

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

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Konstantin S. Tkachenko and Keryea 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(2): 195-210. The aim of this work was to compare coral reef fish communities from a small recently established marine reserve (a no-take area, NTA) with 3 nearby fishing areas within Nanwan Bay, southern Taiwan. Two depth zones (shallow at 3-4 m and deep at 8-10 m) of fringing coral reefs were surveyed at each of the 4 study sites. One of the sites was located within a small NTA (1.5 km²) established in 2005 in the western part of Nanwan Bay. Quantitative data on the composition, abundance, and size of fishes and macroinvertebrates were collected by a visual census using 20 × 5 m belt transects (4 transects per depth zone). The coverage of corals, algae, and substratum was estimated using the photo-quadrat technique (40 quadrats of 1 m² per depth zone). This will serve as the baseline survey within the marine reserve after it was established. Fish species richness and diversity as well as the abundances of 3 fish families and 2 trophic groups were significantly higher in the NTA than in the 3 other sites in which fishing is allowed. Significant differences in the abundances and sizes of fishes belonging to the Lutjanidae suggest that this family can be used as an indicator to reflect impacts of conservation efforts in the reserve. However, results of multiple regression and correlation analyses suggested that differences in certain reef fish families, especially the Chaetodontidae and Pomacentridae, are attributable to the habitat type and structural complexity of the reefs rather than to conservation efforts alone. This study demonstrates that there is the potential for profound changes toward recovery of fish stocks within small marine reserves over a short time frame.
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Key words: Coral reef fishes, Habitats, Marine reserve.

The common goals of marine protected areas (MPAs) are to conserve biodiversity, maintain the productivity of marine ecosystems, and through fish spillover from reserves, help fisheries in adjacent areas avoid the collapse of their fish stocks (Kelleher 1999). Many studies demonstrated the potential for the recovery of fish populations after no-fishing areas were implemented (Roberts 1995, Russ and Alcala 1996, Wantiez et al. 1997, Roberts et al. 2001). Fished and unfished areas were shown to differ

in abundance, biomass, and number of species of fishes (Watson and Ormond 1994, Roberts and Hawkins 1997, McClanahan et al. 1999). On the other hand, spatial and temporal heterogeneities of marine ecosystems lead to protection effects being confused with environmental effects, such as those related to habitat structure (Samoilys 1988, Garsía-Charton and Pérez-Ruzafa 1999, Ferraris et al. 2005). Therefore, it is often necessary to rely on designs that include measurements before and after the establishment of a reserve, both inside

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and outside the reserve. Relatively few reserve assessments explicitly considered habitat. In several studies, differences in fish abundances were influenced by habitat types (Friedlander and Parrish 1998, Bozec et al. 2005, Grober-Dunsmore et al. 2007). It is crucial to account for the effect of habitat when comparing fish abundances in distinct zones, which is necessary to assess the effects of reserve efforts (Ferraris et al. 2005). Monitoring individual habitat types should be part of an assessment, and each habitat should be sampled (Garsía-Charton et al. 2000). The purpose of this study was to identify differences in fish abundances and sizes between a recently established small and well-managed no-fishing area and zones adjacent to it, all within Nanwan Bay, southern Taiwan, and hopefully be able to distinguish natural biotic factors from protective activities, both of which can influence fish stocks.

Most reefs in Taiwan are threatened due to human pressures, with destructive fishing threatening 75 %, overfishing threatening 70 %, and sedimentation and coastal development each threatening about 45 % (Burke et al. 2002). The management effectiveness of MPAs in Taiwan has been rated as poor, with most of them lacking adequate law enforcement to protect the environment (Dai et al. 2002). Long-term monitoring of coral reefs in Taiwan has revealed very low abundances of fishes at most sites (Kimura et al. 2004, Dai et al. 2005). The absence of humphead wrasse, bumphead parrotfish, and reef barracuda, and the extremely low densities of groupers, sweetlips, parrotfishes, and snappers indicate that Taiwan's reefs have been heavily influenced by overfishing. The abundance of butterflyfishes, an indicator of aquarium harvesting, is recorded to be within 2-4 fish/100 m², a value much lower than at most Indo-Pacific reef sites (Dai et al. 2005).

Nanwan Bay, the southernmost area of Taiwan, has been severely overfished for the past 3 decades. Even after the establishment of Kenting National Park in 1982, which includes the entire coastal area of Nanwan Bay, the reef fish status did not improve. Although commercial fishing has become negligible due to depleted fish stocks in the area, recreational fishing from the shore and from small boats is still popular. As a result, fishing pressure is mainly exerted by line fishers and sometimes spear-gun hunters. In the beginning of 2005, a small no-take area (NTA; measuring about 1.5 km²) was established

through the joint efforts of the local community in the western part of Nanwan Bay and park rangers. The Hobihu NTA (named after the nearest village) proved to be the 1st marine reserve in Taiwan with effective protection. This NTA is co-managed by park rangers and the Coast Guard at Hobihu Harbor, with the assistance of operators of recreational dive centers as well as the local community. A Reef Check survey conducted in this area prior to the establishment of the NTA in 2004 revealed neither snappers nor other target species in this area (Dr. T.Y. Fan, pers. comm.). By 2007, an increase in the number of fish was obvious to recreational divers, demonstrating that the reserve was successfully achieving its goals. In this study, we tested 2 hypotheses: (1) there are differences in diversity, abundance, and size of fishes between the protected and unprotected areas, and (2) high abundances of certain functional groups of fishes involved in coral reef dynamics are related to the habitat type and coral composition rather than simply to protective efforts. We were unable to make before and after comparisons because no detailed quantitative data were previously collected in the sanctuary or in the adjacent fished areas. Given this lack of information, the present study can also serve as a baseline, enabling future monitoring and management practices in the Hobihu NTA in Nanwan Bay.

MATERIALS AND METHODS

Survey methods

Surveys were performed at 4 study sites within Nanwan Bay in Apr. 2007 (Fig. 1). The Hobihu site is located in the center of the NTA, and the other 3 sites are fished zones adjacent to the NTA. The Tiaoshi study site exhibits a high sedimentation rate and is subjected to high seasonal nutrient inputs (Dai 1991). The coral communities here experience much more stress from land development than the other 3 sites. The Outlet and the Shanjaowan study sites do not have any special features except for their geographical location on the coastline in relation to the Hobihu and Tiaoshi sites. Two depth zones, a shallow zone at 3-4 m and a deep zone at 8-10 m, were surveyed at each site. As the basis for the fish census and macroinvertebrate counting, we used the Reef Check belt transect survey method (Hodgson et al. 2004), for which 4 belt-transects, 5 m in width and 20 m in length, were deployed

parallel to the depth contour, with a distance of 10 m between them. Unlike the Reef Check protocol, we surveyed all fishes within the transect belts instead of only large target species. Fishes were censused and identified to species whenever possible or at least to genus level otherwise, and fish sizes were visually estimated using objects of known length.

Macroinvertebrates were counted and categorized according to functional groups. Corals, macroalgae, and non-living materials were quantified using the photo-quadrat technique. We photographed the substratum within 1 m² quadrats positioned randomly within the belt-transects ($n =$

10 quadrats per transect, 40 quadrats per depth zone). Coverage was estimated using CPCe software (Kohler and Gill 2006) with 100 equally spaced points within each quadrat. The substrate/benthic categories chosen for analyses are shown in table 1. Rugosity, an index of spatial reef complexity, was measured using a light stainless-steel chain 5 m in length with 1 cm links. Eight replicates were performed (2 measures for each belt-transect) at each depth zone. The ratio of the distance along the reef surface contour to the linear horizontal distance gives an index of spatial reef complexity (McClanahan and Shafir 1990).

Data analysis

One-way analysis of variance (ANOVA) followed by Fisher's post-hoc Protected Least Significant Difference (PLSD) tests were used to determine if there were significant differences in fish abundances among study sites. Data were tested for homogeneity of variance (the Levene test) and were log-transformed when required ($\log_{10}(x + 1)$). If transformation failed to homogenize the variance, nonparametric statistics were used (Kruskall-Wallis ANOVA or Mann-Whitney U -test). Differences in fish trophic groups were tested by the Wilcoxon matched-pairs test. A multiple regression analysis was used to identify the correlation of fish abundances with the substrate category, with R^2 representing the measure of the goodness of fit of the models (multiple determination coefficient). Margalef's

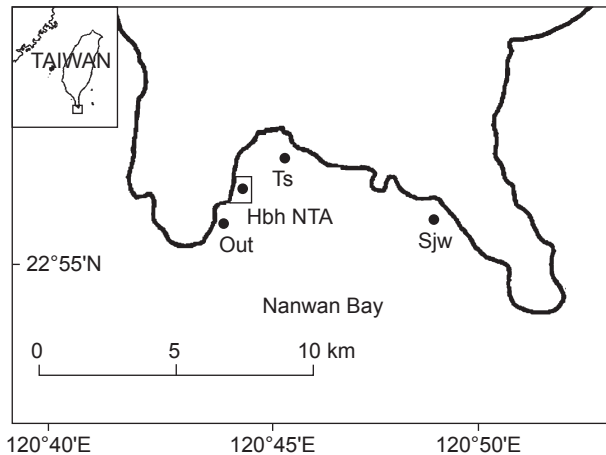


Fig. 1. Map of Nanwan Bay showing the locations of the study sites. Out, Outlet; Hbh NTA, Hobihu No-Take Area (outlined); Ts, Tiaoshi; Sjw, Shanjaowan

Table 1. Description of substrate/benthic categories

Code	Category	Description
BrA	Branching <i>Acropora</i>	All forms of branching <i>Acropora</i>
BMi	Branching <i>Millepora</i>	<i>Millepora tenera</i> , <i>M. dichotoma</i>
BMo	Branching <i>Montipora</i>	<i>Montipora stellata</i>
BrP	Branching <i>Porites</i>	<i>Porites latistella</i> , <i>P. nigrescens</i> , <i>P. horizontalata</i>
Hr	Other branching coral	<i>Hydnophora rigida</i>
EC	Encrusting coral	<i>Hydnophora</i> spp., <i>Montipora</i> spp.
MC	Massive coral	<i>Porites</i> spp., <i>Favites</i> spp., <i>Favia</i> spp., <i>Goniastrea</i> spp., <i>Astreopora</i> spp.
FLC	Foliaceous and laminar coral	<i>Montipora</i> spp., <i>Turbinaria</i> spp., <i>Pachyseris</i> spp.
OT	Other coral	<i>Euphyllia</i> spp., <i>Lobophyllia</i> spp., <i>Pavona</i> spp., <i>Caulastrea furcata</i>
Poc		<i>Pocillopora</i> spp.
SC	Soft coral	All forms of soft corals with the exception of sea fans
Mal	Macroalgae	Green algae: <i>Caulerpa</i> spp., <i>Codium formosanum</i> , <i>Turbinaria</i> spp.; brown algae: <i>Galaxaura</i> spp.
Rock		Bare reef surface
Rubble		
Sand		

species richness index ($d = (S - 1)/\ln N$, where S is the number of species and N is the number of individuals) and the Shannon-Weaver diversity index ($H' = -\sum p_i \ln p_i$ where p_i is the proportion of all individuals related to species i) were determined for each study site. Statistical procedures were performed using the software package Statistica® 6.0 for Windows (StatSoft, Inc. 2001).

RESULTS

Benthic communities

The Hobihu NTA is characterized by high coverage of some branching corals (*Acropora*, *Millepora*, and *Hydnophora rigida*) in the shallow zone, and branching *Porites* spp. in the deep zone (Fig. 2). Soft corals were abundant in both zones of Hobihu, and coral aggregations were separated by sandy spots. Hard-coral coverage was $42.5\% \pm 5.8\%$ in the shallow zone and $28.5\% \pm 4.3\%$ in the deep zone.

The deep zone of the Outlet revealed the largest soft coral coverage among the 4 study sites, and *Pocillopora* spp. were found in the shallow zone in greater abundances here than in the other sites (Fig. 2). Hard-coral coverage in the shallow zone ($37.7\% \pm 12.2\%$) was lower than at Hobihu, but the deep zone of the Outlet presented almost the same coverage ($28.3\% \pm 10.4\%$) as that of Hobihu.

Both zones of Shanjaowan and the deep zone of Tiaoshi were characterized by vast spaces of bare reef surface, very low coverage of branching corals, and a pronounced development of massive and encrusting forms of stony corals (Fig. 2). The shallow and deep zones at Shanjaowan respectively had $37.7\% \pm 12.2\%$ and $42.5\% \pm 3.4\%$ of hard-coral coverage. The deep zones of both Shanjaowan and Tiaoshi also had the greatest coverage of foliaceous and laminar corals (Fig. 2). The Tiaoshi deep zone was the most diverse in terms of growth forms of corals, and it also had the highest hard-coral coverage ($57.3\% \pm 2.2\%$) among the 4 study sites.

The Tiaoshi shallow zone was widely segregated from the other zones due to 4 remarkable features: the highest abundance of macroalgae ($26.8\% \pm 6.3\%$, Fig. 2), especially *Codium formosanum* and *Galaxaura* spp., large rubble aggregations (remnants of former acroporid stands), the occurrence of branching *Montipora stellata* thickets (Fig. 2), and the lowest relative

hard-coral coverage ($26.2\% \pm 7.6\%$). It is worth noting that soft corals were abundant at Hobihu and the Outlet, while at Tiaoshi their coverage was much lower, and at Shanjaowan, soft corals were absent from the samples (Fig. 2).

The occurrence of macroinvertebrates, such as sea cucumbers, starfish, coral shrimp, and giant clams was very low at all study sites and was therefore not analyzed. The occurrence of giant clams (*Tridacna* spp.) was less than 1 individual (ind.)/100 m² at all study sites, and their lengths did not exceed 10 cm. Only echinoids were present in sufficient number for a comparative analysis (Fig. 3). A very high abundance of *Diadema setosum* was discovered in the Tiaoshi shallow zone (119.7 ± 16.4 ind./100 m²). Other urchins (mostly *Echinometra mathaei*) were abundant in shallow zones of the Outlet and Shanjaowan. The absence of macroinvertebrates such as lobsters, large-sized giant clams, and gastropods at all 4 study sites testifies to the heavy overharvesting in Nanwan Bay.

Fish communities

Fish surveys at the 4 study sites revealed 68 species from 21 families (Table 2). The Hobihu NTA had the largest number of species (S) and the highest indices of species richness (d) and diversity (H') ($S = 60$, $d = 12.5$, and $H' = 3.11$) followed by the Outlet ($S = 34$, $d = 8.11$, and $H' = 2.63$), then Tiaoshi ($S = 29$, $d = 6.88$, and $H' = 2.75$); Shanjaowan exhibited the lowest indices ($S = 19$, $d = 5.14$, and $H' = 2.34$). The 10 most abundant families whose densities exceeded 1 fish/100 m² (the Pomacentridae, Chaetodontidae, Acanthuridae, Labridae, Lutjanidae, Mullidae, Serranidae, Tetraodontidae, Holocentridae, and Carangidae) were used for the statistical analyses.

The highest abundance of snappers was found at the Hobihu NTA (Fig. 4). Small schools of soldierfish (Holocentridae) and jacks (Carangidae) were also found mainly within the shallow zone at Hobihu and to a lesser degree in the deep zone of the Outlet (Fig. 4). Six fish families, i.e., the Labridae (wrasses), Pomacentridae (damselfish), Serranidae (groupers), Chaetodontidae (butterflyfish), Acanthuridae (surgeonfish), and Tetraodontidae (pufferfish) made relatively high contributions to differences among the 4 study sites (Fig. 4). It should be noted that the shallow zone of the Hobihu NTA had the highest density of butterflyfish (9.1 ± 1.4 fish/100 m²) and that both zones of the Hobihu NTA exhibited the highest

densities of damselfish (77.7 ± 7.2 and 71 ± 15.4 fish/100 m², Fig. 4).

To exclude the influence of depth ranges, comparisons between sites were made for each depth zone. In addition, to estimate the effect of protection on fish assemblages, the sites were compared using one-way ANOVA and

the Mann-Whitney *U*-test where protection was considered a factor. Differences between sites were significant for the Lutjanidae (both depth zones), Pomacentridae (both depth zones), Chaetodontidae (shallow zones), Acanthuridae (shallow zones), Labridae (shallow zones), and Tetraodontidae (shallow zones) (see Table 3, Fig.

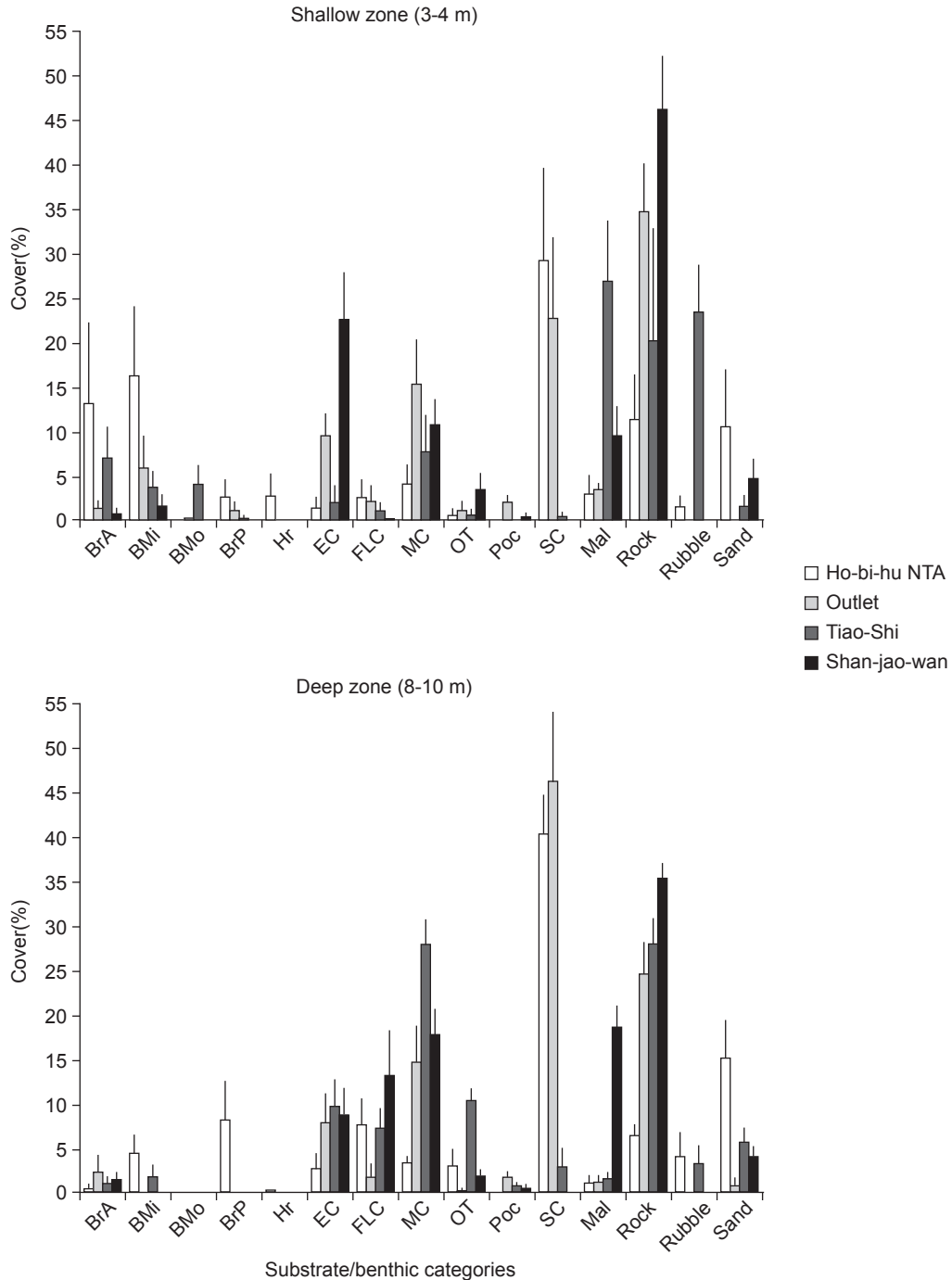


Fig. 2. Substrate/benthic coverage among the study sites (percentage cover + SE). Codes for categories are presented in table 1.

4). The Hobihu NTA was distinguished by high abundances of snappers, butterflyfishes, and damselfishes. An analysis of the protective effect showed that the Hobihu NTA substantially differed from the other study sites in abundances of the Lutjanidae (Mann-Whitney test, $Z = 2.31$, $p = 0.02$), Pomacentridae (ANOVA, $F = 39.04$, $p < 0.01$), Chaetodontidae (ANOVA, $F = 39.04$, $p < 0.01$), and Tetraodontidae (ANOVA, $F = 5.86$, $p = 0.02$).

A multiple stepwise regression analysis was performed to determine if differences in the above fish families were attributable to the effects of the benthic/substrate as well, rather than solely to protection efforts. According to the R^2 coefficient of determination, over 71% of the variability of the Pomacentridae abundance and 43% of the variability of the Chaetodontidae abundance could be explained by variations in the coverage of branching corals, especially branching *Acropora* spp. (Table 4). Determination coefficients of the regression models for the Lutjanidae and Acanthuridae were $< 20\%$, and thus the role of substrate/benthic categories was apparently not important. None of the analyzed fish families had a significant dependence on total hard-coral coverage.

Analysis of the size classes revealed a significant difference in four of the 10 dominant fish families both among sites and between depth zones within each site (Table 5). The Lutjanidae was the most abundant at the Hobihu NTA and was represented by large size classes in the shallow zone (Fig. 5). The Chaetodontidae was found to be the most abundant in the large size class (15-20 cm, Fig. 5) at all 4 sites. Abundances within size classes of the Acanthuridae showed significant

differences between the Hobihu NTA and the other sites. Large (size class 20-25 cm) members of the Acanthuridae were found in both depth zones at Hobihu (Fig. 5). The Labridae significantly differed among sites, with a prevalence of the largest size class (10-15 cm) in the shallow zone of the Outlet.

Abundances of fishes within trophic groups significantly differed among study sites (Table 6). Two patterns of variation in fish abundances were identified from these results. First, the Lutjanidae and Pomacentridae respectively contributed to a pronounced dominance of piscivores/invertivores and omnivores at the protected Hobihu NTA. No significant difference was found in the abundance of herbivores between the reserve and Tiaoshi, even though these sites revealed significantly higher abundances of herbivores than at the Outlet and Shanjaowan (Table 6). In the 2nd pattern, 3 trophic groups showed little variation among sites. Piscivorous fishes, mostly represented by the Serranidae, showed no significant differences in abundance among sites. Differences in invertivore abundances were not significant among the Hobihu NTA, the Outlet, and Tiaoshi, while Shanjaowan showed a significantly lower abundance of invertivores than the other 3 sites. Another finding worth noting is related to the corallivores: the results obtained for the Chaetodontidae did not match those for the trophic group (Hobihu NTA and Tiaoshi had the same proportions of corallivores). The Shanjaowan site had the lowest abundances of all trophic groups.

The rugosity index was found to only be correlated with the abundance of the Chaetodontidae ($r = -0.45$, $p < 0.05$).

DISCUSSION

Benthic communities

Coral reefs in the study sites exhibited pronounced differences regarding substrate characteristics and biotic cover. The reef at the Hobihu NTA appeared quite healthy as indicated by the ratio of coral to algal cover. A high topographic complexity and an abundance of branching corals yielded a high potential for reef metabolism and nutrient uptake as well as providing high value as fish habitat (Miller and Gerstner 2002). Szmant (1997) suggested that topographic complexity is a vital determinant of a reef's capacity to metabolize nutrient inputs without undergoing a "phase shift" to macroalgal dominance. In comparison to the

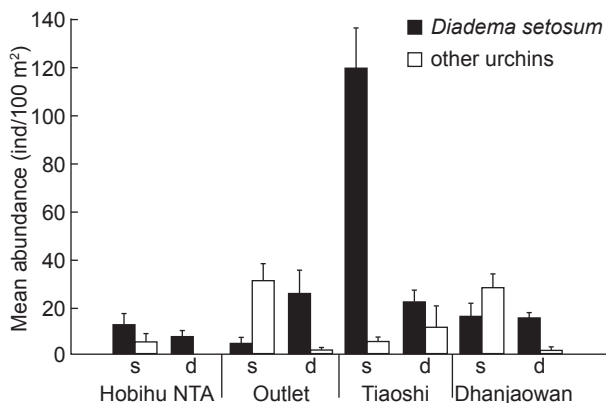


Fig. 3. Abundance (individuals/100 m² + SE) of *Diadema setosum* and other sea urchins in the study sites; s and d are the respective shallow and deep zones.

other study sites, Tiaoshi was the most remarkable in the variability of its coral species composition and coverage between deep and shallow zones. While the deep zone was occupied by diverse coral communities with high coverage of stony corals, the shallow zone demonstrated poor coral coverage with the highest abundance of macroalgae and an extremely dense population of the long-spined urchin *Diadema setosum*. The inner part of Nanwan Bay where the Tiaoshi reef is located, receives domestic sewage and terrestrial

runoff during the rainy season resulting in high eutrophication (Tsai et al. 2005), algal overgrowth (Hwang et al. 2004, Tsai et al. 2005), and evidently a sea anemone outbreak (Tkachenko et al. 2007). High abundances of macroalgae and of the sea urchin *D. setosum* observed in this study may be related. Changes in water quality as a result of human impacts, natural disturbances, and seasonal fluctuations in nutrient concentrations contribute to algal overgrowth (Hughes 1994, McCook et al. 2001, Lapointe et al. 2004) that

Table 2. List of fish species that occurred within the study sites

Taxa	Study site			
	Hobihu No-Take Area	Outlet	Tiaoshi	Shanjaowan
Acanthuridae				
<i>Naso unicornis</i>	+	+	+	
<i>Acanthurus dussumieri</i>	+		+	
<i>A. nigricans</i>	+	+		+
<i>A. lineatus</i>	+			
Ballistidae				
<i>Ballistes bursa</i>		+		
Carangidae				
<i>Caranx melampygus</i>	+	+	+	+
Chaetodontidae				
<i>Chaetodon auriga</i>	+		+	+
<i>C. xanthurus</i>	+	+		
<i>C. speculum</i>	+			
<i>C. melannotus</i>	+		+	
<i>C. plebeius</i>	+			
<i>C. trifasciatus</i>	+		+	+
<i>C. vagabundus</i>	+	+		+
<i>C. kleini</i>	+		+	
<i>Heniochus acuminatus</i>	+	+	+	+
Cirrhitidae				
<i>Paracirrhites fosteri</i>	+		+	
Diodontidae				
<i>Diodon holocanthus</i>	+	+	+	
Haemulidae				
<i>Plectorhynchus flavomaculatus</i>		+		
Holocentridae				
<i>Myripristis</i> sp.	+	+		
<i>Neoniphon sammara</i>	+			
Labridae				
<i>Cheilinus undulatus</i>	+			
<i>Halichoeres</i> sp.	+			+
<i>Thalassoma lunare</i>	+	+		+
<i>T. rueppellii</i>	+	+		
<i>T. lutescens</i>	+	+	+	+
<i>Labroides dimidiatus</i>	+	+	+	
<i>Gomphosus varius</i>	+	+		
Lethrinidae				
<i>Lethrinus nebulosus</i>	+		+	

Table 2. (Continued)

Taxa	Study site			
	Hobihu No-Take Area	Outlet	Tiaoshi	Shanjaowan
<i>L. olivaceus</i>		+		
Lutjanidae				
<i>Lutjanus kasmira</i>	+	+		
<i>L. quinquelineatus</i>	+	+	+	
<i>L. fulviflamma</i>	+			+
<i>L. fulvus</i>	+	+		
<i>L. rufolineatus</i>	+			
<i>Lutjanus</i> sp.	+			
Mullidae				
<i>Mulloides vanicolensis</i>	+		+	+
<i>Parupeneus cyclostomus</i>	+			
<i>Parupeneus</i> sp.	+	+		
Muraenidae				
<i>Gymnothorax favagineus</i>	+			
Pomacanthuridae				
<i>Pomacanthus semicirculatus</i>	+	+	+	+
<i>P. imerator</i>	+			
<i>Pygoplites dicanthus</i>	+			
Pomacentridae				
<i>Abudefduf sexfasciatus</i>	+	+	+	
<i>A. vaigiensis</i>	+	+		
<i>Chromis antripectoralis</i>	+	+	+	+
<i>C. viridis</i>	+			
<i>Chromis</i> sp. 1	+		+	+
<i>Chromis</i> sp. 2	+	+	+	+
<i>Dascyllus trimaculatus</i>	+		+	
<i>D. carneus</i>	+		+	
<i>Neoglyphidodon melas</i>		+		
<i>Amphiprion clerkii</i>	+			
<i>A. frenatus</i>	+	+		
<i>Amphiprion</i> sp.			+	
Scaridae				
<i>Cetoscarus bicolor</i>	+	+		+
<i>Scarus quoyi</i>	+			
<i>Scarus</i> sp.	+			
Scorpaenidae				
<i>Pterois volitans</i>	+	+	+	+
<i>Dendrochirus zebra</i>			+	
<i>Scorpaenopsis</i> sp.	+			
Serranidae				
<i>Epinephelus tauvina</i>	+			
<i>Epinephepus</i> sp. 1	+	+	+	+
<i>Epinephepus</i> sp. 2	+			+
Synodontidae				
<i>Synodus variegates</i>	+	+	+	
<i>Synodus</i> sp.		+		
Tetraodontidae				
<i>Canthigaster valentini</i>	+	+	+	+
<i>Arothron stellatus</i>		+		
Zanclidae				
<i>Zanclus cornutus</i>	+		+	

may trigger an increase in *Diadema* populations. However, despite the well-known regulatory effect of *Diadema* on coral overgrowth by macroalgae (Hughes et al. 1987 1999, Hughes 1989), this echinoid plays an important role in the erosion of the reef substratum through grazing activity and spine abrasion (Sammarco 1980, Bak 1994). The structural composition of coral reefs at the Outlet and Shanjaowan sites was mostly explained by their geographical position within Nanwan Bay and

by the degree of exposure to storm disturbances and strong currents in this area (Dai 1993).

Fish communities

The highest abundances of the Chaetodontidae and Pomacentridae at the Hobihu NTA can be explained by the availability of branching corals and the pronounced reef complexity. Bouchon-Navaro et al. (1985) suggested that

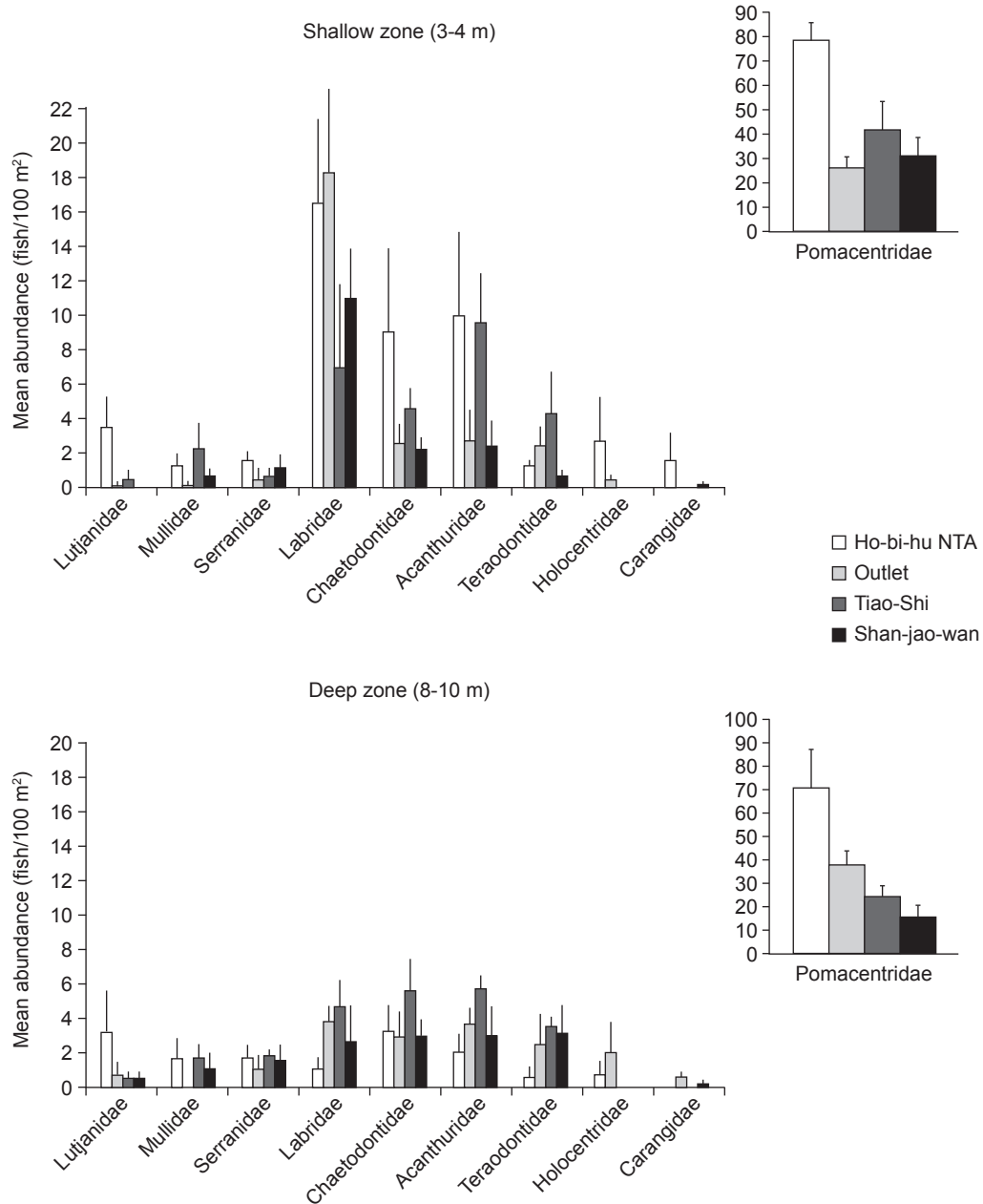


Fig. 4. Abundance (individuals/100 m² + SE) of the dominant fish families in the study sites.

the abundance of large branching corals rather than total live cover is of primary importance in determining the development of a rich chaetodontid community. We observed the same phenomenon in our study: chaetodontid abundance was not dependent on the total coral cover, while the coverage of branching *Acropora* had a significant influence on the chaetodontid distribution. Greater contrasts in total coral cover among the study areas resulted in more-

pronounced differences in abundance and species composition of butterflyfish, as was shown in several studies (Khalaf and Crosby 2005, Temraz and Abou Zaid 2005, Crosby and Reese 2005). On coral reefs, trophic groups of fishes that are most dependent on structural complexity are those using the substratum for food and shelter; the Chaetodontidae and Pomacentridae are among the major users of the living coral framework (Sano et al. 1987, Jones 1991, Roberts et al.

Table 3. Differences in the abundances of 6 dominant fish families among the study sites based on the results of the ANOVA with post-hoc comparisons and the Kruskal-Wallis test

Taxon	Abundance differences: test, <i>p</i> level	Post-hoc comparisons by Fisher's PLSD test
Lutjanidae	Shallow zones Kruskal-Wallis (K-W) test, $H = 16.23, p = 0.001$	
	Deep zones K-W test, $H = 16.23, p = 0.001$	
Labridae	Shallow zones K-W test, $H = 7.88, p = 0.041$	
	Chaetodontidae ANOVA, $F = 8.81, p = 0.005$	Hbh NTA > *Tsh = Out = Sjw
Pomacentridae	Shallow zones ANOVA, $F = 7.65, p < 0.001$	Hbh NTA > ***Out = Tsh = Sjw
	Deep zones ANOVA, $F = 7.63, p < 0.001$	Hbh NTA > ***Out > *Sjw = Tsh
Acanthuridae	Shallow zones ANOVA, $F = 2.86, p = 0.041$	Hbh NTA = Tsh > *Out = Sjw
Tetraodontidae	Shallow zones ANOVA, $F = 5.86, p = 0.021$	Tsh > *Hbh NTA = Out = Sjw

Hbh NTA, Hobihu No-Take Area; Out, Outlet; Tsh, Tiaoshi; Sjw, Shanjaowan. * $p < 0.05$; *** $p < 0.001$.

Table 4. Results of the multiple linear regression analysis for the abundance of dominant fish families. The sign for the coefficient of each independent variable is in parentheses; all variables were log-transformed

Dependent variable	Independent variables	R^2	F	p
Pomacentridae (Damsel-fishes)	Br. <i>Acropora</i> (+)	0.711	12.79	< 0.001
	Br. <i>Millepora</i> (+)			
	Massive coral (-)			
	Sand (+)			
	Macroalgae (-)			
Chaetodontidae (Butterflyfishes)	Br. <i>Millepora</i> (+)	0.435	11.19	< 0.001
	Br. <i>Acropora</i> (+)			
Labridae (Wrasses)	Rock (+)	0.324	6.96	0.003
	Massive coral (-)			
Tetraodontidae (Pufferfishes)	Macroalgae (+)	0.219	8.13	0.007

Br., branching.

1992, Chabanet and Letourneur 1995, Chabanet et al. 1997). A greater variety of living corals supports more fish species by increasing the variety of microhabitats (Williams 1986, Sano et al. 1987, Galzin et al. 1994, Chabanet et al. 1997). Destruction of reef complexity and elimination of or a profound decrease in cover of branching stony corals, especially *Acropora*, result in drastic decreases in the diversity and abundances of butterflyfishes and damselfishes (Sano et al. 1984, Chen et al. 2008). Obligate corallivore chaetodontids are among the 1st to die during mass coral mortality events (Samways 2005). Further, specialized corallivore butterflyfishes, such as *Chaetodon trifasciatus*, are more susceptible to deprivation of their coral prey than are generalist corallivores (Berumen and Pratchett 2008).

No significant differences were found between the reserve and the Tiaoshi site of herbivorous fishes that matched the distribution of the Acanthuridae, the main contributor to this trophic group in our study. This illustrates that the reserve effect may be difficult to evaluate for non-territorial fishes when the reserve is rather small and close to an unprotected area. A similar phenomenon was found for the Acanthuridae between a reserve and fished areas in New Caledonia (Ferraris et al. 2005). Reserve effects

supposedly depend on species mobility, because mobile species are less likely to be protected than others (Allison et al. 1998). However, species with the same mobility may respond differently to a reserve status because of other factors, such as targeting by fisheries (Ferraris et al. 2005). The dependence of the Pomacentridae on habitat type is reflected in the distribution of the omnivorous group. Almost all observed damselfishes were related to this trophic group, and thus the greatest abundance of both omnivores and damselfishes was observed at the Hobihu NTA. The absence of a match between the distributions of the Chaetodontidae and corallivore fishes can be explained by the mixed trophic composition of observed butterflyfishes including corallivores and omnivores. The trophic group with mixed feeding types (piscivores/invertivores) represented mainly by the Lutjanidae revealed the greatest abundance within the NTA and is apparently the most obvious indicator of a reserve effect.

Marine reserve effects

Fish species richness and diversity, and the abundance of 3 fish families (the Lutjanidae, Chaetodontidae and Pomacentridae) and 2 trophic groups (piscivores/invertivores and

Table 5. Summary table of Kruskal-Wallis test values with the level of significance for comparisons of differences in the average size of the most abundant fish families among sites and between depth zones within sites

	Kruskal-Wallis test				
	Among study sites		Between depth zones within study sites		
Lutjanidae	H = 12.34	$p = 0.007$	Hobihu NTA	H = 14.23	$p < 0.001$
			Outlet	H = 7.41	$p = 0.008$
			Tiaoshi	H = 6.87	$p = 0.037$
			Shanjaowan	ns	
Chaetodontidae	ns		Hobihu NTA	H = 8.63	$p = 0.013$
			Outlet	ns	
			Tiaoshi	ns	
			Shanjaowan	ns	
Labridae	H = 10.34	$p = 0.008$	Hobihu NTA	H = 9.78	$p = 0.006$
			Outlet	H = 6.31	$p = 0.043$
			Tiaoshi	ns	
			Shanjaowan	H = 10.52	$p = 0.002$
Acanthuridae	H = 8.83	$p = 0.024$	Hobihu NTA	ns	
			Outlet	H = 6.75	$p = 0.033$
			Tiaoshi	H = 7.97	$p = 0.017$
			Shanjaowan	ns	

ns, not significant.

omnivores) were significantly higher at the Hobihu NTA than at the other study sites. In addition, this marine sanctuary was distinguished by larger average sizes of 2 families: the Lutjanidae and Acanthuridae. The Lutjanidae appeared to be the main indicator family reflecting the effects of a fishing prohibition. The abundance of snappers was not significantly related to habitat type. Apparently, the significant increase in abundance and average size of snappers at the Hobihu NTA can be attributed to protective efforts. The Lutjanidae is one of the major edible and exploited fish families, and restocking of its populations is very important for fisheries in the Nanwan Bay area. The majority of the surveyed Lutjanidae was related to blue-lined snappers *Lutjanus kasmira*. Given that their doubling time is 1.4-4.4 yr (Allen 1985) and that snappers had the largest abundances in 2 size classes of 10-15 and

20-25 cm, we suppose that a stable aggregation of snappers formed after the period of establishment of the NTA, i.e., over the previous 2 yr. Dense populations of damselfishes on which snappers feed (Allen and Talbot 1985, Allen 1997) together with other food resources allowed a stable increase in snapper population at the Hobihu reef. Fishing prohibition, appropriate habitat, and food availability may have allowed this species-group to form aggregations within the Hobihu NTA via self-recruitment and in part via migration from adjacent fished reefs. Another commercially important family, the Acanthuridae, showed a larger average size within the NTA although their abundance was not higher than that at Tiaoshi. The occurrence of large target species such as Napoleon wrasse (*Cheilinus undulatus*) and moray eel (*Gymnothorax favagineus*) testify to the effects of protection. These differences between the Hobihu NTA and

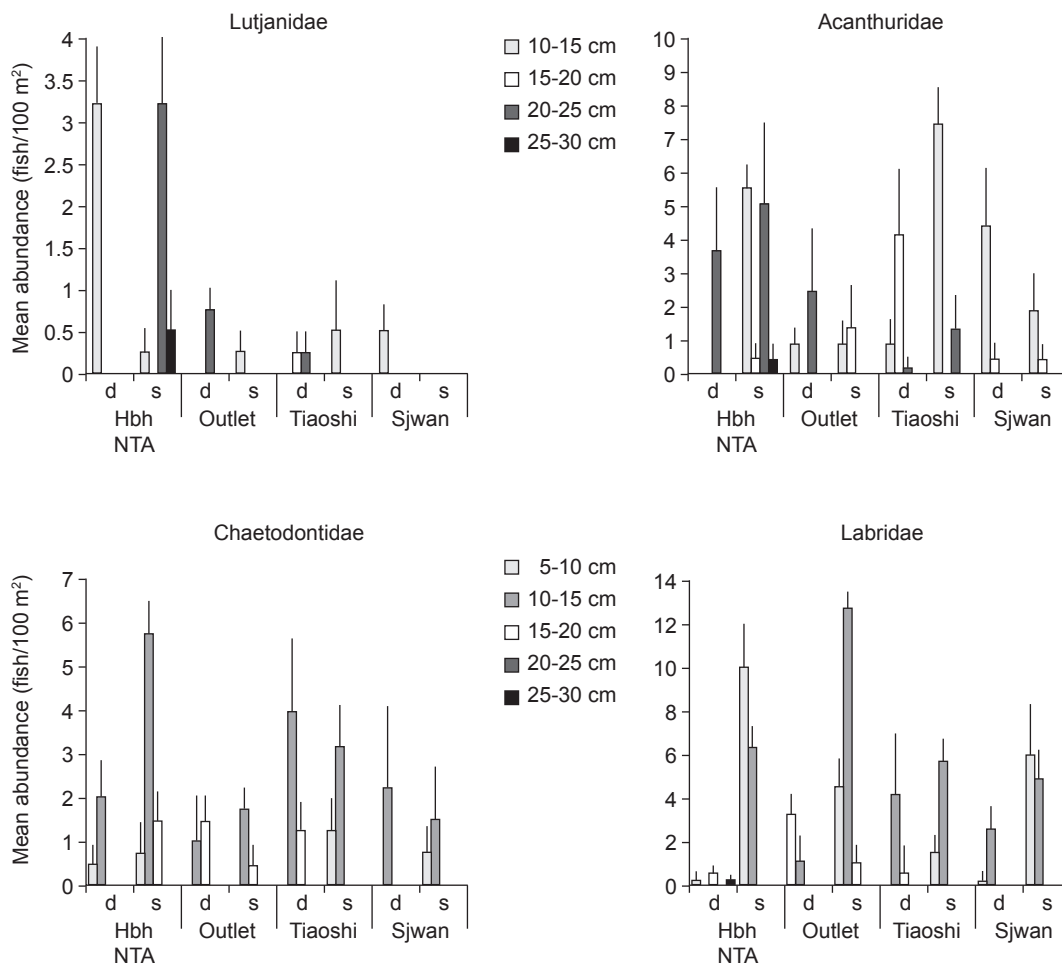


Fig. 5. Abundance of individual size classes of 5 dominant fish families in the study sites; s and d are respective shallow and deep zones. Hbh NTA, Hobihu No-Take Area, Sjw, Shanjaowan.

adjacent fished areas demonstrate the potential effectiveness of a small marine reserve over a short period of time.

The higher diversities and abundances of butterflyfishes and damselfishes within the Hobihu NTA could have been the result of a combination of a marine reserve effect, a diverse coral composition with dominance of branching corals, and changes in recruitment patterns over time. Our results as well as a number of previous studies (White 1986, Polunin and Roberts 1993, Wantiez et al. 1997, Halpern 2003) support the hypothesis that the establishment of marine reserves allows fish stocks to develop and increases the average size of target species (Russ 1985, Roberts and Polunin 1991, Westera et al. 2003). Compared to other study sites, the Hobihu NTA possesses high potential as a marine reserve in terms of its high coral diversity with a healthy stage of branching corals providing habitats for reef fishes. The small size of the Hobihu NTA and its proximity to the office of enforcement officers allows year-round monitoring and effective management. Even the smallest no-take reserves (~1-5 km²) are known to provide conservation benefits in terms of enhancing the biomass of sedentary target species within their boundaries (Halpern 2003) and by providing some fish spillover into adjacent unprotected areas (Halpern 2003, Gell and Roberts 2003, Russ et al. 2004). NTAs may also have an important fishery management role

if situated in crucial locations such as spawning aggregation sites (Beets and Friedlander 1999).

Despite the obvious improvement after providing protection, abundances of the fishery target family, the Serranidae, within the reserve were lower than 2 fish/100 m² and did not differ from other fished sites. Moreover, the size of groupers was still < 20 cm, which is smaller than commercial size (see Hodgson et al. 2004). The other indicator family, the Scaridae (parrotfishes), one of the major functional groups of fishes that play important roles in coral reef dynamics (Bellwood et al. 2004, Hughes et al. 2006, Mumby et al. 2006), occurred sporadically in all 4 study sites with an abundance of < 1 fish/100 m², and their size did not exceed 20 cm. Many commercially important fish families such as the Lethrinidae, Haemulidae, and Sphyraenidae were scarce or absent both within the NTA and in the fished study sites. Macroinvertebrates were also dramatically overharvested at all 4 sites as demonstrated by the absence of lobsters, and the scarcity and small sizes of clams *Tridacna* spp. and top-shells *Trochus* spp. These results indicate that the fish sanctuary may be too small and fishing pressure in the surrounding waters may be too great to produce more-pronounced increases in commercial fish and invertebrate stocks. Despite the obvious improvement in its fish community, the Hobihu NTA still does not host a healthy fish community as do other successful

Table 6. Average abundances (individuals/100 m²) and number of species (in parentheses) within trophic groups. Differences in abundances were significant by Wilcoxon matched pairs test ($\alpha = 5\%$); ns, not significant. Sites: Hbh NTA, Hobihu No-Take Area; Out, Outlet; Tsh, Tiaoshi; Sjlw, Shanjaowan. *The cleaner trophic group represented by *Labroides dimidiatus* (Labridae) feeds on crustacean ectoparasites and mucus of other fishes (Randall et al. 1990)

Trophic group	Hobihu NTA	Outlet	Tiaoshi	Shanjaowan	Comparison
Herbivores	9.5 (7)	3.3 (3)	7.4 (2)	2.9 (2)	Hbh NTA = Tsh > Out = Sjlw
Corallivores	3.1 (6)	0	3.3 (4)	1.3 (2)	Hbh NTA = Tsh > Sjlw
Invertivores	10.1 (12)	8.8 (10)	5.2 (3)	3.3 (3)	Hbh NTA = Out = Tsh > Sjlw
Omnivores	65 (15)	29.1 (9)	27.6 (10)	26.7 (7)	Hbh NTA > Out = Tsh = Sjlw
Piscivores	2.5 (7)	1.1 (4)	2.1 (5)	1.5 (3)	Hbh NTA = Tsh > Out = Sjlw
Pisc/invertivores	3.7 (9)	0.6 (4)	0.6 (3)	0.2 (2)	Hbh NTA > Out = Tsh = Sjlw
Planktivores	2.2 (2)	1.2 (1)	0	0	ns
Plankt/herbivores	14 (1)	7 (1)	10 (1)	0	ns
Cleaner*	0.4 (1)	0.2 (1)	0.6 (1)	0	ns
Total	110.5 (60)	51.3 (34)	56.8 (29)	36 (19)	

ns, not significant.

MPAs in the Indo-Pacific region. Further efforts must be made to preserve the biodiversity of coral reefs in the Nanwan area.

Conclusions

Small marine reserves have the potential to produce profound changes toward recovering fish stocks within a short period of time. Among commercially important fishes, the Lutjanidae (snappers) can be an effective indicator reflecting protection efforts by increases in their abundance and size. Reef complexity and coral diversity are important factors in MPA design and deployment since many fish families inhabiting coral reefs are strongly dependent on the type of habitat. Factoring out habitat types when studying MPA success makes the process of recovery of certain fish families more detectable over a short time frame. The Hobihu NTA exhibited the most diverse and healthiest coral community, and thus site selection for the marine reserve may have contributed to the high level of recovery and diversity of reef fishes.

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