Effects of habitat modification on coastal fish assemblages

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The purpose of this study was to assess the influence of anthropogenic modification of coastal habitats on fish assemblages in Taiwan, comparing the abundance, species richness and taxonomic composition of fishes on natural *v.* artificial habitats. While there was no significant variation in the abundance or richness of fishes between natural and artificial habitats, the species composition of fishes in artificial habitats was significantly different from that of natural habitats. Natural reefs were characterized by greater abundance of *Stethojulis* spp. (Labridae), *Abudefduf* spp. (Pomacentridae) and *Thalassoma* spp. (Labridae), whereas anthropogenic habitats were dominated by *Parupeneus indicus* (Mullidae), *Pempheris oualensis* (Pempheridae) and *Parapriacanthus ransonneti* (Pempheridae). In general, it appears that specialist reef-associated species are being replaced with fishes that are much more generalist in their habitat-use. The loss of natural coastal habitats may threaten some species that cannot live in anthropogenically altered habitats, though the overall abundance and diversity of coastal fishes was not significantly different between natural and artificial habitats in Taiwan.   © 2010 The Authors

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Key words: breakwaters; disturbance; habitat degradation; structural complexity; urbanization.

INTRODUCTION

With rapid urbanization and coastal development throughout the world, natural coastal habitats are increasingly being degraded and converted to anthropogenically altered habitats (Airoldi *et al*., 2009; Jordan *et al*., 2009). The reclamation of foreshore areas and changes in coastal geomorphology led to changes in current patterns and sedimentation, as well as greatly altering the biological and the physical structure of nearshore habitats (Bhattacharya & Giosan, 2003; Ten Brinke *et al*., 2004; Turner, 2006). Most importantly, artificial habitats vary greatly from natural habitats in their surface and structural complexity. Most anthropogenically altered coastal habitats are dominated by concrete structures, the surface of which is much smoother compared to natural rocky reef substrata, and this can reduce the availability of refuges

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for small fishes and microhabitats necessary for species recruitment and colonization (Bulleri, 2005). Conversely, the large-scale structural complexity provided from interlocking concrete tetrapods or dolosse is generally much higher than the coastal habitats that they replaced, which could favour larger and more mobile species, such as fisheries species (Clark & Edwards, 1999). Consequently, the species structure of organisms associated with anthropogenically altered coastal habitats is likely to be very different from the natural habitats they replaced. Accordingly, studies on intertidal sessile organisms have clearly shown that concrete breakwaters and sea-walls support very different invertebrate assemblages compared to natural rocky reefs (Chapman & Bulleri, 2003; Bulleri & Chapman, 2004; Airoldi *et al*., 2005*a*; Bulleri *et al*., 2005; Pinn *et al*., 2005).

Nearshore shallow-water fish assemblages are economically and ecologically important (Horn *et al*., 1999) but are also strongly affected by anthropogenic activities including overfishing, pollution and habitat modification (McManus, 1988; Greene & Shenker, 1993; Boreman, 1997; Bussotti *et al*., 2003; Guidetti, 2004; Guidetti *et al*., 2005). Throughout south-east Asia, nearshore habitats are naturally dominated by low-relief rocky and coral reefs, which support high densities of coastal fishes and are important fishing grounds (McManus, 1988). Moreover, rocky and coral reef habitats are important breeding and feeding grounds for fishes (Gibson, 1982; Rangeley & Kramer, 1994). These habitats, however, are increasingly threatened by human alteration, whereby natural coastal rocky reefs are replaced by artificial concrete habitats, often formed by interlocking tetrapods (Wang, 2005). Previous studies have shown that artificial concrete habitats do provide significant habitat for coastal fish assemblages, in so much as they provide large-scale complexity that is necessary to support high diversity and biomass of coastal fishes (Clark & Edwards, 1995, 1999). These artificial habitats, however, do not effectively simulate the natural habitats which they replace, potentially causing major changes in community structure of fish assemblages (Clark & Edwards, 1999).

Large-scale structural complexity of benthic habitats, which is enhanced by increased topographic relief and availability of interstitial spaces, has a significant influence on the local abundance and diversity of fishes in tropical marine habitats. Numerous studies have demonstrated strong positive relationships between structural complexity of coastal habitats and the abundance or diversity of fishes (Wilson *et al*., 2007). In instances where structural complexity of shallow marine habitats has been reduced following catastrophic disturbances (Graham *et al*., 2006) or experimental manipulations (Syms & Jones, 2000), the abundance and diversity of fishes has also declined. These findings indicate that structural complexity plays a key role in enhancing the persistence and coexistence of marine fishes, either by increasing food availability or moderating outcomes of predatory and competitive interactions (Pratchett *et al*., 2008).

In Taiwan, >50% of the coastline has been anthropogenically altered, whereby natural coastal rocky reefs have been replaced with extensive concrete seawalls and breakwaters, mostly to protect coastal highways along the west coast (Wang, 2005). The purpose of this study was to assess the extent to which human alteration of coastal habitats has affected the abundance, diversity and species composition of nearshore fish assemblages. Specifically, this study compared fish assemblages on artificial concrete breakwaters *v.* adjacent natural rocky reefs at five sites around

Taiwan. If community structure of fish assemblages differs between natural *v.* artificial habitats, this will demonstrate the importance of habitats in structuring coastal fish assemblages. Alternatively, if community structure is essentially similar between natural *v.* artificial habitats, but varies among sampling sites around Taiwan, this may suggest that local fish assemblages are structured according to large-scale process and regional species abundance (Sale *et al.*, 1984). Changes in habitat structure (especially, structural complexity) may simply alter the overall abundance and diversity of fishes that coexist within the local environment, while community structure remains largely unchanged.

MATERIALS AND METHODS

FIELD SAMPLING

This study was conducted in 2005, with sampling conducted in both summer and winter to account for seasonal variation in the abundance and community structure of coastal fish assemblages. Sampling was conducted at five locations across northern and southern Taiwan (Fig. 1). In northern Taiwan (Taipei county), sampling was conducted at three distinct locations; Ao-Di (AD, 25° 03′ N; 121° 55′ E), Lon-Men (LM, 25° 02′ N; 121° 55′ E) and Mei-Yan-Shan (MYS, 25° 04′ N; 121° 55′ E). Only two locations were sampled in southern Taiwan; Hai-Ko (HK, 22° 05′ N; 120° 42′ E) and Hong-Chai-Keng (HCK, 21° 58′ N; 120° 42′ E).

At each location, sampling was conducted along a concrete breakwater, as well as within corresponding natural reef habitats located within 500 m of the artificial habitat. Variation in the biological and physical structure of benthic habitats (*e.g.* coral cover and topographic variation) between natural *v.* artificial habitats was recorded as part of a companion study (Hsieh *et al.*, 2005). In northern Taiwan, the natural coastal habitats comprise rocky reefs colonized by occasional hard corals (Table I). Although breakwaters have been in place for several decades, coral cover in these artificial habitats is negligible. In south Taiwan, the natural coastal habitats generally comprise fringing coral reefs. Here, the anthropogenic modification of coastal habitat has occurred much more recently, but already there is significant coral growth within these habitats (Table I). Topographic variation, recorded as the S.D. in measurements of water depth recorded along a transect, was always much higher in natural habitats compared to the homogeneous habitat structure of concrete breakwaters (Hsieh *et al.*, 2005).

Underwater visual census (UVC) was used to survey fishes within each habitat at each location, following McCormick & Choat (1987). Fishes were sampled along three replicate 10 m transects positioned at least 2 m apart along the 4 m depth contour. All fishes located within 2 m on either side of the transect line were identified to species. To maximize detection of small and cryptic fishes, divers moved slowly and carefully searched within all caves and crevices. All transects were surveyed during daytime spring high tides. The overall abundance, species richness and species composition of fish assemblages were compared between artificial *v.* natural coastal habitats within each location.

DATA ANALYSIS

Variation in abundance and species richness of coastal fishes was analysed using three-way ANOVA, testing for differences between natural *v.* artificial habitats, among locations and between seasons. Count data were $\log_{10}$ transformed prior to analyses. Variation in the taxonomic composition of fish assemblages was analysed using MANOVA with Pillia's trace test statistic, testing for variation in the abundance of different fishes between natural *v.* artificial habitats, among locations and between seasons. All species for which fewer than five individuals were recorded or which were recorded on fewer than five different transects

TABLE I. Date of construction for concrete breakwaters considered during this study in Taiwan, and comparative structure (coral cover and topographic variation) of natural *v.* artificial habitats in each location from Hsieh *et al.* (2005)

Region	Coral cover		Site	Constructed	Topographic variation	
	Natural (% of hard substratum)	Artificial (% of hard substratum)			Natural (S.D. of water height)	Artificial (S.D. of water height)
North	1·18	0·22	Ao-Di	1989	6·65	0·39
			Mei-Yan-Shan	1983	1·11	0·71
			Lon-Men	1995	—	—
South	4·94	1·16	Hai-Ko	2000	4·66	0·48
			Hong-Chai-Keng	1998	2·49	0·42

were excluded from the analysis, and counts of all remaining fishes (40 species) were $\log_{10}$ transformed prior to analysis. Variation in taxonomic composition of coastal fishes was further explored using canonical discriminant analysis, whereby the fish assemblages in each habitat, at each location and in each season are represented as centroids with 95% C.I. on bi-plots. The relative proximity of these centroids indicates the relative similarity in community structure. Separate bi-plots were prepared for each season (summer *v.* winter), thereby relating the differential importance of key fish species in driving spatial patterns for each season.

RESULTS

ABUNDANCE

A total of 4416 fishes were recorded during this study, corresponding with a mean ± S.E. of 73·6 ± 14·2 fishes per transect. The abundance of fishes varied among locations and between seasons, but did not vary between artificial *v.* natural habitats within each location (ANOVA; Table I). The abundance of fishes averaged across all locations was higher in summer (97·5 ± 86·5 fishes per transect) compared with winter (49·7 ± 17·1 fishes per transect), but differences in abundance of fishes were only apparent at three (out of five) study locations. At Ao-Di and Hai-Ko, the abundance of fishes recorded in summer was significantly higher than the abundance of fishes recorded in the same sites during winter. At Hai-Ko, the extraordinary number
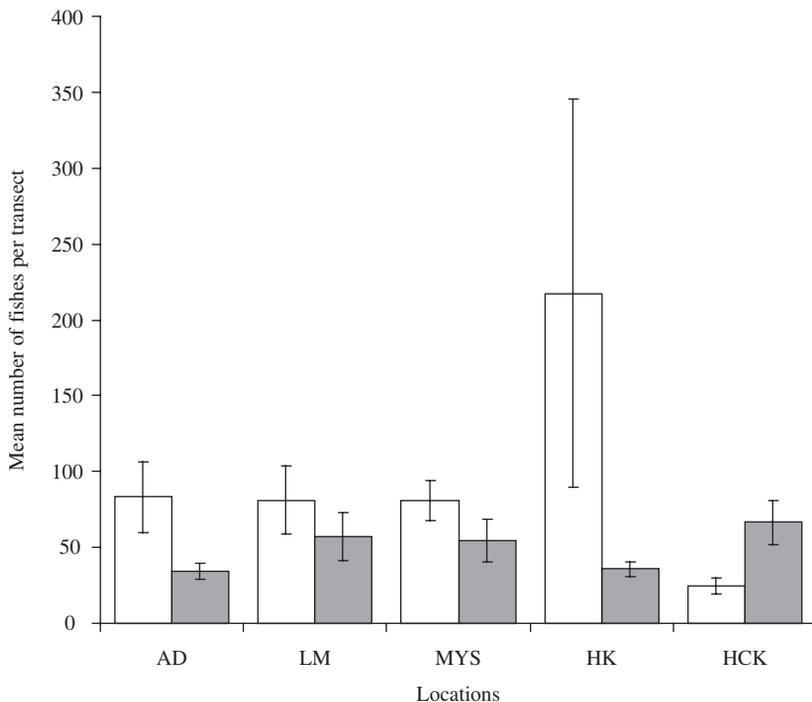

FIG. 1. Mean ± S.E. abundance of fishes recorded in summer (□) and winter (■) at five locations: Ao-Di (AD), Lon-Men (LM), Mei-Yan-Shan (MYS), Hai-Ko (HK) and Hong-Chai-Keng (HCK).

of fishes recorded in summer was due to the localized abundance of *Parapriacanthus ransonneti* Steindachner. There were as many as 800 individuals recorded on a single transect, though this species was not recorded at any other time or in any other location. At Hong-Chai-Keng, densities of fishes were higher in winter compared with summer.

SPECIES RICHNESS

A total of 126 different species were recorded during this study, though nearly half of these species (61 out of 126 species) were represented by fewer than five individuals across all surveys. A further 25 species were observed on fewer than five different transects. The maximum number of species recorded on a single transect was only 25 species and mean $\pm$ S.E. species richness was 11.6 ± 0.6 species per transect. Average species richness was slightly higher in winter (12.4 ± 0.8 species per transect) compared to summer (10.9 ± 0.9 species per transect), but these differences were not significant (ANOVA; Table II). Further, there was no significant variation in species richness between natural *v.* anthropogenically modified habitats, nor among locations (ANOVA; Table II). Moreover, there was no variation in the abundance or species richness of fishes among different breakwaters, which vary in their age.

TABLE II. ANOVA results for $\log_{10}$ transformed abundance and species richness of coastal fishes among locations (Ao-Di, Lon-Men, Mei-Yan-Shan, Hai-Ko and Hong-Chai-Keng), between habitats (natural *v.* anthropogenically modified habitats) and between seasons (summer *v.* winter) in Taiwan

Source	SS	d.f.	MS	F	P
Abundance					
Location	0·48	4	0·12	1·90	>0·05
Habitat	0·00	1	0·00	0·00	>0·05
Season	0·04	1	0·04	0·66	>0·05
Location × habitat	0·59	4	0·15	2·36	>0·05
Location × season	0·99	4	0·25	3·92	<0·01
Habitat × season	0·01	1	0·01	0·09	>0·05
Location × habitat × season	0·46	3	0·15	2·41	>0·05
Error	2·33	37	0·06		
Total	158·47	56			
Species richness					
Location	65·59	4	16·40	0·75	>0·05
Habitat	1·43	1	1·43	0·07	>0·05
Season	18·86	1	18·86	0·86	>0·05
Location × habitat	52·02	4	13·01	0·59	>0·05
Location × season	206·40	4	51·60	2·35	>0·05
Habitat × season	0·99	1	0·99	0·05	>0·05
Location × habitat × season	84·55	3	28·18	1·28	>0·05
Error	813·33	37	21·98		
Total	9041·00	56			

TABLE III. MANOVA results for $\log_{10}$ transformed abundance of coastal fishes among locations (Ao-Di, Lon-Men, Mei-Yan-Shan, Hai-Ko and Hong-Chai-Keng), between habitats (natural *v.* anthropogenically modified habitats) and between seasons (summer *v.* winter) in Taiwan

Effect	Value	F	d.f.	Error d.f.	P
Intercept	1·00	245·98	40	1	>0·05
Location	3·98	17·63	160	16	<0·001
Habitat	1·00	35·22	40	1	>0·05
Season	1·00	63·74	40	1	>0·05
Location × habitat	3·94	6·39	160	16	<0·001
Location × season	3·89	3·51	160	16	<0·001
Habitat × season	0·99	2·95	40	1	>0·05
Location × habitat × season	3·92	4·65	160	16	<0·001

COMMUNITY STRUCTURE

Despite limited variation in the abundance and species richness of fishes between natural *v.* anthropogenically modified coastal habitats, the structure of fish assemblages was significantly different between these habitat types (MANOVA; Table III). The assemblage structure also varied among locations and between seasons (MANOVA; Table III). Variation in the structure of fish assemblages were primarily attributable to variation in abundance of 13 species [*Abudefduf sexfasciatus* (Lacépède), *Abudefduf vaigiensis* (Quoy & Gaimard), *Acanthurus xanthopterus* Valenciennes, *Chaetodon auripes* Jordan & Snyder, *Chaetodon vagabundus* L., *Parupeneus indicus* (Shaw), *Pempheris oualensis* Cuvier, *Petroscirtes breviceps* (Valenciennes), *Pomacentrus coelestis* Jordan & Starks, *Stethojulis terina* Jordan & Snyder, *Thalassoma lunare* (L.), *Thalassoma purpureum* (Forsskål) and *Thalassoma quinquevittatum* (Lay & Bennett)]. There were, however, a total of 36 species, such as *Ptereleotris evides* (Jordan & Hubbs), *Ablabys taenianotus* (Cuvier), *Chromis xanthura* (Bleeker), that were only found in natural habitats and never on anthropogenically modified habitats. Most of these species were rare, though there were several species that were much more abundant in natural habitats compared to adjacent artificial habitats (Fig. 2). Further, there were 33 species that were recorded only in artificial habitats including *P. ransonneti*, *Chromis notatus* (Temminck & Schlegel) and *Chromis fumea* (Tanaka), which were relatively abundant (Fig. 2).

The community composition of fishes in artificial habitats in summer showed strong and consistent directional differences from natural habitats within the same location [Fig. 3(a)]. The overall assemblages, however, were not clearly differentiated into fish assemblages characteristic of natural *v.* artificial habitat types. Differences in community structure of fish assemblages between natural *v.* artificial habitats were relatively minor at Ao-Di (AD) and Lon-Men (LM), whereas there were marked differences in community structure at Hai-Ko (HK) and Hong-Chai-Keng (HCK) [Fig. 3(a)]. Within each location, natural habitats tended to have higher abundance of *T. purpureum*, *T. quinquevittatum* and *S. terina*. In contrast, anthropogenically altered habitats were characterized by higher abundance of *P. oualensis* and *A. vaigiensis*, whereas *A. xanthopterus* and *P. coelestisa* were consistently more abundant at Mei-Yan-Shan compared to all other locations. The composition of fishes in artificial
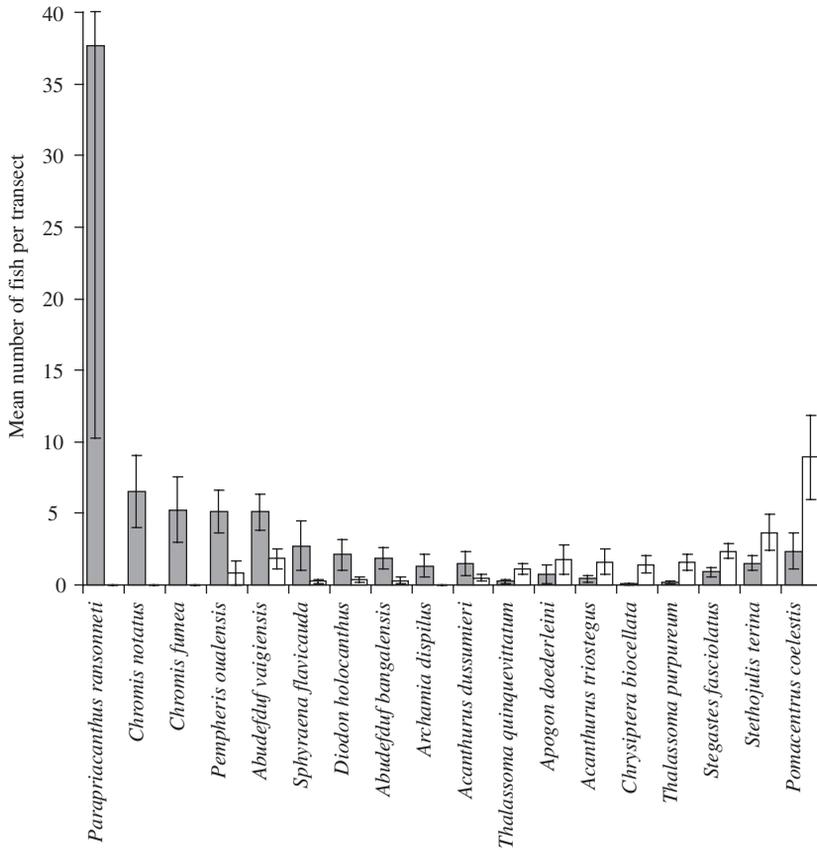
FIG. 2. Mean ± S.E. abundance of fishes recorded in anthropogenically modified (■) *v*. natural habitats (□).
Data were pooled from surveys conducted in summer and winter across five locations (Ao-Di, Lon-Men,
Mei-Yan-Shan, Hai-Ko and Hong-Chai-Keng).

habitats varied greatly among locations, but there were no consistent patterns with
respect to geographical location (north *v*. south) or years since construction.

The overall distinction in fish assemblages between natural and anthropogenically
modified habitats was much more pronounced in winter compared to summer. In
winter, there were strong similarities in the fish assemblages of artificial habitats
regardless of location, though there was overlap with the natural habitats at some
locations, especially Lon-Men. Differences in community structure of fish assem-
blages between natural and artificial habitats were most pronounced at Ao-Di and
Mei-Yan-Shan, which are also the oldest of the artificial habitats (Table I). Differ-
ences in composition of fish assemblages between artificial and natural habitats,
however, were similar between Lon-Men and Hai-Ko, which were constructed in
1995 and 2000, respectively. Overall, artificial habitats were characterized by higher
abundance of *C. vagabundus*, *A. vaigiensis* and *C. notatus*, whereas natural habitats
tended to have higher abundance of *P. coelestis*, *P. indicus*, *P. breviceps*, *T. lunare*
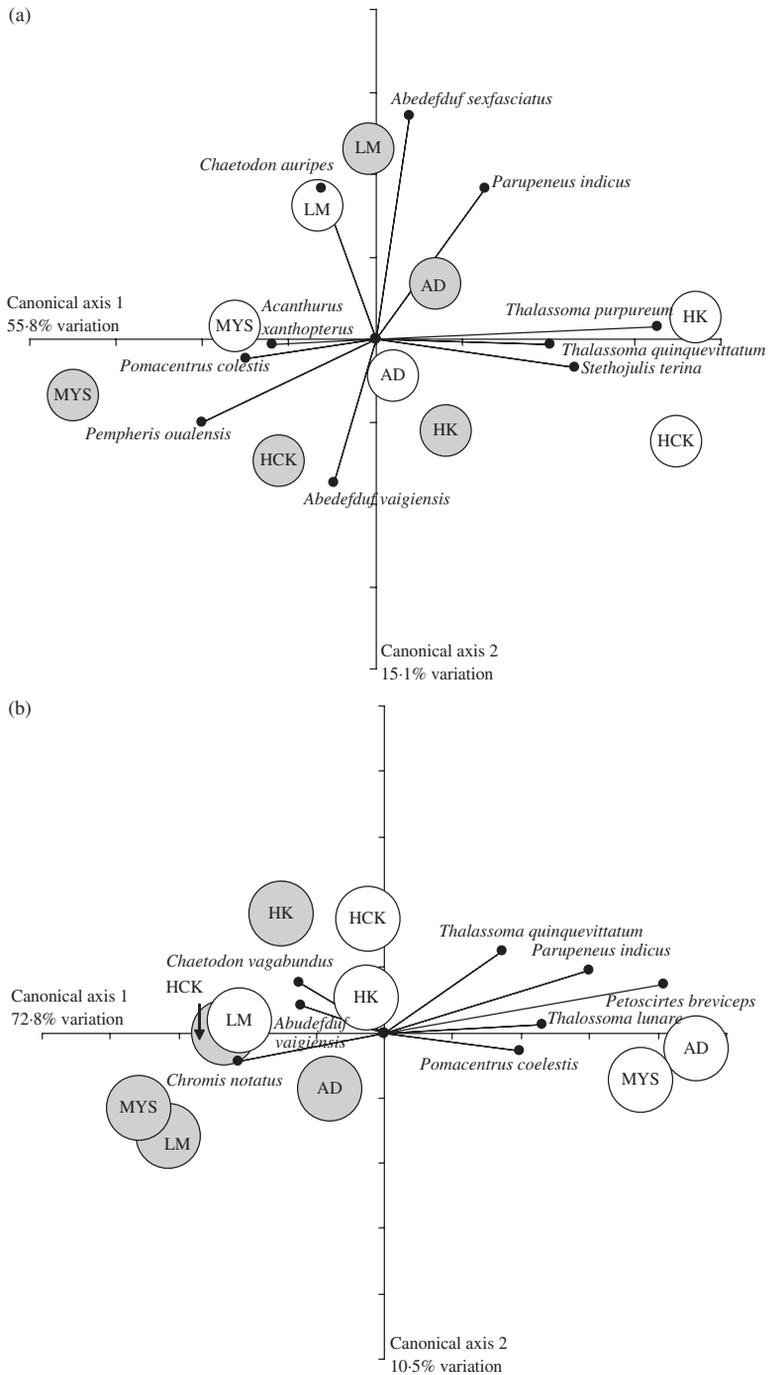and *T. quinquevittatum*.

FIG. 3. Canonical discriminant analyses of coastal fish assemblages in (a) summer and (b) winter, comparing community structure between anthropogenically modified (◉) *v.* natural habitats (○), at five locations; Ao-Di (AD), Lon-Men (LM), Mei-Yan-Shan (MYS), Hai-Ko (HK) and Hong-Chai-Keng (HCK).

DISCUSSION

This study revealed marked differences in the structure of coastal fish assemblages in natural v. anthropogenically altered coastal habitats in Taiwan, though there were no significant differences in overall abundance or species richness of fishes between these habitats. These results reinforce the insensitivity of commonly used metrics for measuring responses of fish assemblages to disturbances and habitat degradation, whereby stasis in abundance and diversity of fishes may belie marked changes in taxonomic composition (Bellwood *et al.*, 2006). Variation in the taxonomic composition of fish assemblages between natural and artificial habitats is likely to result from marked differences in the biological and physical structure of benthic habitats. The role of habitat structure in moderating fish assemblages is well known (Sano *et al.*, 1984; Garpe *et al.*, 2006; Graham *et al.*, 2006), and marked differences in the habitats considered in this study would reflect the most extreme differences between natural habitat types. In Taiwan, Hsieh *et al.* (2005) showed that natural rocky reefs support higher diversity of abiotic and biotic habitat types (*i.e.* cracks, crevices, boulders, algal turf and coral reefs) compared to artificial habitats. The artificial breakwaters considered in this study all comprised uniform concrete blocks laid on rocky and sandy bottoms, providing very limited diversity in habitat structure (Hsieh *et al.*, 2005). Despite their age (up to 22 years since construction), these artificial habitats also supported very low cover of habitat-forming sessile organisms, such as corals (Table I).

Given the diversity of habitats (Hsieh *et al.*, 2005), it would be expected that natural reefs would contain a much higher diversity of fishes compared to concrete breakwaters, especially for coral associated species such as *S. terina* (Labridae), *A. sexfasciatus* (Pomacentridae), and *T. quinquevittatum* and *T. purpureum* (Labridae). On the other hand, the breakwaters provide alternative habitat structure which is not provided by natural reefs. The large crevices between the concrete blocks effectively provided large holes that are utilized by fishes such as *P. ransonneti* and *P. oualensis*, which were among the most abundant fishes on the artificial habitats. The level of habitat complexity that is important for fishes (*e.g.* the size of refuge holes) scales with body size (Shulman, 1984; Hixon & Beets, 1993). Whereas, smaller bodied fishes (<10 cm total length L_T) are expected to benefit from fine scale surface complexity, larger and more mobile species benefit from increased availability of larger crevices (Wilson *et al.*, 2007), such as those provided by gaps between concrete blocks. When placed within areas of highly degraded or low-relief habitat, concrete breakwaters often lead to marked increases in abundance and biomass of fishes (Bohnsack, 1989). The extent to which artificial breakwaters support a greater or lesser number of fishes (species and individuals) clearly depends on differences in the availability of specific niches and habitat types.

The abundance of fishes in coastal habitats is often regulated by the availability of habitat, and especially the availability of predator refuge v. availability of prey (Sale, 1980). Interactions between predators and prey vary greatly between natural reefs and breakwaters, thus affecting species composition within these habitats (Guidetti, 2004). In general, breakwaters provide limited refuges for smaller prey fishes and therefore, attract species that make use of the larger shelter holes, but do not necessarily feed on benthic or sessile prey within these habitats. This is apparent from differences in the taxonomic composition of fishes on natural v.

artificial habitats in Taiwan; artificial habitat had fewer fishes with highly specialist food and habitat requirements, such as *P. coelestis* which often inhabits low-relief reef fronts (Doherty *et al*., 1996) and *P. indicus* which feeds over sand (Lukoschek & McCormick, 2001), and more species that feed in the water column and only associate with reef structures to avoid predation (*e.g. P. ransonneti*).

With increased development and alteration of coastal habitats, it appears that the normal inhabitants of coastal habitats in Taiwan are being replaced by species adapted to live within the habitat provided by concrete breakwaters. Notably, there were several species (*e.g. P. ransonneti*, *C. notatus* and *C. fumea*) in altered habitats that were never observed on the adjacent natural habitats. This may reflect effective partitioning of habitats by ecologically equivalent species (Anderson *et al*., 1981), though it is more likely that the altered habitats fail to provide essential resources for normally reef-associated species. The localized loss of specific species and corresponding declines in biodiversity may become even more apparent if sampling is increased to include the full range of intertidal habitats that are replaced during construction of artificial breakwaters. For example, there are a large number of fishes, mostly from the families Gobiidae and Blenniidae, that inhabit rocky tidepool habitats around Taiwan (Wen *et al*., 2005); they do not exist along coastal margins with concrete breakwaters which intentionally have high vertical relief and no retention of water during tidal movements.

The age of artificial habitats is often critical in determining the local abundance of different benthic and sessile organisms (Anderson & Underwood, 1994; Thompson *et al*., 1996; Walters & Wethey, 1996) and could therefore, further influence the abundance and composition of fishes associated with artificial habitats. Hsieh *et al*. (2005) showed that several benthic invertebrates, including barnacles, sponges and macroalgae, increased in abundance with increasing age of breakwaters in Taiwan, but this did not hold for corals, which are the most important habitat-forming organisms in tropical shallow marine habitats (Bellwood *et al*., 2006). Accordingly, there did not appear to be any major differences in species composition of fishes among different artificial habitats, despite the large differences in the time since construction. While there is likely to be a rapid change in the abundance and composition of fishes in the first few years after construction (associated with differential patterns of colonization and succession), it appears that each of the artificial habitats considered in this study is sufficiently old to be at a similar successional stage, at least for coastal fishes.

The influence of natural *v*. anthropogenically altered coastal habitats is not only limited to changes in habitat structure. Rather, the anthropogenic impacts on coastal habitats tend to increase with coastal development due to increased boating and fishing activity, resulting in increased turbidity, slop-oil contamination and waste pollution (Airoldi *et al*., 2005*b*). In addition, the seawall will obstruct the circulation of sea water inside the harbour and the concentration of pollution will increase. Some reports also demonstrated that the noise from motors can impair the hearing system of larval and adult fishes (Saito *et al*., 2001; Smith *et al*., 2004*a*, *b*). Damaged hearing systems may prevent fishes from avoiding predators or locating prey (Popper *et al*., 2003; Scholik *et al*., 2004; Hastings & Popper, 2005). These changes do not arise directly from the introduction of artificial habitat structures, but represent additive effects of natural coast urbanization.

In conclusion, significant and ongoing development and anthropogenic alteration of Taiwan's coastline does not appear to have greatly affected the localized diversity and abundance of coastal fishes. The fish assemblages associated with anthropogenically altered habitat are, however, significantly different from the fish assemblages on natural heterogeneous habitats, which they have replaced. Consequently, further loss of natural coastal habitats may lead to regional extinction of some highly specialized fishes that are critically dependent upon certain features of natural coastal habitats.

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