

A Comparative Study of Fish Assemblages Near Aquaculture, Artificial and Natural Habitats

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(Received August 18, 2013; revised November 18, 2013; accepted August 29, 2014)

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Abstract Habitat plays a critical role in regulating fish community structure. Using the data collected from a monthly trammel net survey in Ma'an archipelago off the east coast of China, we evaluated impacts of five different habitats (artificial reefs, mussel farms, cage aquaculture, rocky reefs and soft bottom) on fish assemblages. This study suggests that artificial reefs (AR) have significantly higher species richness, abundance and diversity than mussel farms (MF) or soft bottom (SB) habitats during most seasons, and that fish taxa in the AR habitats are similar to those in the rocky reef (RR) habitats. Two different fish assemblage patterns were revealed in the study area using non-metric multidimensional scaling ordination: an assemblage dominated by reef fishes (especially by Scorpaenidae species) in AR, RR and cage aquaculture (CA) habitats and an assemblage dominated by Sciaenidae species in MF and SB habitats. We suggest that reef fishes play a key role in differentiating fish community structures in the study area. Although few differences in fish abundance and diversity were found between the CA and SB habitats, a more diverse age structure was observed in the CA habitats. A much more complex fish assemblage and enhanced population of local species were established as a result of the presence of both floating and fixed artificial structures, probably through improved survival rates.

Key words artificial reef; species diversity; fish culture; mussel culture; aquaculture facility; fish assemblage

1 Introduction

The relationship between fish assemblage and habitat is an important research topic in ecology (Benaka, 1999; Fogarty, 1999; França *et al.*, 2009; Simon *et al.*, 2011; Burta *et al.*, 2013). Most of these studies focus on coastal and estuarine habitats, such as shallow lagoons and straits (*e.g.*, Hajisamiae and Chou, 2003; Martin *et al.*, 2009), seagrass beds, mangroves, coral reefs and kelp forests (*e.g.*, Dorenbosch *et al.*, 2006; James, 1988; Nagelkerken *et al.*, 2007), rocky, sandy and soft bottom and algal-reefs (*e.g.*, Johan *et al.*, 2007; Beyst *et al.*, 2001). Understanding the fish assemblage-habitat relationships is particularly important because human activities such as fishing, aquaculture, oil and gas operations, offshore renewable energy developments and coastal development put considerable stress on natural habitats (Fraschetti *et al.*, 2008). Such stress can lead to habitat degradation, destruction, fragmentation or loss (Sih *et al.*, 2000; Gill, 2005; Hansson *et al.*, 2007; Murdoch *et al.*, 2007; Rybicki and Hanski, 2013). Approaches such as stock enhancement, sea ranching, and use of artificial reefs are

often integrated into fishery management as an ecosystem approach to levitate habitat degradation (Leber *et al.*, 2004).

The presence of artificial structures in aquatic systems may cause habitat fragmentation at different scales depending on the type of structures (Bulleri, 2005; Rybicki and Hanski, 2013). Structures such as artificial reefs and aquaculture facilities may increase habitat complexity by providing refuges and barriers that fragment the area, resulting in more heterogeneous assemblages (Sebens, 1991) and in turn changing fish community structure (Anderson *et al.*, 2009; Fernández *et al.*, 2009).

Marine structures, both natural and artificial, are known to aggregate fish (Pickering and Whitmarsh, 1997; Simon *et al.*, 2011; Campbell *et al.*, 2011). This has led to the development of fish aggregation devices (FADs) in fisheries using artificial structure (*e.g.*, Stanley and Wilson, 2000; Machias *et al.*, 2004; Valle *et al.*, 2007; Pizzolon *et al.*, 2008). Other studies claim that the presence of artificial structures can increase fish biomass (*e.g.*, Bohnsack, 1989; Santos and Monteiro, 1997, 1998; Fabi *et al.*, 2004). However, most of the studies only included a single artificial habitat. Few studies have compared fish assemblages among more than 3 artificial habitats within a relatively small area (Clynick *et al.*, 2008a; Burta *et al.*, 2013). Since these structures act as substitutes for natural

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habitat (e.g., rocky shores), it is important to understand whether they support fish assemblages that are comparable to those found on natural substrata and if the environmental factors operating between and within artificial habitats and natural habitats are similar.

Mussel farming and fish cage aquaculture activities are widespread around coastal waters in many countries. Mussel farms can be found in New Zealand (Morrissey *et al.*, 2006), Canada (Clynick *et al.*, 2008b), Western Europe (Theodorou *et al.*, 2010), China (Wang *et al.*, 2010) and cage aquaculture in Western Europe (Machias *et al.*, 2004; Valle *et al.*, 2007; Fernandez-Jover *et al.*, 2009), Southeast Asia (San Diego-McGlone *et al.*, 2008; Sudirman, 2009) and China. Unique fish assemblages have been observed around deployed aquaculture facilities (Machias *et al.*, 2004; Clynick *et al.*, 2008b; Sudirman, 2009; Dempster *et al.*, 2010), raising interesting questions about ecological roles of these structures in natural fishery ecosystems.

The objective of this study is to evaluate impacts of different habitats, in particular artificial structures and aquaculture facilities, on the dynamics of fish assemblages. Ma'an archipelago on the east coast of China provides an ideal experimental area for addressing this objective. This region features both aquaculture facilities set on soft bottom habitat and two artificial reef systems built in 2005–2006 and 2008 in the western marine reserve. All these artificial structures are situated near rocky shores. We test the following hypotheses: 1) the presence of additional structures on soft bottom habitat offers new living space for residents and transients, and thus increases both fish abundance and diversity on the whole, and 2) by attracting additional individuals to those artificial habitats, a

more complex assemblage structure and age pattern can be formed within these areas.

The highlights in the present work are:

i) Aquaculture structures provide extra habitats for more local fishes and migrating fishes, and thus contribute to a small scale fisheries based on those species.

ii) Meta-habitats including both aquaculture and artificial habitats serve to establish a more complicated fish community structure. However, no significant differences can be found between them if reef fish are excluded.

iii) Age structure of fish community composition can be an effective tool in testing the population enhancement effects contributed by both aquaculture and artificial habitats.

2 Materials and Methods

2.1 Study Area and Site Selection

The western Ma'an archipelago off the Yangtze River estuary (Fig. 1) is a traditional anchorage ground for international cargo ships and for offshore discharging. There are mainly two types of substrate in the subtidal area: rock-algal and clay. Less than 1% of this area is covered by rocky reefs. Most of the open waters share the same substrate, which is fine clay with particle diameter, ranging from 0.03 to 0.1 mm. This soft bottom area is an important fishing ground for gill-netting and trawling. The area's high productivity can be attributed to the runoff from the Qiantang and Yangtze Rivers interacting with the offshore Kuroshio current (Wang *et al.*, 2010). It is an important habitat for the Chinese sturgeon (*Acipenser sinensis*) as well as other endangered species (Wang *et al.*, 2010).

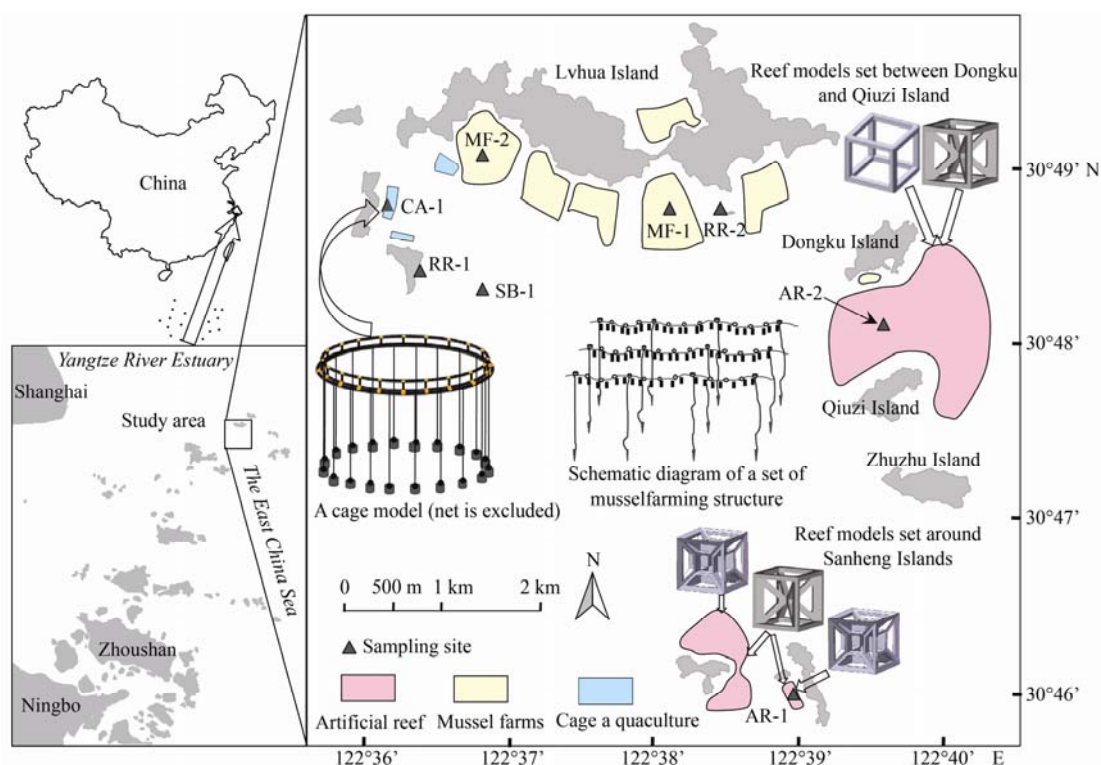


Fig. 1 Spatial distribution of sampling sites and artificial habitats in western Ma'an Archipelago, East China Sea.

Many artificial structures were deployed in the Ma'an archipelago region in the last decade. About 1.8 km² of mussel farms, divided into 6 regions, were developed during 2000–2008 in western Ma'an Archipelago. Nearly 140 fish cages were set in the south of western Lvhua Island between 2002 and 2004, covering an area of 1.6 ha. In 2005 and early 2006, 554 individual concrete reef units of the same design (length × width × height = 3 m × 3 m × 3 m = 27 m³) were deployed between Dongku and Qiuzi Islands to form 13 clustered artificial reef groups, each consisting of 42–43 individual units with a reef area of approximately 330 ha. In the vicinity of Sanheng Island, an additional 342 individual concrete reef units with two similar separate designs (length × width × height = 3 m × 3 m × 3 m = 27 m³) were deployed in early 2008 to form 9 clustered artificial reef groups, each consisting of 37–39 units with a combined reef area of 200 ha.

Eight sites were selected for our monthly fish sampling survey to examine the effects of artificial structures on fish assemblages (Fig. 1). Sanheng (AR-1, average water depth = 12.3 ± 0.5 m) and Dongku (AR-2, average water depth = 15.3 ± 1.3 m) are two artificial reef (AR) sites located in the southeastern and eastern study areas. Two mussel farm (MF) sites, East Lvhua (MF-1, average water depth = 10.1 ± 0.3 m) and West Lvhua (MF-2, average water depth = 7.7 ± 0.3 m), are located in the northeast and northwest parts of the study area, respectively. Only one site, East Mandui (CA-1, average water depth = 10.1 ± 0.2 m), was selected for cage aquaculture (CA) habitat due to limited spaces for trammel nets deployment. Three natural habitat sites, including 2 rocky reef (RR) sites (East Mantou (RR-1, average water depth = 6.3 ± 0.4 m) and Tongqian reefs (RR-2, average water depth = 6.2 ± 0.1 m)), and 1 soft bottom (SB) site (South Lvhua (SB-1, average water depth = 9.7 ± 0.7 m)), were set as control sites because they are not artificially enhanced and share similar environmental characteristics (Carr and Hixon, 1997). All of the artificial structures were originally set in soft bottom habitats.

2.2 Field Sampling and Laboratory Analysis

We used multi-mesh trammel nets (MTNs) to sample our fish assemblage since most of the habitats are not easily trawled or seined. MTNs were set randomly each month in our selected 8 sites (each site is about 200 m in length and 100 m in width), *i.e.*, no overlaps for the consecutive months. Multi-mesh gillnets and trammel nets were shown to be effective sampling tools for fish on various substrates (Acosta, 1997).

Four groups of experimental MTNs were deployed for approximately 24 h on the same day at 4 sites. Thus it took 48 h to sample all the 8 sites in each month. We sampled each site only once per month to avoid local overfishing (Olin *et al.*, 2004) which can impact small-scale fish assemblages by severely reducing reef fish abundance over a small area. Monthly surveys at the sites were carried out over the same area (a transect of about 200 m in length and 100 m in width) within each habitat

with the help of a GPS. All nets were set close to the bottom with anchors and placed in a direction perpendicular to the main tidal current (oriented northeast-southwest). Nets were set on top of natural reefs and soft bottom habitats and kept perpendicular to the main tidal current direction. They were deployed across the reef models in the AR habitats to make sure each part of the habitat was sampled effectively. In the CA habitat, nets were set around cages which were fixed to bottom structures. We set nets through gaps in the MF habitat and kept them perpendicular to tidal currents as well. Nets were checked twice a day in the summer to reduce mortality of captured fish.

Each group of trammel nets was composed of 2 nets (*i.e.*, smaller-mesh net and larger-mesh net) that had 8 mesh sizes ranging from 2.5 cm to 8.0 cm. The panels in each net were ordered randomly. The size of smaller-mesh net was 1.5 m × 15 m × 4 panels with mesh sizes of 2.5 cm, 3.4 cm, 4.3 cm and 5.8 cm; and 27 cm for covers. The size of larger-mesh net was 2.4 m × 30 m × 4 panels with mesh sizes of 5.0 cm, 6.0 cm, 7.0 cm and 8.0 cm; and 33 cm for covers. Thus, the total length of our sampling transect was about 180 m at each site. Due to high concentrations of juveniles and other small fish observed during previous sampling, we used only the 2.5 cm mesh panel in the smaller-mesh net from January to August to ensure the efficiency of catching these size classes. Panels with mesh sizes of 3.4 cm, 4.3 cm and 5.8 cm were included for smaller-mesh net from September to December. The larger-mesh net was kept the same throughout the year.

A total of 96 hauls were conducted in the 5 habitats from January to December in 2009. Fish collected in each survey were identified to species as well as measured, weighed and sexed. Stomach contents were collected for analyzing food selection preferences and otoliths were extracted for ageing. For each species, up to five individuals were aged in a 1 cm-gap size group (if abundance ≤ 5, all individuals were aged).

2.3 Data Analysis and Statistical Methods

Fish abundance and biomass data were standardized for sampling (soak) time since the soak time was not exactly 24 h for each net. Abundance per unit effort (APUE, ind h⁻¹) and biomass per unit effort (BPUE, g h⁻¹) were used to represent the relative abundance of fishes in the targeted habitats.

Margalef's species richness index D and Whilm's species diversity index H' were used to compare the diversity levels among 5 habitats. We used the Whilm's index because, based on our sampling experience, some species change habitat utilization strategies over their life history stages. For example, juvenile reef fishes such as *Sebastes marmoratus* tend to be associated with algae and other structures while adult individuals choose mostly rocky reefs or hard bottom. The abundance-based diversity index cannot discern such differences if juvenile and adult fishes have similar abundance.

The number of species, APUE, BPUE and species di-

versity were analyzed seasonally (January–March=winter; April–June= spring; July–September= summer; October–December= autumn; the classification was based on the average seawater temperature recorded monthly in 2009) in order to better understand temporal variability of fish assemblage. Analyses of variance (ANOVA) were used for spatial, seasonal comparisons of those four indices among 5 habitats and 4 seasons. Posteriori comparison of means (relative abundance, relative biomass, species number and species diversity) was performed using the Turkey test.

Seasonal differences in fish assemblages among 5 habitats were examined using non-metric multidimensional scaling (NMDS) based on a Bray-Curtis similarity matrix. We used biomass matrix for ordination plots because some species might change favorable habitats in their life history stages, and the differences could be easily examined using individual weight rather than abundance data. Analysis of similarity (ANOSIM) was used for evaluating differences between groups (defined by two types of substrate samples and two types of habitats, *i.e.*, artificial and natural habitats). Two thousand permutations were run in the analysis. Rare species were excluded from the analyses (Araújo *et al.*, 1999) and a square root transformation was performed on the biomass data before the analysis. All multivariate analyses were performed using PRIMER software package v5 (Clarke and Gorley, 2001). A significance level of 5% was used in all statistical analyses.

3 Results

3.1 Fish Abundance and Diversity

In total 66 fish species were identified belonging to 38

families (Table 1). Fish taxa, by either family or genus, were more abundant in the purpose-built AR habitats (27 families and 36 genera at AR-1; 23 families and 32 genera at AR-2) compared with those in other non purpose-built artificial habitats and natural habitats (16 families and 23 genera at MF-1; 16 families and 21 genera at MF-2; 20 families and 27 genera in the CA habitat; about 20 families and 28 genera for the 2 RR habitats; and 15 families and 20 genera in the SB habitat). Fewer taxa were found in the RR and CA habitats. The lowest number of species in taxa was observed in the SB and MF habitats. Species diversity and fish abundance were highest in the AR habitat (Table 1). Site RR-1 had the lowest abundance (only 290 individuals were collected in 2009), but its total biomass was higher than biomass found in more than half of the study sites. Habitats with concrete structures on the seabed such as AR and CA had much higher concentration and occurrence (see Appendix A) of species like *Sebastes marmoratus* and *Hexagrammos otakii*, than natural RR, SB and MF habitats. Those two species were observed in the CA habitat only. Fishes such as *Thryssa kammalensis*, *Anchoviella commersonii*, *Engraulis aponicas* and *Larimichthys polyactis* were most attracted to sites with artificial reefs (Appendix A). *Johnius grypotus* was also a common species, found most often in the MF habitat. Some seasonal species like *Decapterus maruadsi* and *Plotosus anguillaris* were also common at AR sites (Appendix A).

Species richness, relative abundance (APUE&BPUE) and species diversity varied considerably among the four seasons (Table 2). Significant seasonal differences were found within different habitats for species richness, Whilm's diversity and APUE. However, differences in BPUE among the study sites were smaller (Table 2).

Table 1 The total number of species, abundance and biomass during the whole survey period

Category	AR-1	AR-2	MF-1	MF-2	CA-1	RR-1	RR-2	SB-1	Total
Species number	42	34	24	24	31	32	32	24	66
Abundance (ind)	1090	1529	566	576	552	290	421	411	5435
Biomass (g)	37115.3	50262.1	24218.1	21585.1	29110.6	28289.7	24798.7	26324.1	241703.7
Taxa composition order/family/genus	9/27/36	8/23/32	7/16/23	8/16/23	6/20/27	7/19/27	7/20/28	7/15/20	12/38/53

Table 2 Two-fixed-factor ANOVA

Source	df	Species number		Species diversity		APUE		BPUE	
		MS	F	MS	F	MS	F	MS	F
Season	3	224.135	35.195**	2.850	23.237**	266.528	19.817**	116142.587	10.399**
Habitat	4	58.893	9.248**	1.147	9.356**	34.042	2.531*	12794.731	1.146 ^{NS}
Season×Habitat	12	8.213	1.290 ^{NS}	0.119	0.968 ^{NS}	17.067	1.269 ^{NS}	14488.206	1.297 ^{NS}
Error	76	6.368		0.123		13.450		11168.269	

Notes: Species number, species diversity, abundance per unit effort and biomass per unit effort serve as functions of habitats (artificial reef, mussel farm, cage aquaculture, rocky reef and soft bottom) and seasons includes spring, summer, autumn and winter. NS, $P > 0.05$;

* $P < 0.05$; ** $P < 0.01$.

Many more species were found in the AR habitats than in the SB habitat in spring and summer (Fig.2a). AR-1 and AR-2 sites were found to be significantly higher in Margalef's species richness than MF-2, MF-1 and CA-1

in autumn, and higher than RR-2 in winter. No other significant differences were found among those habitats during other seasons. Species collected in MF were similar to those from the SB habitat in each season; it also displayed

low species richness. The habitat exhibiting the highest abundance was RR-2 in summer, which was significantly higher than the SB and MF habitats (Fig.2a).

The average APUE was higher at AR sites than that at the other sites in most of the seasons except for autumn (Fig.2b). Significantly higher APUE was found at AR-2 in both spring and summer, which was higher than those at MF-2 ($P=0.036$) and SB-1 ($P=0.027$) in spring and

RR-1 ($P=0.026$) in summer. AR-1 had a much higher APUE in winter than most of the sites (Fig.2b). Spatial variability of BPUE over the 8 sites in each season followed similar trends to that of APUE. All of the sites with concrete reefs (AR-1, AR-2&CA-1) had a significantly higher BPUE than one of the mussel farm sites in spring (Fig.2c). The highest BPUE was found at AR-2 in summer, much higher than those for the sites of RR-1 and SB-1.

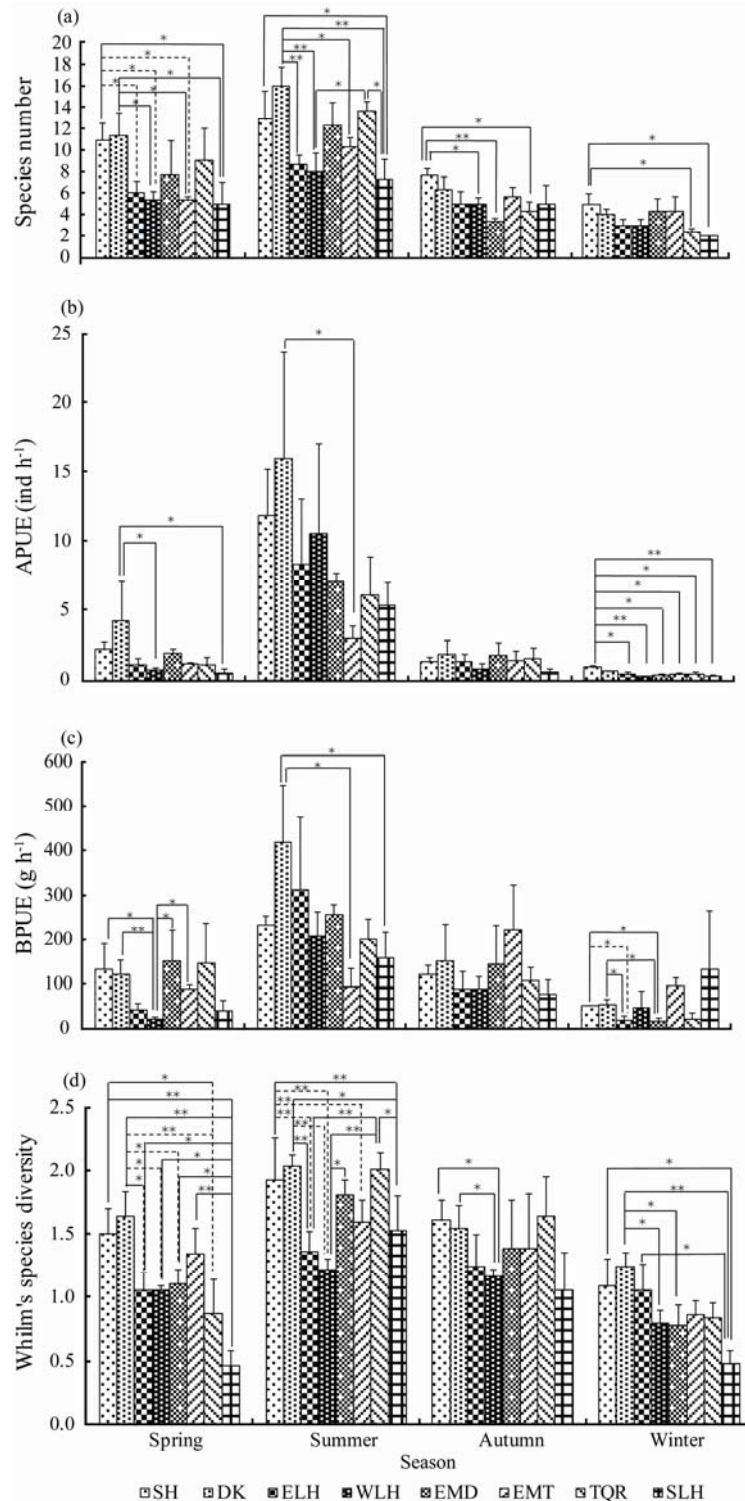


Fig.2 Seasonal variations of fish abundance and diversity in 2009. (a), number of species; (b), abundance per unit effort (APUE); (c), biomass per unit effort (BPUE); (d), Whilm's species diversity. Results are expressed as means $\pm$ SD. The error bars represent the standard error. '*' and combined lines indicate the significance level between the compared groups. * $P<0.05$; ** $P<0.01$. Post hoc Turkey-HSD test was used.

No significant differences were found in autumn among the 8 sites. Though some sites like RR-1 and SB-1 had a higher BPUE than the other sites on average, only the sites with artificial reefs were found to have a significantly higher BPUE than MF-1 and CA-1 in winter (Fig.2c).

Significantly higher Whilm's species diversity was observed in all seasons for the 2 AR sites (Fig.2d). Only CA-1 had a higher diversity than MF-2 in summer for

other artificial habitats. Sites without natural rocks or concrete reefs (*i.e.*, MF-2, MF-1 and SB-1) were found to be much lower in fish diversity in most seasons.

3.2 Fish Assemblage Patterns and Age Structures

Two types of assemblage patterns, reef bottom and soft bottom, were identified based on seasonal fish community (left four panels in Fig.3). This classification was

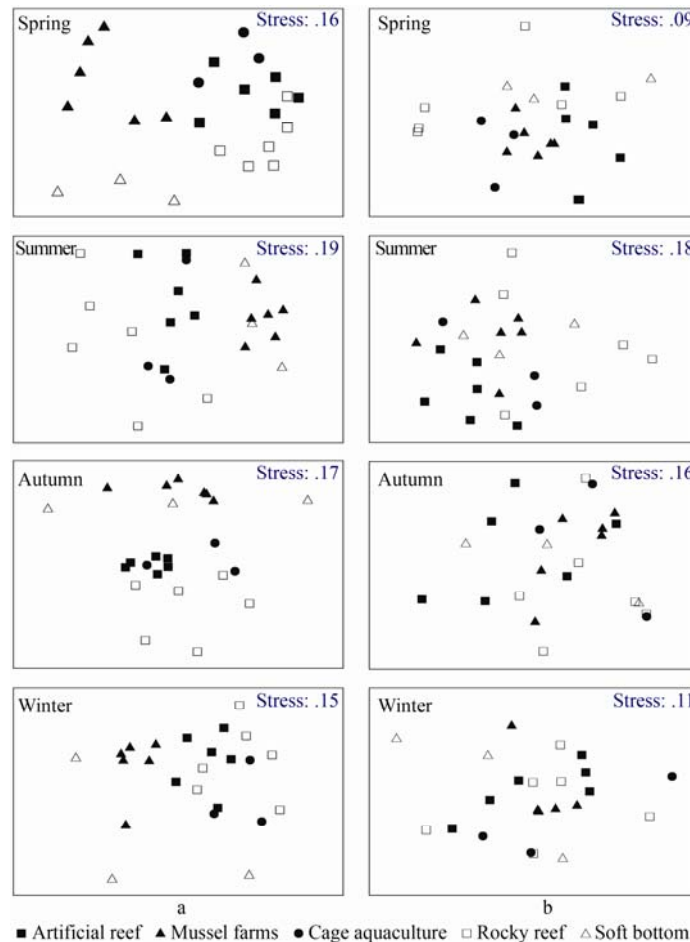


Fig.3 NMDS plots on the assemblages of fish in 5 habitats at 8 sites (column a: reef fish included; column b: reef fish excluded). The biomass matrix was used in non-metric multidimensional scaling analysis. All original data was square-root transformed.

Table 3 The list of R values from analysis of similarity (ANOSIM) between 3 groups

Season	Reef fishes included			Reef fishes excluded		
	A-B	D-E	C-F	A-B	D-E	C-F
Spring	0.279*	0.741*	0.801**	0.168 ^{NS}	0.463*	0.006 ^{NS}
Summer	0.447*	0.494*	0.476**	0.431*	0.025 ^{NS}	0.041 ^{NS}
Autumn	0.417*	0.361*	0.588**	0.036 ^{NS}	0.241 ^{NS}	-0.027 ^{NS}
Winter	0.121 ^{NS}	0.679*	0.604**	-0.091 ^{NS}	0.639*	-0.021 ^{NS}

Notes: A=habitat with manmade reefs on bottom (AR&CA); B=habitat with natural reefs on bottom (RR); C=habitat with man-made or natural reefs on bottom (AR, CA&RR); D=soft bottom without any artificial structures (SB); E=soft bottom with mussel farming structures (MF); F=soft bottom with or without mussel farming structures (SB&MF). One Way Global Test for groups of C-F and One Way Pairwise Tests for groups of A-B and D-E. NS, $P>0.05$; * $P<0.05$; ** $P<0.001$.

significant for all seasons (Table 3). However, there were no significant differences between reef habitats (AR, CA and RR) and soft bottom habitats (MF and SB) when reef fishes were excluded (right four panels in Fig.3, Table 3). Reef fishes, especially dominant ones such as *Sebastiscus marmoratus*, *Lateolabrax maculatus*, *Nibea albiflora*, *Paralichthys olivaceus* and *Hexagrammos otakii*, made major contributions to the reef bottom fish assemblage structures (Appendix A). Species such as *Johnius grypus*, *Lophius litulon*, *Trichiurus haumela*, *Muraenesox cinereus* and *Pelates quadrilineatus* were much more abundant in SB and MF habitats than those in reef bottom habitats, and contributed to the formation of fish assemblage in soft substrate habitats (Appendix A). In spring, summer and autumn, fish assemblage patterns identified for those habitats containing artificial reefs were signifi-

cantly different from those in sites where there were only natural rocky reefs (left four panels in Fig.3, Table 3). When reef fish were excluded, only the summer assemblages showed significant difference between those two types of habitats (Fig.3, Table 3). The fish assemblages in MF were significantly different from those in SB habitats in all seasons. However, the data in summer and autumn showed no differences when reef fish were not included (Fig.3, Table 3).

In considering age structure, many more individuals older than 2 years were sampled from sites in the AR, CA

and RR habitats than those from sites in the MF and SB habitats, especially at site CA-1 in the CA habitat (Fig.4). A greater variety of age groups and wider range of age structure were observed in the CA habitat, and most of those 3- or 4-year-old individuals were scorpion fish (*Sebastes marmoratus*). Age structure in the AR habitats was similar to that in the RR habitat with low abundance of fish in the 3-4 years old groups. Few individuals with ages older than 2 years were collected in the MF and SB habitats. Most individuals collected in our monthly sampling were under 1 year old in all sites (Fig.4).

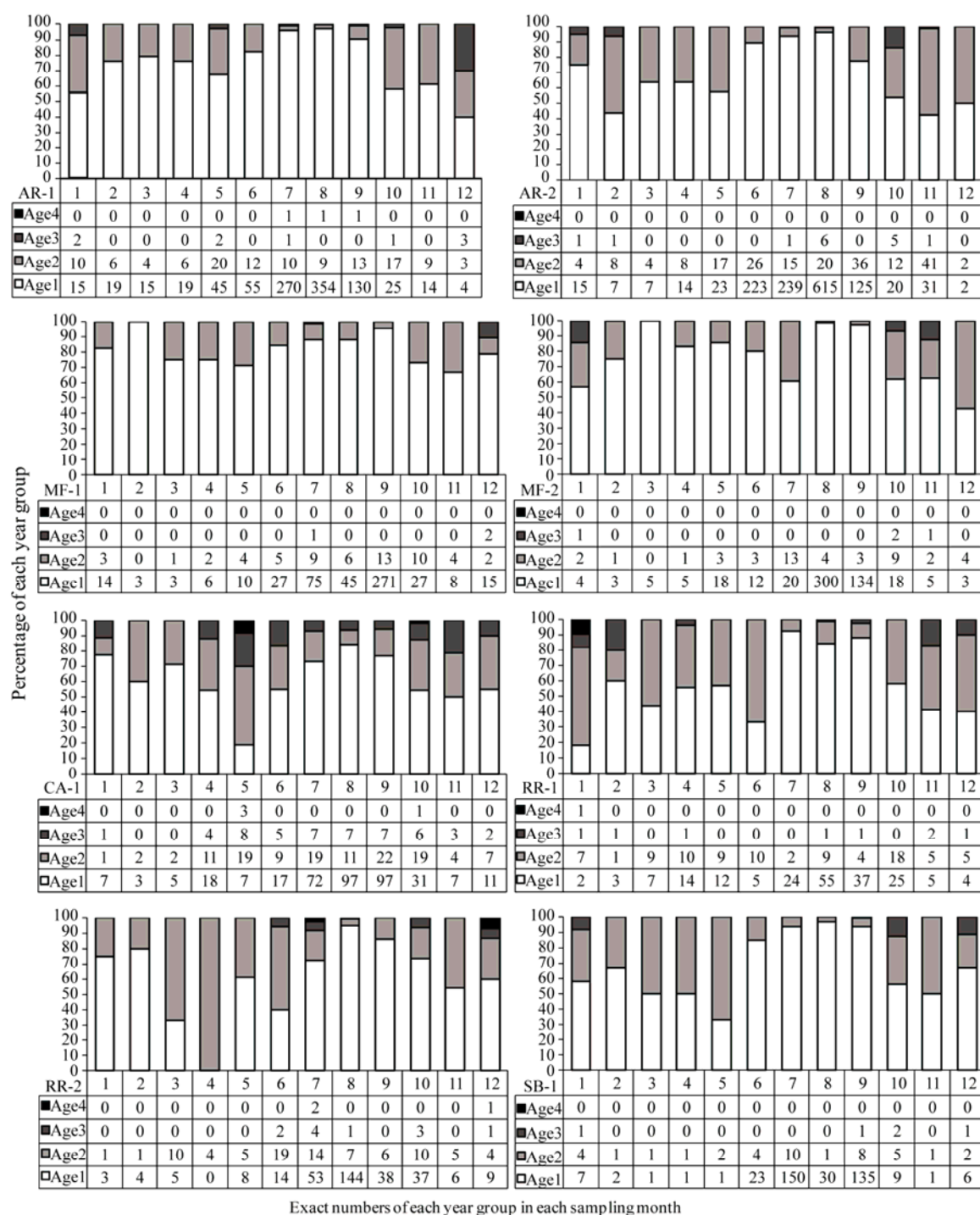


Fig.4 Monthly variation of percentage of four age groups for all fishes at 8 sites during the study period. age1=0⁺, age2=1⁺, age3=2⁺, age4=3⁺. The relative percentage of each year group is shown by bars and the exact number of each age group is given in the table down below.

4 Discussion

4.1 The Differences in Species Composition, Fish Abundance and Diversity Among 5 Habitats

In our investigation three different types of artificial structures were found on natural SB habitat, each of which was showed to contribute differently to seasonal variations in species composition, fish abundance, and diversity. Masuda *et al.* (2010) compared fish richness and density among three types of ARs and found significant differences among them during most of the sampling years. Walker *et al.* (2002) also compared fish assemblages between concrete aggregates and quarry stone, and found significant seasonal variation of fish abundance and species richness for both types of ARs. However, the differences between these types of ARs were not significant. Although these studies may offer some evidence as to the functions of different types of ARs, few studies have compared fish assemblages in AR habitat with other artificial habitat, such as MF and CA. This makes it difficult to draw a comparable conclusion. Many studies suggest that marine structures can attract certain aquatic animals to colonize on them (Pickering and Whitmarsh, 1997), or just offer temporary uses for activities such as feeding, protection from predators and serving as spawning ground for migrating species (DeMartini *et al.*, 1994).

In this study AR habitats had different fish taxa, abundance and species diversity compared with SB habitats in most seasons. However, indices for these characteristics did not differ greatly between the areas with aquaculture structures and natural habitats. Complex fish taxa composition and higher abundance and diversity of fishes were found mostly in the AR habitat, indicating that the AR tended to enhance local fish fauna complexity and diversity. This is consistent with many previous findings that artificial reef deployment has the potential to enhance fish assemblages and increase species diversity (e.g., Santos *et al.*, 1997; Rilov and Benayahu, 2000; Relini *et al.*, 2007). However, a few positive changes have been noted in areas with improperly designed or sited artificial reefs (Baine, 2001; Polovina, 1994; Bortone *et al.*, 1994). It has been reported that artificial reefs could provide additional carrying capacity and therefore abundance and biomass of reef biota, which explains why fish tended to be most abundant in the AR habitat in our study.

Although both MF and CA were established in SB areas, the composition of their dominant fish species was different. The MFs shared similar taxonomic structure with soft bottom, and only *Johnius grypotus* was found to be more abundant than in the natural SB habitat. However, species composition in the CA habitat was similar to that in the AR and RR habitats, especially for reef fish. The primary cause could be the difference in materials and spatial locations of the studied artificial structures. Residual food from feeding caged fish from April to November could be another reason why there were many wilder reef fishes sampled in this habitat. These wild fishes might not

directly use food pellets dropped under the cages, but might prey on shrimp or crabs attracted by feeding events (Machias *et al.*, 2004; Sudirman *et al.*, 2009). By definition, fish species that respond directly to artificial or natural reefs and make them a permanent or seasonal habitat are referred to as reef-associated fishes (Bellwood, 1998). This might result in fish species composition in the CA and AR habitats being similar to that in the natural RR habitat.

Increased habitat complexity is considered favorable for promoting diversity and abundance (Fernández *et al.*, 2009). Ambrose and Swarbrick (1989) compared fish assemblages on artificial and natural reefs and found a greater number and density of benthic fish species in AR habitats compared to natural habitats, but species richness, diversity and total individuals were not different between artificial and natural reefs. Similar results were also found in other studies (Machias *et al.*, 2004; Clynick *et al.*, 2008b). Some other studies identified significantly higher abundance and diversity of wild fish around aquaculture structures (Valle *et al.*, 2007; Sudirman *et al.*, 2009). We believe that this might result from different sampling approaches in different studies. The three dimensional extension of aquaculture structures is quite different from the bottom set of ARs (Perkol-Finkel *et al.*, 2008). Most of the facilities are suspended from the water surface for the MFs and CA habitats. Our bottom nets could barely sample those fishes near bottom and pelagic fishes, especially juvenile fish. Sudirman *et al.* (2009) reported that wild fishes are significantly more abundant in near-surface depths around the margins of the cages in the morning than at other times of the day. Similarly, we found species such as *Mugil cephalus* and *Hyporvthus sajori* in great numbers around MFs during our field investigation, but we could not effectively sample them. This was probably due to their sensory ability to detect obstacles (Duffy, 1987). Taking those pelagic individuals into consideration, there should be a much higher level of fish diversity in the MFs or CA habitats compared with the adjacent SB habitats.

4.2 Fish Assemblage Patterns and Age Structures

One of the key objectives of habitat restoration by deploying artificial structures is to enhance fish assemblages in a designated area and to maintain higher population densities of target species (Pickering and Whitmarsh, 1997). The deployed artificial reefs and established aquaculture structures around our study area are mostly acting as combined habitat enhancement systems and FADs, rather than habitat replacements. Thus new fish assemblage pattern could be easily found due to change of available food and living space. Masuda *et al.* (2010) demonstrated that deployment of ARs does not reduce the number of fish species or density of individuals in the adjacent areas. This also suggests that introduction of ARs in certain areas may have limited impacts on the adjacent natural habitat.

In our study two major fish assemblage patterns have

been revealed, including the assemblage dominated by reef fishes (especially by Scorpaenidae species) in the AR, RR and CA habitats and the assemblage mainly dominated by Sciaenidae species such as Belenger's croaker (*Johnius grypotus*) and small yellow croaker (*Larimichthys polyactis*) in the MF and SB habitats. There are significant differences between fish assemblages in artificial habitats and natural habitats for most seasons except winter. Ambrose and Swarbrick (1989) claimed that the fish assemblages on artificial reefs are generally similar to the assemblages on natural reefs, similar to our findings here. A recent study suggested that artificial reef can hardly retain reef fishes effectively, especially for groupers (Addis *et al.*, 2013), indicating that they have an equal chance to choose habitat between natural and artificial reefs. If reef fish are excluded, the differences are found only in summer between the AR and RR habitats and in spring and winter between MF and SB habitats, which might result from seasonal changes in density of migratory species. This indicates that permanent residents or reef fishes are the driving factors in differentiating fish assemblages in the studied area. Early studies, such as the comparison of fish populations on artificial and natural reefs in the Florida Keys by Stone *et al.* (1979), suggested that ARs could be used to expand reef fish stocks. This explains why the AR and CA have similar fish assemblage pattern to that for the natural RR habitat. This study supports the hypothesis that deployment of artificial structures can enhance local fish assemblages and change community structure compared with natural habitats as a result of the newly formed reef fish aggregations.

Although our study did not identify any differences in abundance, biomass or diversity between CA habitat and RR habitats, an interesting result was revealed by examining the age structure of fish assemblages across the sampling sites. Many more individuals older than two years were sampled in CA habitat than any other artificial or natural habitats, indicating that permanent species inhabiting the CA habitat had higher survival rates than those in other habitats, and/or the CA habitat was more attractive to older fish than the other habitats. Most of the older individuals were species like scorpion fish (*Sebastes marmoratus*) and Fat greenling (*Hexagrammos otakii*), which are the most important economic species in the region. Ogawa (1973) stated that properly constructed ARs or submarine forests could increase survival, growth, and feeding efficiency of certain juvenile fishes, thus increasing the total biomass of reef fishes (Stone *et al.*, 1979). This conclusion can explain why the CA habitat could act as a reef fish stock enhancement system in our study. The higher food availability and lower disturbance from fishing activities in artificial habitats may explain the age structure observed in the artificial habitat in this study. No fishing around or within the CA area was allowed since the establishment of the cages except for our monthly sampling in 2009. However, gillnetting and fish trapping were often found to appear in the AR and MF habitats. It seems logical that population enhancement for specific species through deployment of artificial struc-

tures should at least involve protection measures as a prior consideration in habitat management.

5 Conclusions

The development of aquaculture structures and deployment of artificial reefs established a more complex and diversified habitat for fish species. This also restricts the use of mobile fishing gear and creates more undisturbed or minimally disturbed areas, providing extra habitats for local species (Burta *et al.*, 2013) and enhancing populations of demersal fish in the area. A more complex age structure can be found in the CA habitat due to limited fishing. Migrating species also benefit from the existence of artificial structures, especially in the AR habitat.

Acknowledgements

We would like to thank Mrs. Zhang Zhiguo, Xu Ming, Tong Wujun, Chen Mingchao, Chen Qingman, and Ye Linna for their assistance in the fieldwork. This research was supported by the National High Technology Research and Development Program of China (863 Program; No. 2006AA100303) and the National Basic Research Program of China (No. 2011CB111608). Z. Wang and Y. Chen's involvement in the project was partially supported by the Maine Sea Grant College Program at the University of Maine in the USA.

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(Edited by Qiu Yantao)

Appendix

A List of taxa recorded and their total individual numbers and frequency of occurrence (% in 12 months) in associated habitats during the study period

Category /species	Family	Sites in artificial habitats				Sites in natural habitats			
		SH	DK	ELH	WLH	EMD	EMT	TQR	SLH
Permanent residents									
<i>Sebastiscus marmoratus</i>	Scorpaenidae	138/100	144/100	20/41.7	27/58.3	194/100	68/100	97/91.7	1/8.3
<i>Hexagrammos agrammus</i>	Hexagrammidae	1/8.3	3/25		2/8.3	9/41.7	4/33.3	4/25	
<i>Hexagrammos otakii</i>	Hexagrammidae	30/83.3	38/91.7			35/75	16/58.3	4/25	
<i>Platycephalus indicus</i>	Platycephalidae	35/50	61/66.7	5/16.7		6/16.7	2/8.3	5/25	13/58.3
<i>Paralichthys olivaceus</i>	Bothidae	5/33.3	19/58.3	1/8.3		2/16.7	11/33.3	6/25	
<i>Zebrias japonica</i>	Cynoglossidae	1/8.3	2/16.7			1/8.3		2/16.7	
<i>Cynoglossus abbreviates</i>	Cynoglossidae	7/16.7			1/8.3		1/8.3		2/8.3
<i>Cynoglossus joyneri</i>	Cynoglossidae	1/8.3	5/8.3	2/16.7				1/8.3	3/16.7
<i>Odontamblyopus rubicundus</i>	Taenioididae	1/8.3		1/8.3					
<i>Amblychaeturichthys hexanema</i>	Gobiidae		1/8.3	3/8.3		6/8.3			7/16.7
<i>Nibea albiflora</i>	Sciaenidae	35/58.3	36/66.7	22/50	6/41.7	39/58.3	24/58.3	23/66.7	39/41.7
<i>Johnius grypotus</i>	Sciaenidae	19/58.3	25/33.3	186/100	116/91.7	54/58.3	20/33.3	19/41.7	62/75
<i>Miichthys miuy</i>	Sciaenidae	13/25	49/41.7	17/25	63/8.3	41/16.7	5/33.3	7/16.7	
<i>Muraenesox cinereus</i>	Muraenesocidae	1/8.3	3/25	3/16.7	3/16.7		1/8.3		9/41.7
<i>Raja porosa</i>	Rajidae	2/8.3							
<i>Acanthopagrus schlegeli</i>	Sparidae		1/8.3			1/8.3	8/41.7	13/41.7	

(to be continued)

(continued)

Category /species	Family	Sites in artificial habitats					Sites in natural habitats		
		SH	DK	ELH	WLH	EMD	EMT	TQR	SLH
<i>Acanthopagrus latus</i>	Sparidae	1/8.3							
<i>Rhabdosargus sarba</i>	Sparidae	2/16.7				2/8.3	4/16.7	5/25	
<i>Pagrus major</i>	Sparidae	2/16.7	9/25			3/8.3	1/8.3	1/8.3	
<i>Lateolabrax maculates</i>	Serranidae		4/25		2/16.7	2/16.7	13/33.3	4/33.3	
<i>Microcanthus strigatus</i>	Kyphosidae	5/8.3				2/16.7			
<i>Oplegnathus fasciatus</i>	Oplegnathidae					1/8.3	2/8.3	2/8.3	1/8.3
<i>Parapristipoma trilineatum</i>	Pomadasyidae				1/8.3	1/8.3	1/8.3	3/25	
<i>Harpadon nehereus</i>	Harpodontidae	2/16.7	2/16.7	1/8.3	1/8.3	3/25	1/8.3		
Seasonal residents									
<i>Apogon semilineatus</i>	Apogonidae	6/16.7	3/25			4/25	1/8.3	1/8.3	
<i>Decapterus maruadsi</i>	Carangidae	60/16.7	14/25	7/16.7	5/16.7	6/16.7	11/16.7	24/16.7	27/8.3
<i>Psenopsis anomala</i>	Centrolophidae	1/8.3	1/8.3						
<i>Chaetodon modestus</i>	Chaetodontidae	3/8.3	1/8.3				1/8.3		
<i>Goniistius zonatus</i>	Cheilodactylidae	3/8.3				2/8.3	6/8.3	1/8.3	
<i>Clupanodon punctatus</i>	Clupeidae			14/16.7					
<i>Harengula thrissina</i>	Clupeidae	1/8.3	1/8.3	11/16.7					1/8.5
<i>Thryssa kammalensis</i>	Engraulidae	501/41.7	693/33.3	201/25	254/25	106/33.3	73/33.3	129/33.3	199/33.3
<i>Coilia ectenes</i>	Engraulidae	3/16.7	2/8.3				1/8.3		
<i>Setipinna tay</i>	Engraulidae	2/8.3				1/8.3	1/8.3		
<i>Anchoiella commersonii</i>	Engraulidae	46/16.7	100/25	7/16.7	2/16.7	1/8.3		4/16.7	2/8.3
<i>Engraulis aponicas</i>	Engraulidae	22/25	119/25	8/16.7	6/8.3	1/8.3	1/8.3	12/16.7	1/8.3
<i>Thrissa mystax</i>	Engraulidae	23/16.7	4/25	2/8.3	2/16.7	3/16.7	1/8.3	2/8.3	11/16.7
<i>Sphyræna japonica</i>	Hemiramphidae	1/8.3							
<i>Lophius litulon</i>	Lophiidae				2/8.3				6/16.7
<i>Stephanolepis cirrhifer</i>	Monacanthidae	2/16.7	2/16.7			6/25	4/8.3	7/25	
<i>Plotosus anguillaris</i>	Plotosidae	6/25	66/25					10/25	1/8.3
<i>Eleutheronema tetradactylum</i>	Polynemidae	2/8.3	5/16.7			1/8.3	1/8.3		2/8.3
<i>Collichthys lucidus</i>	Sciaenidae			1/8.3					
<i>Argyrosomus argentatus</i>	Sciaenidae	3/8.3				1/8.3			
<i>Larimichthys crocea</i>	Sciaenidae	4/25			2/16.7				1/8.3
<i>Larimichthys polyactis</i>	Sciaenidae	92/58.3	95/41.7	44/75	36/66.7	17/8.3	4/16.7	15/33.3	17/33.3
<i>Nibea japonica</i>	Sciaenidae				39/8.3		1/8.3	11/8.3	
<i>Scomberomorus niphonius</i>	Scombridae		5/8.3						2/16.7
<i>Scomber japonicas</i>	Scombridae		10/16.7						
<i>Pampus argenteus</i>	Stromateidae	3/16.7	5/16.7	2/8.3					
<i>Takifugu oblongus</i>	Tetrodontidae				1/8.3			3/8.3	
<i>Pelates quadrilineatus</i>	Theraponidae			2/8.3	1/8.3			2/8.3	
<i>Trichiurus haumela</i>	Trichiuridae	1/8.3		5/16.7	2/8.3				
<i>Chelidonichthys kumu</i>	Triglidae	3/8.3							2/8.3
Casual/rare species									
<i>Navodon modestus</i>	Aluteridae				1/8.3	1/8.3			
<i>Goniistius quadricornis</i>	Cheilodactylidae							1/8.3	
<i>Ilisha elongata</i>	Clupeidae				1/8.3				1/8.3
<i>Cynoglossus gracilis</i>	Cynoglossidae								1/8.3
<i>Elops saurus</i>	Elopidae			1/8.3					
<i>Oplegnathus punctatus</i>	Oplegnathidae						1/8.3		
<i>Hapalogenys mucronatus</i>	Pomadasyidae						1/8.3		
<i>Epinephelus akaara</i>	Serranidae							1/8.3	
<i>Sillago sihama</i>	Sillaginidae							1/8.3	
<i>Sillago japonica</i>	Sillaginidae		1/8.3						
<i>Hyporhamphus sajori</i>	Sphyraenidae							1/8.3	
<i>Takifugu niphobles</i>	Tetrodontidae	1/8.3							
67 species	39 families	1090	1529	566	576	552	290	421	411