemones, which provide the hosts refuges against predators (Cleveland et al. 2011). Those anemones use photosynthetic zooxanthellae to fix carbon and synthesise amino acids (Lipschultz and Cook 2002, Ollerton et al. 2007, Cleveland et al. 2011). As they mostly depend on photosynthate components produced by endosymbionts, *Heractis* anemones are often restricted to shallow depths (Hattori 2006, Scott et al. 2011).

Conversely, the major corallivore species were *Chaetodon octofasciatus* (Block 1787) and *Chaetodon lineolatus* (Cuvier 1831). The results are in line with those of Van Long (1996), who showed that tropical butterflyfish were more abundant in shallow reef slopes. *Chaetodon octofasciatus* is an obligate corallivore species, whereas *Chaetodon lineolatus* have less specialized diets (Steene 1978, Myers 1991). Although Chaetodontidae are able to exploit a wide range of dietary resources, both species directly rely on corals for food and protection (Pratchett 2005, Pratchett et al. 2013). Altogether, the high density of both planktivore and corallivore species in shallow reef slopes appears to be mainly driven by the distribution of hard branching corals and *Heractis* anemones.

No significant differences were found in herbivores densities between shallow and deep reef slope habitats. This conclusion is surprising, as most studies (Nemeth and Appeldoorn 2003, Brokovitch et al. 2010) found a negative correlation between herbivore density and depth. The herbivore assemblages of this study are mainly driven by Scaridae, which are specialise in scraping algae and detritus off rocks and dead corals (Nemeth and Appeldoorn 2009). A recent study by Goatley and Bellwood (2012) showed that coral reef grazing activity might be affected by high sedimentation rates. Hence, future studies should examine coral reef fish assemblages across depth

gradients in association with detailed substrate observations and consideration of other human-induced environmental pressures (e.g. sedimentation).

The influence of benthic structure

Reef fish density was higher in hard-coral dominated habitats. Hard coral cover was also found to be the primary driver affecting assemblage structure of reef fish. Those conclusions are in line with published literature (Parrish et al. 1985, Friedlander and Parrish 1998, Pratchett et al. 2013). High coral cover is often associated with high structural complexity and rugosity (Caley and John 1996, Friedlander and Parrish 1998). Corals presumably provide shelter for invertebrates (potential food source) (Parrish et al. 1985, Hixon 1991) and against predators (Caley and John 1996, Friedlander and Parrish 1998). Corals are also the major food source for corallivores that feed on coral polyps, which may explain the positive correlation between *Chaetodon octofasciatus* density and hard coral cover found in the present study (Pratchett et al. 2013). Moreover, *C. octofasciatus* is a microhabitat specialist settling solely within live corals, especially *Acropora* (Srinivasan 2003). On the other hand, an inverse correlation was found between the density of *Dascyllus reticulatus* and hard coral cover. Although Friedlander and Parrish (1998) found that coral cover was inversely associated with planktivore biomass, *D. reticulatus* is an obligate coral-dwelling species usually associated with live hard coral cover (Pratchett et al. 2012). My results are thus surprising, and it is likely that the present study lacks details regarding hard coral components. Pratchett et al. (2012) found that *D. reticulatus* could be more affected by the biological and physical variations of coral health and structural complexity than direct loss of coral cover. Also, because *D. reticulatus* only use a limited variety of coral species, it is possible that our analysis of benthic components is not fine-scale enough to differentiate the coral species associated with *Dascyllus reticulatus*.

The study revealed that Serranidae were more abundant in rocky habitats. This finding is in line with previous literature (Robins and Ray 1986, Gibran 2007). Interestingly, this result suggests

that MPAs should not necessarily be implemented on coral reef areas when aiming to protect fisheries targeted species over the long-term. First, it is known that non-corallivore species are more abundant in low coral cover areas (Emslie et al. 2010). Also, Serranidae are known to feed on a wide variety of fish species, and are considered as opportunistic species (Samoilys 1997, Gibran 2007). The result appears logical, as opportunistic non-corallivore species are presumably more likely to cope with variations in resource availability (Fox and Morrow 1981, Pratchett et al. 2013). *Cheilinus fasciatus* and *Stegastes obreptus* were abundant in hard coral dominated habitats. *Cheilinus fasciatus* is a carnivorous wrasse that primarily feeds on benthic invertebrates (Rice et al. 2008). As coral reefs provide a multitude of shelter for invertebrates, the presence of *Cheilinus fasciatus* in coral dominated habitats is likely to be caused by this predator favouring high-abundance prey areas (Parrish et al. 1985, Hixon 1991). Conversely, *S. obreptus*, a highly territorial damselfish, ‘cultivates’ large mixed species algal farms and is thus known to strongly shape local benthic community structures and herbivore distributions (Hata and Nishihira 2002, Hata and Kato 2004, Emslie et al. 2012). *S. obreptus* is known to live in rocky areas associated and dead reef areas (Lieske and Myers 1994). Because the transects used to monitor benthic composition were different to those used to record fish, it is possible that the spatial-scale of sampling of *Stegastes obreptus* did not correspond to the spatial distribution of live hard corals. As *S. obreptus* is known to mainly occur in shallow reef slopes, the very high number recorded in this study may account for the relative scarcity of herbivores in shallow reef slopes (Lieske and Myers 1994).

The influence of recreational activities

A large body of literature (Dearden et al. 2010, Edgar et al. 2010, Jung and Swearer 2011, Holles et al. 2013) support the fact that snorkelling, SCUBA diving, and boat sound could have detrimental effects on reef fish assemblages. Yet, results showed that *Cheilinus fasciatus* was more abundant in high recreational use areas. First, fish could become accustomed to the presence of divers and snorkelers, especially if feeding activities occur (Milazzo 2011). In the case of Koh Tao,

such habituation is likely to occur, as fish feeding is a major selling argument for most snorkelling and diving companies. Moreover, a recent study by Di Franco et al. (2013) showed that divers and snorkelers could involuntarily feed fish by moving substrate components and dislodging benthic invertebrates, making them more accessible to predatory fish. The presence of *Cheilinus fasciatus* in high use sites may thus reflect a direct behavioural response to sudden short-term availability of invertebrate prey. No studies to date have investigated such ‘involuntary fish feeding’ in tropical coral reef ecosystems. Conversely, Serranidae and Chaetodontidae were less abundant as recreational pressure increased. The majority of boats recorded at the six study sites used very noisy high speed propellers (on traditional Thai long-tail boats). The present study suggests that both Serranidae and Chaetodontidae should be considered as sensitive species with respect to stress induced by boat sound or underwater disturbances (Hardiman and Burgin 2010). Hence, both families could be valuable indicators for future studies investigating the influence of recreational activities on reef fish assemblages. Future studies should focus on the effects of boat noises on Serranidae and Chaetodontidae found around Koh Tao, as some species are known to use sound for mating and behavioural (e.g. threeband butterflyfish, *Heniochus chrysostomus*) interactions (Ladich and Fine 2006, Parmentier et al. 2011, Schärer et al. 2012).

Finally, no significant variations in Pomacentrid densities occurred between sites under different recreational pressures. This result appears logical, as the study focused on highly territorial and specialized Pomacentridae species, which are presumably less likely to be affected by the presence of divers and snorkelers underwater (Myers 1991, Lieske and Myers 1994, Bonin 2012, Pratchett et al. 2012).

Conclusion

This study found no significant effects on reef fish density or assemblage structure due to Marine Protected Areas one year after their establishment. This result supports the need for MPA enforcement over the long-term, as many fisheries targeted species have K-selected life history traits. The study also showed that physical variables, such as depth and benthic structure, were the primary structural drivers of reef fish assemblage structure. Despite the fact that there is a large body of literature (Hughes et al. 2006, McClanahan et al. 2006, Mora 2006, Mumby et al. 2006, Botsford et al. 2009, Selig et al. 2012, Halpern et al. 2013) advocating the use of MPAs in coral reef areas, the present study supports the need to consider other less productive habitat types as well, such as rocky areas. Serranidae were notably found to be highly abundant in areas dominated by rocky habitats. This supports the need to increase the representativeness of habitat types when implementing MPAs and MPA networks. Also, future studies investigating MPA effectiveness around Koh Toa should combine fish population surveys with more detailed biological monitoring, such as size estimation (Costa et al. 2006) and age determination (e.g. otolith samples) (Buxton 1993, Campana and Thorrold 2001, Lou et al. 2005) of fish. Finally, the study indicated that reef fish densities may be affected by recreational activities (e.g boating, snorkelling, SCUBA diving), but such effects are likely to be species-specific. Most importantly, this study provides an essential baseline to continue monitoring the effects of MPAs around Koh Tao.

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