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Long-term variations in trophic groups of coral reef fishes in the lagoon of Meiji Reef in the South China Sea

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Fishes play significant ecological functions though many ways in coral reef, and feeding process is one of the most important. To understand responses of reef fish communities to external disturbances, we studied variations in trophic groups of fishes in the lagoon of Meiji Reef in the South China Sea based on fish specimens collected by hand-line and gillnet in 1998–2018, databases and literatures. Differences in species richness, abundance, weight and size of fish in different trophic groups among years were analysed, especially herbivorous and high-economy fish. The results indicated that the percentages of species number and weight of herbivores, piscivores and detritivores decreased significantly from 1998–1999/2016–2018. Herbivorous fishes saw the biggest decline. In the gillnet surveys, the percentages of species number and weight of herbivorous fishes in 1999 were 33.33% and 56.14%, respectively, while the percentages in 2016–2018 were all zero. The species number percentage of large-sized fishes (maximum total length ≥ 65 cm) in 1998–1999 was significantly larger than that in 2016–2018. Thirty-two fish species being found in the lagoon of Meiji Reef during 1998–1999 were not discovered during 2012–2018. Contingency table analysis showed that the disappearance of fish was not significantly related to the vulnerability or resilience of fish rather than economic value. The mean body weight of very high & high-value fish in 1998–1999 was significantly larger than that in 2016–2018. Simple linear regression showed that coral cover had the greater effect on the species number and weight of herbivorous fishes as compare to fishing power. Both fishing power and coral cover had significant effects on the mean body weight. To protect fish on Meiji Reef, we propose to strengthen the conservation initiatives (e.g., creating protected areas, prohibiting fishing, and reconstructing habitat).

KEYWORDS

trophic group, herbivorous fishes, coral cover, fishing, contingency table analysis

Introduction

Coral reefs are among the most productive and diverse marine ecosystems, and provide a multitude of ecosystem services and support a myriad of fishes (Moberg and Folke, 1999; Bellwood et al., 2004; Smith, 1978). However, over the past few decades, coral reefs and associated fishes have sharply degraded because of multiple threats (e.g. rising ocean temperature and unsustainable fishing (Allgeier et al., 2016; Hughes et al., 2017; Munday et al., 2008). The South China Sea (SCS) is a globally significant area because of its shallow coral reefs and high biodiversity (Chen and Li, 2005; Arai, 2015; Li et al., 2021; Lu et al., 2021; Dai et al., 2022; Li et al., 2022). Under multiple stressors of human activities and climate change, the coral cover in the SCS has severely declined within the past few decades, and coral reef fish populations have receded (Hughes et al., 2013; Zhao et al., 2013; Zhao et al., 2016; Hughes et al., 2017; Zhang et al., 2021a; Zhang et al., 2021b).

Fish are important components of coral reefs, play significant ecological functions though many ways in coral reef, and feeding process is one of the most important (Berumen et al., 2005; Munday et al., 2008; Cole et al., 2010; Roberts, 1995). Therefore, the knowledge of reef fish feeding is of great significance for protecting fishery resources and diagnosing health status of coral reefs (Letourneur et al., 2013; Hempson et al., 2017; Morillo-Velarde et al., 2018). Dividing reef fish into different trophic groups according to their prey is helpful to study their ecological roles and how fishing and climate alter the structure of reef fish (Gao et al., 2014; Wilson et al., 2021; Dai et al., 2022). For example, herbivorous fishes in coral reef can inhibit algal overgrowth and promote coral growth, which is important for the recovery of bleached coral (Cramer et al., 2017; Rempel et al., 2020; Wilson et al., 2021). Piscivorous fish are probably the most significant consumers of fish biomass and in most reef systems will consume considerably more fish biomass than is removed by fishing (Grigg et al., 1984). The removal of piscivorous fish may have repercussions throughout the ecosystem (Jennings et al., 1995). In the SCS, Although some studies have focused on feeding and trophic levels of reef fish (Zhang et al., 2006; Yang et al., 2012; Gao et al., 2014; Zhang et al., 2022), little research has revealed the long-term variations in the structure of their trophic groups.

Meiji Reef (9°55′N, 115°32′E) is located in the SCS near the western border of the Coral Triangle, and is a typical atoll (Figure 1). The reef is a semi-closed and oval-shaped shallow tropical atoll, which is 9 km long (east-west) and 6 km wide (north-south) and covers a total area of 56.6 km^2. This reef is characterized by a large lagoon with a maximum water depth of 30 m, which is surrounded by a ring of reef flat, which is typically 0—3 m below the low tide level (Zhao et al., 2013). Three channels connect the lagoon to the open ocean. The reef flat in the northwest is about 3 km long and 0.8 km wide, and the reef flat in the southeast is more than 4 km long and 0.3 km wide. Meiji Reef was rich in fish, although fishing activity was frequent (Li et al., 2007). Regular surveys of fish in the lagoon of Meiji Reef conducted by South China Sea Fisheries Research Institute since the 1990s provided the foundation for studying long-term variations in reef fish communities.

To understand responces of coral reef fish communities under external disturbances in the SCS and provide some valuable information for their conservation, we studied variations in trophic groups of fishes in the lagoon of Meiji Reef based on fish specimens collected by hand-line and gillnet in 1998—2018, databases and literatures. Differences in species richness, abundance, weight and size of fishes in different trophic groups among years were analysed, especially herbivorous and high-economy fish. The relationships between fish disappearance and diet, resilience, vulnerability, and economic value were explored by contingency table analysis. The effects of fishing effort and coral cover on herbivorous and high-economy fish were tested by simple linear regression model.

Materials and methods

Study area and fish specimen collection

The study site was located at the lagoon of Meiji Reef in the SCS (Figure 1). Fish specimens were collected by hand-line in 1998—1999 and 2017—2018 and gillnet in 1999, 2012, 2016—2018 (Table 1). The working depth of hand-lines with barbed hooks was ~20 m, with fresh shrimp as bait and sampling was performed during the day (08:00—10:00 and 14:00—18:00). The working depth of gillnets was ~20 m, and sampling was usually performed during the day, although occasionally extended to the next morning (06:00). For each survey, four sites were established to cover the lagoon. GPS was used to ensure that the same sites are being sampled. The sampling sites were restricted to the lagoon. South China Sea Fisheries Research Institute conducted all surveys.

The time, site, and fish-catcher of each specimen were recorded. Each specimen was identified to the lowest taxonomic category based on morphological characteristics and Nelson's classification system (Nelson, 2006). Live fish were euthanized using MS-222 before being processed. Specimens were immersed in seawater and frozen (−20°C) for shore-based analysis. Wet body weight was measured using electronic scales to the nearest 0.01 g.

In 1998 and 1999, surveys were undertaken onboard the vessel R/V *Fisheries Administration* (300 GT, 44.40 m long, and 8.00 m wide) and commercial fishing vessel F/V *Yueyu 730* (98 GT, 26.50 m long, and 5.30 m wide). During 2012—2018, surveys were undertaken onboard the R/V *Nanfeng* (1537 t GT, 66.66 m long, and 12.40 m wide) equipped with a motorboat for samping (1 GT, 7.85 m long, 1.50 m wide, and compression-ignition internal combustion engine). The total species number, abundance, weight and sampling effort of fish specimens were presented in Table 2.

Trophic groups and fish size

Based on published literatures (Jennings et al., 1995; Gao et al., 2014), fishes were categorized into seven trophic groups:

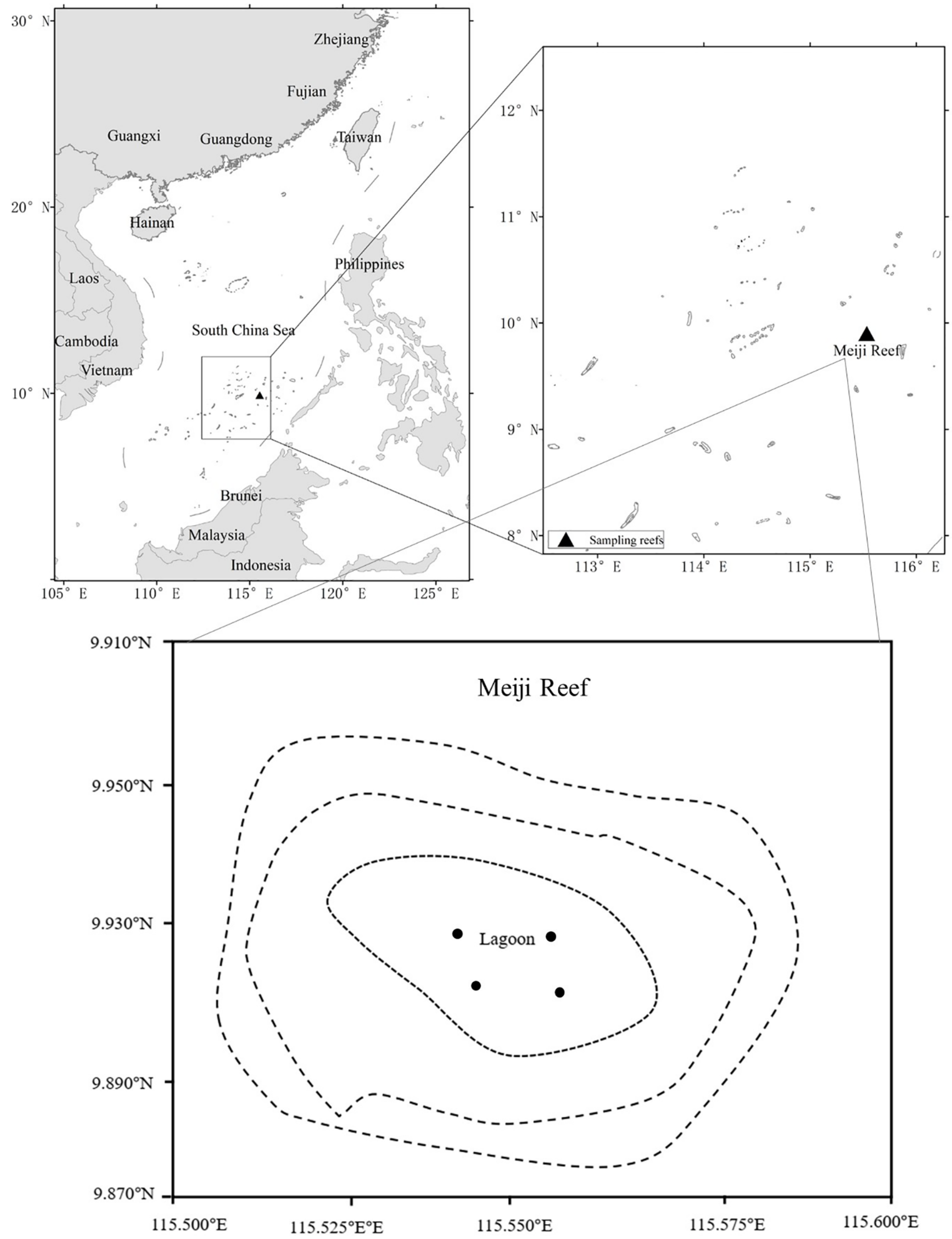

FIGURE 1
Study area (Meiji Reef lagoon) in the South China Sea. ●: approximate fishing sites.

piscivores (pi), invertebrate feeder & piscivores (ip), invertebrate feeders (iv), omnivores (om), planktivores (pk), detritivores(dt), and herbivores (hb). The primary information on the trophic groups of fishes was from literatures and databases (Zhang et al., 2006; Gao et al., 2014; Shao, 2019; Froese and Pauly, 2020; Liveaquaria, 2022). Those fish whose diet could not be determined were analyzed separately by gastric contents. The species composition of fish specimen among years was analysed, including corresponding number and weight. Differences in fish species richness and weight of different trophic groups among years were analyzed using the Mann-Whitney (M–W) and Kolmogorov-Smirnov (K–S) tests. In this study, the species percentage and weight percentage of fish across trophic groups among different surveys were calculated as follows:

$$Species\ \ percentage_{i,y} = Species\ \ number_{i,y} / \sum_{j=1}^{m} Species\ \ number_{j,y} \times 100\,\%$$

TABLE 1 Specifications of hand-line and gillnet used for fish collection in the lagoon of Meiji Reef in the South China Sea.

M/Y	Net and specifications
05/1998	Hand-line, hook with barb, size: 26.0 mm total length, 10.0 mm gape size, 1.0 mm thickness, 0.33 mm diameter nylon wire, # of lines: 9, working time: 3 h
05/1999	Hand-line (same specifications as May 1998), # of lines: 10, working time: 2 h; gillnet: 40 m length, 1.1 m height, 5.5 cm mesh size, 0.20 mm diameter nylon wire, # of sets: 26, working time: 2 h
09/2012	gillnet: (same specifications as May 2016), # of sets and working time: no valid record
05/2016	gillnet: 50 m length, 1.5 m height, 3.3 cm inner mesh size, 7.8 cm inner mesh size, 0.20 mm diameter nylon wire, # of sets: 7, working time: 4 h
05/2017	Hand-line (same specifications as May 1998), # of lines: 20, working time: 8 h 15 min; gillnet: (same specifications as May 2016), # of sets: 9, working time: 11 h 30 min
12/2017	Hand-line (same specifications as May 1998), # of lines: 15, working time: 5 h 12 min; gillnet: (same specifications as May 2016), # of sets: 3, working time: 6 h 48 min
05/2018	Hand-line (same specifications as May 1998), # of lines: 20, working time: 6 h 38 min; gillnet: (same specifications as May 2016), # of sets: 9, working time: 8 h
09/2018	Hand-line (same specifications as May 1998), # of lines: 20, working time: 7 h 18 min; gillnet: 50 m length, 1.1 m height, 2.0 cm inner mesh size, 7.0 cm inner mesh size, 0.20 mm diameter nylon wire, # of sets: 6, working time: 7 h

$$Weight\ \ percentage_{\mathrm{i,\,y}} = Weight_{i,\,y}/\sum_{j=1}^{m} Weight_{\mathrm{j,\,y}} \times 100\,\%$$

where species $\mathrm{number}_{\mathrm{i,y}}$ and $\mathrm{weight}_{\mathrm{i,y}}$ are the species number and weigtht of fish in *i*th trophic group in the *y*th survey, respectively, and species $\mathrm{number}_{\mathrm{j,y}}$ and $\mathrm{weight}_{\mathrm{j,y}}$ are the species number and weigtht of fish in the *j*th trophic group (pk、pi、om、iv、ip、hb or dt) in the *y*th survey, respectively.

Maximum total length of fish was obtained from FishBase (Froese and Pauly, 2020). According to the maximum total length, fishes were divided into three types, namely small-sized fish: maximum total length< 35 cm, medium-sized fish: 65 cm > maximum total length ≥ 35 cm, large-sized fish: maximum length ≥ 65 cm (Wang et al., 2022). We analyzed difference of fish size between 1998—1999 and 2016—2018. The species number and

TABLE 2 Total species number, abundance, weight and sampling effort of fish specimens in the lagoon of Meiji Reef in the South China Sea during 1998—2018.

Method	Year	Species number	Abundance (individual)	Weight (g)	Sampling effort
gillnet	05/1999	30	106	17237	2282
	09/2012	12	/	/	/
	05/2016	12	34	4116	2100
	05/2017	14	71	3312	7762
	12/2017	13	39	6365	1538
	05/2018	9	25	12103	5400
	09/2018	13	67	12876	2310
Hand-line	05/1998	19	76	24600	2700
	05/1999	19	42	8047	2000
	05/2017	43	462	34278	16500
	12/2017	33	273	39389	7800
	05/2018	29	295	16539	13250
	09/2018	39	445	23247	14600

The unit of sampling effort in gillnet surveys was "m^2 h". The sampling effort in the gillnet is calculated by the following formula: $n_G \times L_{G\times} H_G \times T_G$, where n_G and T_G (h) are # of gillnets and working time, respectively; and L_G (m) and H_G (m) are length and height of gillnet, respectively. The unit of sampling effort in hand-line surveys is "100 lines h". The sampling effort in the hand-line is calculated by the following formula: $n_H \times T_H$, where n_H and T_H (h) are # of lines and working time, respectively (Dai et al., 2022).

total weight of hb fish in gillnet surveys among years were analyzed in particular, as was the total weight and mean body weight of high-value fish among years.

Fish disappearance and contingency table analysis

Using Fishbase database (Froese and Pauly, 2020), we collected information on resilience, vulnerability, and economic value of fish. Resilience included four grades: i.e., very low (VL), low (L), moderate (M), and high (H). Vulnerability included six grades: i.e., low (L), low-moderate (L-M), moderate (M), moderate-high (M-H), high (H), and very high (VH). Economic value included four grades: i.e., low (L), moderate (M), high (H), and very high (VH). We used contingency table analysis to explore the relationships between fish disappearance and diet, resilience, vulnerability, and economic value (significance = 0.05). The size of fish that disappeared was also analysed.

Fishing effort and coral cover

The fishing effort of coral reef fish on Meiji Reef was from the Fishermen's Association of Nansha Islands Taishan City, China. The association is a voluntary civil organization of fishermen. Fishermen in Taishan City are the main catchers of coral reef fish in the Nansha Islands. They have been catching coral reef fish on Meiji Reef and adjacent reefs since the early 1990s. The main methods of operation were hand-line, diving and gillnet. The fishing effort from 1998 to 2018 is indicated by the total horsepower of fishing boats.

Information on the coral cover of Meiji Reef in this paper came from published literatures and personal communication. Zhao et al. (2013) reported that the coral cover of Meiji Reef was 28.31% in 2007. According to literatures (Hughes et al., 2013; Zhao et al., 2013), we simply speculated that the coral cover of Meiji Reef was between 60% and 50% in 1998 and 1999. During 2016—2018, the coral cover of Meiji Reef ranged from 12%—15% with an average cover of 14% (personal communication).

Simple linear regression model (SLM) was used to test the effects of fishing effort and coral cover on the percentages of species number and weight of hb fish in gillnet surveys, and the weight percentage and mean body weight of very high & high-value fish in gillnet and hand-line surveys.

Results

Fish list

From 1998 to 2018, there were 166 fish species sampled in present study in the lagoon of Meiji Reef, belonging to 33 families. The composition of diet, trophic level, resilience, vulnerability and economic value of these fishes was present in the Figure 2 and Supplementary 1.

Among 166 species, there were fourteen hb fish species, including 10 parrotfishes, 3 rabbitfishes and 1 surgeonfish. The lowest trophic level of fish was 2.00, including twelve hb fish species and four dt fish species. The highest trophic level of fish was 4.50, including two ip fish species and two ip fish species. The vulnerability of most fishes was not high. The number of fish species with vulnerability ≥ H only accounted for 10.2% of total species. As viewed from resilience, the number of fish species with resilience = M and H accounted for 44.6% and 36.1% of total species, respectively. Six fish species had extremely low resilience, including *Taeniurops meyeni*, *Maculabatis gerrardi*, *Neotrygon kuhlii*, *Acanthurus nigricans*, *Epinephelus bruneus* and *Gymnothorax undulatus*. Regarding economic value, the number of fish species with economic value ≥ H accounted for 50.6% of total species. Among 31 high-value species, there were 15 parrotfishes. Among 53 very high-value species, there were 17 Serranidaes, 14 Lethrinidae, 11 Labridae and 6 Lutjanidae.

Variations in trophic group and size distribution

The species richness, abundance percentage and weight percentage of different trophic fish in 1998—1999 and 2016—2018 are presented in Figure 3 and Figure 4. The absolute abundance and weight of different trophic fish in the lagoon of Meiji Reef between 1998—1999 and 2016—2018 in a figure as support information (Supplementary 2). The species richness and weight composition of trophic groups in 2016—2018 were significantly different with 1998—1999 (M−W and K−S tests, $p< 0.01$). In 1999, the fish by gillnet was framed by six trophic groups, except there was no pk fish. In contrast, in 2016—2018, some trophic groups disappeared (e.g. hb and pi fish) and the structure of trophic groups became incomplete.

The species number and weight percentages of hb, pi and dt fish had a significantly decline from 1998—1999/2016—2018 (ANOVA, $p< 0.01$). The hb fish saw the biggest decline. However, there was a noticeable rise in the species number and weight percentages of om and iv fish from 1998—1999/2016—2018. For example, from 1999 to 2018, the species number percentages of om fish increased from 5.3% to 10.3%, and the corresponding weight percentages increased from 1.0% to 16.4%. Notably, the species richness, frequency and weight of pk fish was very low.

Regarding fish size, the species number percentages of large-sized fishes in 1998—1999 were significantly larger than that in 2016—2018 (ANOVA, $p< 0.01$) (Figure 5).

Disappeared fishes

According to survey period, we divided fish specimens into two groups (1998—1999 and 2012—2018) and found 64 fish species in 1998—1999, of which 32 were not present in 2012—2018 (Table 3). These disappeared fish included 14 families, with marked reductions in fish of Scaridae, Siganidae and Lethrinidae, and the composition of

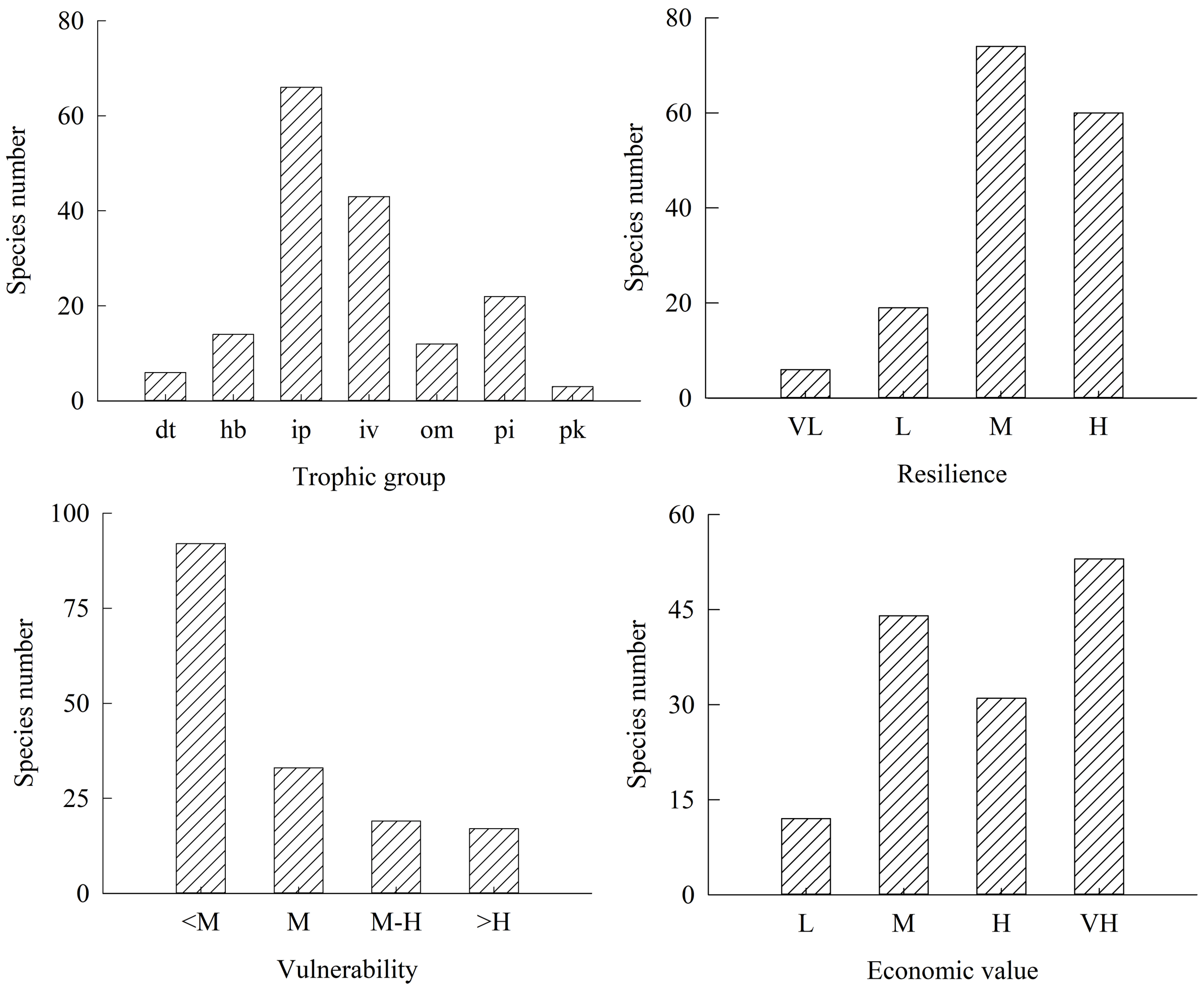

FIGURE 2
Number of fish species for different diet, vulnerability, resilience and economic value in the lagoon of Meiji Reef in the South China Sea. The dt, hb, ip, iv, om, pi and pk mean detritivores, herbivores, piscivores, invertebrate feeders, omnivores, invertebrate feeder & piscivores, and planktivores, respectively. The VL, L, M, M-H, H, and VH mean very low, low, moderate, moderate-high, high, and very high levels, respectively.

their diet, vulnerability, resilience and economic availability of these disappeared fish species was presented in the Figure 6.

Among disappeared fish, hb and ip fish accounted for the highest percentages. Species with high resilience and species with low vulnerability accounted for the highest percentages of disappeared fish, suggesting that high resilience and low vulnerability did not prevent disappearance. Very high and high-value species accounted for 34.37% and 37.50% of disappeared fish, respectively, indicating that the higher the economic value of fish, the higher the disappearance risk.

Contingency table analysis indicated that economic value was significantly associated with the disappearance of fish ($p< 0.01$). The disappearance of high economic hb and ip fish was the most noticeable. There were no significant correlations between disappearance of fish and resilience and vulnerability ($p > 0.05$).

Among disappeared fish, medium-sized fish was the most abundant, accounting for 53.13%, followed by small-sized fish with 31.25%, and large-sized fish with 15.63% (Figure 7).

Variations in weight and mean body weight of fish with high economic value

In gillnet and hand-line surveys, the mean body weight of very high & high-value fish in 1998—1999 was significantly larger than that in 2016—2018 (ANOVA, $p< 0.01$) (Figure 8). in gillnet surveys, the weight percentage of very high & high-value fish in 1999 was significantly larger than that in 2016—2018 (T-test, $p< 0.01$). In hand-line surveys, the weight percentage in 1999 has barely changed from the percentages in 2016—2018, which was attributed to the fact that hand-line has been selective in catching carnivorous high value fish (ANOVA, $p > 0.01$).

Effects of fishing effort and coral cover on fish

In the gillnet surveys, the percentages of species number and weight of hb fish in 1999 were 33.33% and 56.14%, respectively,

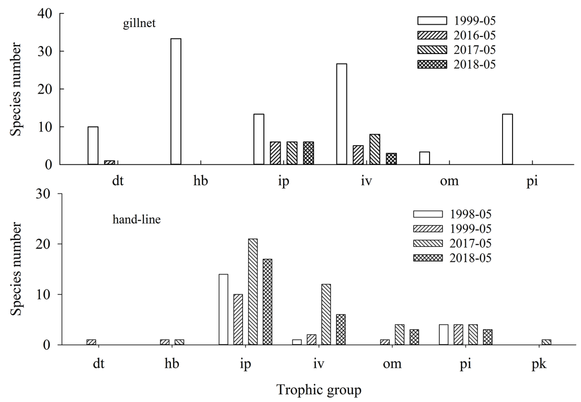

FIGURE 3
Species number of different trophic fish in the lagoon of Meiji Reef in the South China Sea between 1998—1999 and 2016—2018. The dt, hb, ip, iv, om, pi and pk mean detritivores, herbivores, piscivores, invertebrate feeders, omnivores, invertebrate feeder & piscivores, and planktivores, respectively.

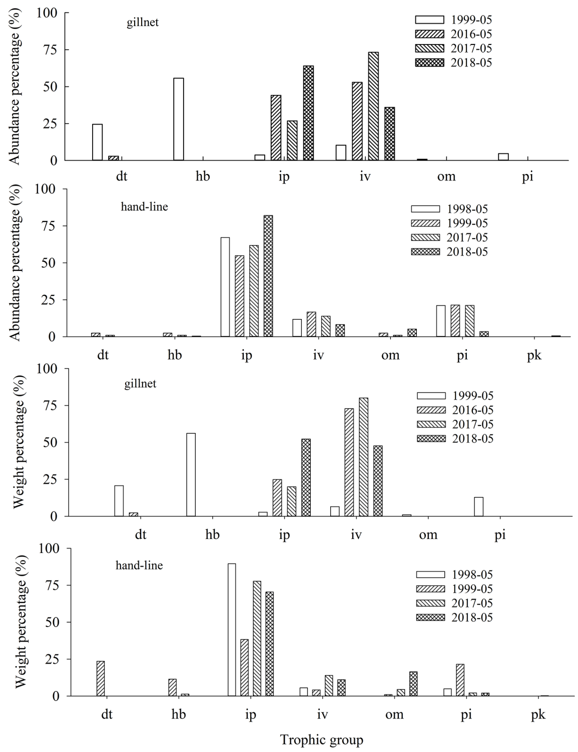

FIGURE 4
Abundance and weight percentage of different trophic fish in the lagoon of Meiji Reef in the South China Sea between 1998—1999 and 2016—2018. The dt, hb, ip, iv, om, pi and pk mean detritivores, herbivores, piscivores, invertebrate feeders, omnivores, invertebrate feeder & piscivores, and planktivores, respectively.

while the percentages in 2016—2018 were all zero (Figure 9). Results of linear regression indicated that coral cover had the greater effect on the percentages of species number and weight of hb fish as compare to fishing power (Figure 9; Table 4).

In addition, results of linear regression indicated that coral cover had the greater effect on the weight percentage of very high & high-value fish as compare to fishing power in gillnet surveys (Figure 10; Table 5). The effect of coral cover on weight percentage of very high & high-value fish was more pronounced in gillnet surveys than in hand-line survey. Both fishing power and coral cover had significant effects on the mean body weight of high

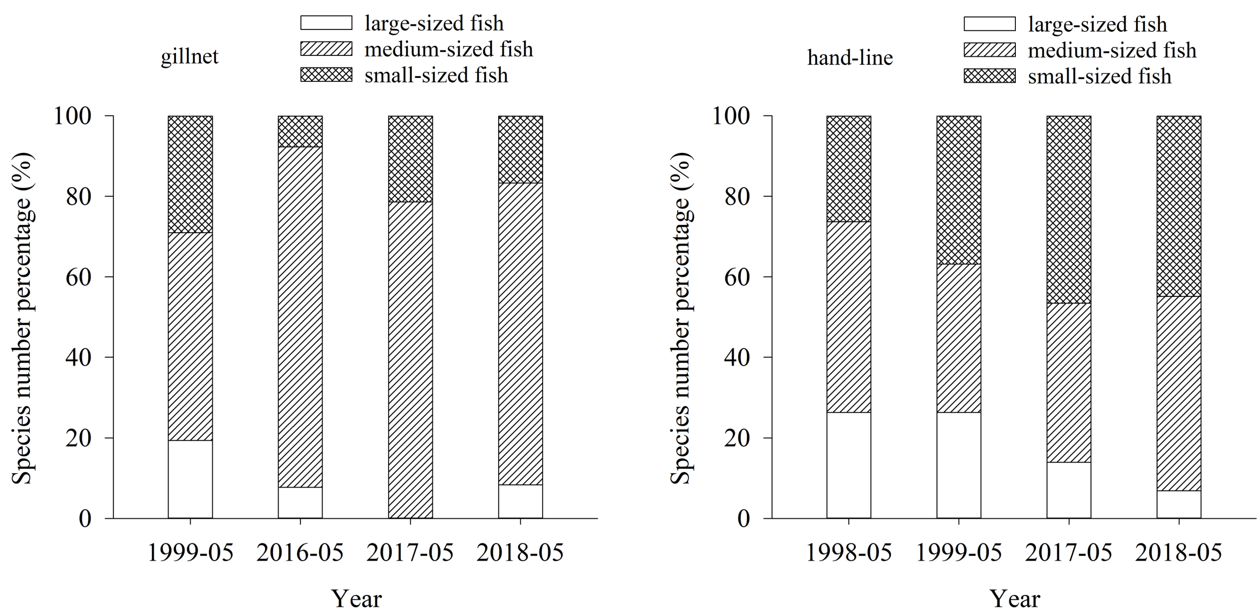

FIGURE 5
Distribution of fish size in the lagoon of Meiji Reef in the South China Sea between 1998—1999 and 2016—2018.

TABLE 3 32 fish sampled in 1998—1999 from the lagoon of Meiji Reef were not detected in 2012—2018.

Order	Family	Species	Diet	Resilience	Vulnerability	Economic value
1	Acanthuridae	*Acanthurus nigrofuscus*	dt	M	L–M	M
2	Acanthuridae	*Acanthurus triostegus*	dt	M	L	M
3	Scaridae	*Calotomus spinidens*	hb	H	L	H
4	Scaridae	*Scarus longiceps*	hb	H	L–M	H
5	Scaridae	*Scarus dimidiatus*	hb	H	L–M	H
6	Scaridae	*Scarus forsteri*	hb	H	L–M	H
7	Scaridae	*Scarus janthochir*	hb	M	M	H
8	Scaridae	*Scarus psittacus*	hb	H	M	H
9	Scaridae	*Scarus scaber*	hb	H	L	H
10	Siganidae	*Siganus fuscescens*	hb	H	L	H
11	Siganidae	*Siganus oramin*	hb	M	L	H
12	Siganidae	*Siganus vulpinus*	hb	M	L	H
13	Labridae	*Epibulus insidiator*	iv	L	H	VH
14	Labridae	*Choerodon anchorago*	iv	M	M–H	VH
15	Labridae	*Anampses meleagrides*	iv	M	L–M	VH
16	Pentapodidae	*Pentapodus macrurus*	om	H	L	Unknown
17	Apogonidae	*Apogon trimaculatus*	iv	H	L	Unknown
18	Chaetodontidae	*Chaetodon selene*	iv	H	L	Unknown
19	Chaetodontidae	*Chaetodon trifasciatus*	iv	H	L	Unknown
20	Balistidae	*Melichthys vidua*	om	M	L–M	M
21	Lutjanidae	*Aphareus furca*	ip	M	M	VH
22	Lutjanidae	*Aphareus rutilans*	ip	M	H	VH
23	Carangidae	*Carangoides ferdau*	ip	M	M	M
24	Serranidae	*Epinephelus areolatus*	ip	L	M	VH
25	Serranidae	*Epinephelus fasciatus*	ip	L	M–H	H
26	Serranidae	*Epinephelus trimaculatus*	ip	M	M	VH
27	Lethrinidae	*Lethrinus haematopterus*	ip	M	M	VH
28	Lethrinidae	*Lethrinus kalloperus*	ip	M	M–H	VH
29	Lethrinidae	*Lethrinus lentjan*	ip	M	L	VH
30	Lethrinidae	*Lethrinus variegatus*	ip	M	L–M	VH
31	Sparidae	*Monotaxis grandoculis*	ip	M	M	VH
32	Holocentridae	*Sargocentron furcatum*	ip	H	L	M

& high-value fish. Overall, coral cover had a larger impact than fishing power on the mean body weight (Table 5).

Discussion

Gao et al. (2014) reported that the dominant coral reef fishes belonged to the iv and pk trophic groups in the Xisha Islands of SCS (six reefs: Yongxing Island, Dongdao Island, Lingyang Atoll, Jinyin Island, Huaguang Atoll, and Zhongjian Island), and the abundance and biomass of other trophic groups were both low (e.g. pi, om, and hb), and the proportion of same trophic group between reefs differed greatly. Our present analysis indicated that the species richness and biomass percentage of pk fish were the smallest among trophic groups in the lagoon of Meiji Reef, and the biomass percentage of pk fish in the lagoon of Meiji Reef was also much lower than the six reefs in the Xisha Islands mentioned above, and also lower than the lagoon of Zhubi Reef in the Nansha Islands. The

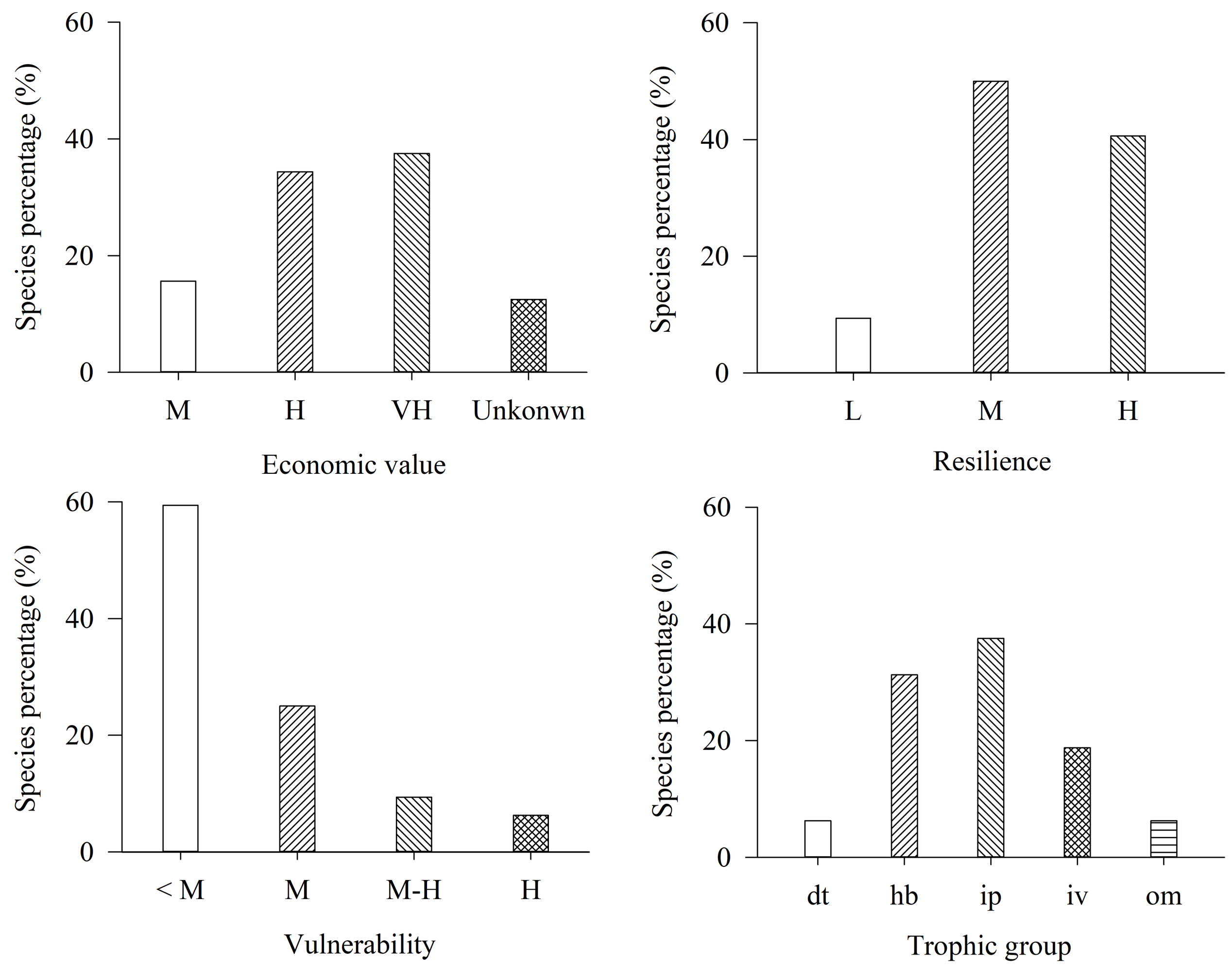

FIGURE 6
Composition of economic value, resilience, vulnerability and trophic group of 32 fish appearing in 1998—1999 but not in 2012—2018 in the lagoon of Meiji Reef. The dt, hb, ip, iv, and om mean detritivores, herbivores, piscivores, invertebrate feeders, and omnivores respectively. The L, M, M-H, H, and VH mean low, moderate, moderate-high, high, and very high levels, respectively.

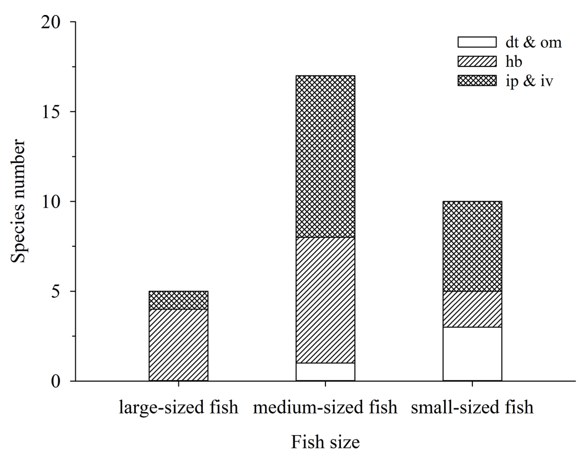

FIGURE 7
Composition of size and trophic group of 32 fish appearing in 1998—1999 but not in 2012—2018 in the lagoon of Meiji Reef. The dt, hb, ip, iv, and om mean detritivores, herbivores, piscivores, invertebrate feeders, and omnivores respectively.

studies of Du et al. (2015) and Yin et al. (2011) indicated that Zhubi Reef had higher densities of planktivores than Meiji Reef. Thus, the low density and biomass of zooplankton in the lagoon of Meiji Reef may be an important factor in shaping low species richness and biomass of pk fish. In coral reef ecosystems, there are generally multiple pathways for nutrient delivery (Thomas and Cahoon, 1993; Morillo-Velarde et al., 2018). Yamamuro et al. (1995) also mentioned that zooplankton was not the main source of nutrient for corals because the $\delta^{15}C$ values of zooplankton were higher or close to the nitrogen isotopic composition of coral. Thus, zooplankton may be not the main hub in the nutrient transfer from primary producers to fishes in the lagoon of Meiji Reef. However, the low species and richness and biomass of pk fish may also be the result of sampling area and fishing tools. Planktivores are much more abundant on outer slope of reefs for the ideal hydrodynamic conditions. Hand-line and gillnet have their limitations on collecting different fish species. Many pk fish may not be easy to be caught in the lagoon by hand-line and gillnet.

In marine ecosystem, in addition to phytoplankton, organic detritus is also the source of nutrients in the food web (Vetter and

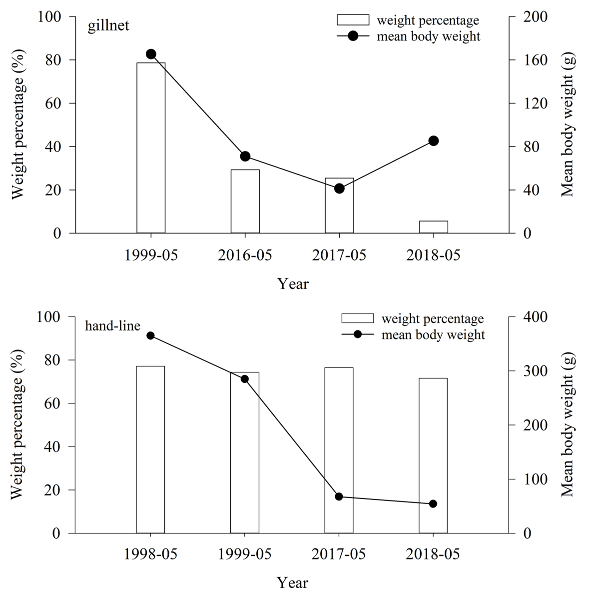

FIGURE 8
Variations in weight percentage and mean body weight of very high & high-value fish between 1998—1999 and 2016—2018 in the lagoon of Meiji Reef.

Dayton, 1999; Anderson et al., 2016; Jensen et al., 2019). Guo et al. (2002) studied trophic relationships among various organisms from Zhubi Reef ecosystem in the Nansha Islands by stable carbon isotope technique, and the great variation in δ^{15}C of zooplankton (-20.4%~-10.9%) in their results suggested that there might be two trophic sources: phytoplankton and detritus. Xu et al. (2010) reported that the Bohai Sea ecosystem could be simplified into three major food chains: phytoplankton→zooplankton→zooplanktivorous fish→nektivore fish (the first food chain), phytoplankton and detritus→benthos→benthivorous fish and cephalopod→nektivore fish (the second food chain), and detritus→detrivorous fish (the third food chain), and since late 1950s, the percentage of biomass made up by fisheries in the third food chain increased continuously and became the second primary fisheries in the Bohai Sea in recent years. Similarly, the study of Letourneur et al. (2013) in two contrasted bays in Moorea of Polynesia indicated that sedimented organic detritus was an important food for fishes *Stegastes nigricans* and *Chaetodon citrinellus*, and the main sources of organic detritus involved in the food webs ending with these species were algal turfs and surface sediments. Thus, the hb and dt fish may also represent two separate nutrient pathways in the lagoon of Meiji Reef.

Compared with that in 1998—1999, some apparent variations were found in the trophic groups of fishes in the lagoon of Meiji Reef in 2016—2018, such as dramatic decrease of hb fish, noticeable increase of om fish, disappearances of some fish, and decline of large-sized fishes. These variations may profoundly impact the structure and function of coral reef ecosystem. For example, the loss of herbivorous fish can hinder recovery of bleached coral and accelerate regime shifts from coral- to algae-dominated states (Rempel et al., 2020; Wilson et al., 2021). Large carnivorous fishes are the top predators in coral reef and control the structure of the ecosystem through predation, and their loss can lead to the explosion of bait species and destroy the balance of coral reef (Roberts, 1995; Bellwood et al., 2004).

In our study, the number of fish species sampled in 1998—1999 was lower than that in 2012—2018, mainly because the survey effort in 1998—1999 was much lower than that in 2012—2018. The total fishing efforts by gillnet and hand-line in 2012—2018 were at least 8 and 11 times that in 1998—1999. Despite this, 32 fish species that were present in 1998-1999 were not sampled in 2012—2018. These disappeared fish may have migrated from the lagoon of Meiji reef, or they have just been fished out and not migrated from the slope,

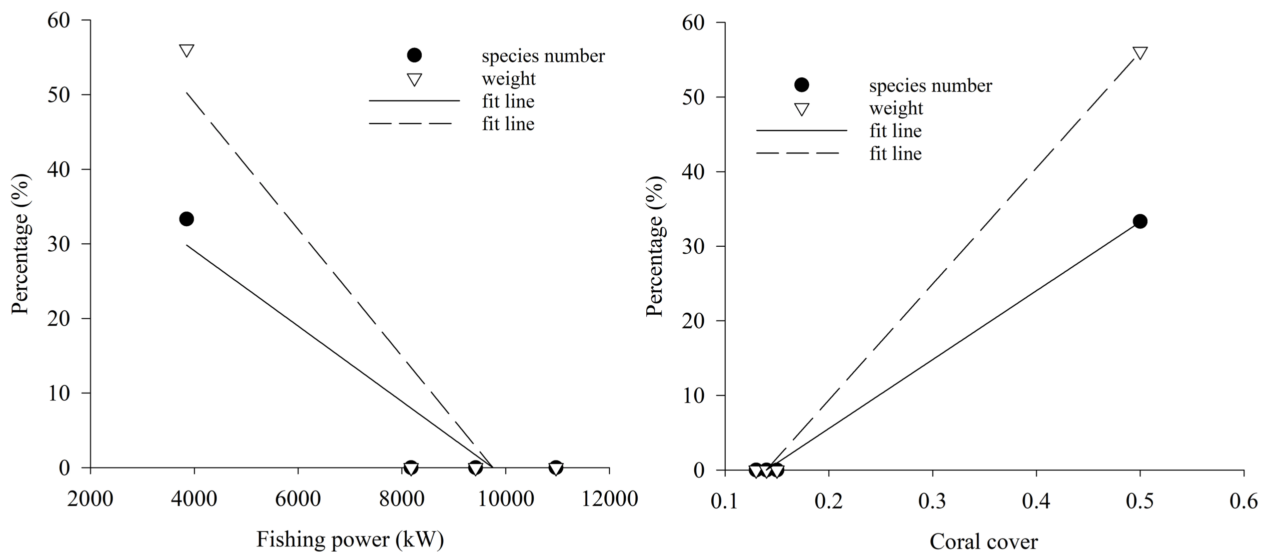

FIGURE 9
Scatter plot and linear fit between percentages of species number and weight of herbivorous fishes by gillnet in the lagoon of in Meiji Reef and fishing power and coral cover in 1999 and 2016—2018.

TABLE 4 Linear fit parameters between percentages of species number (*SN*) and weight (*W*) of herbivorous fishes by gillnet in the lagoon of in Meiji Reef and fishing power (*F*) and coral cover (*CC*).

Fomular	Coefficient	Std. Error	*t*	*p*	R^2_{adj}	AIC
SN% = y0 + a**F*	y0 = 49.316	12.286	4.01	0.057	0.791	30.834
	a = -0.005	0.001	-3.51	0.073		
W% = y0 + a**F*	y0 = 83.067	20.694	4.014	0.057	0.791	35.006
	a = -0.0085	0.002	-3.51	0.073		
SN% = y0 + a**CC*	y0 = -12.918	0.824	-15.70	0.004	0.997	17.259
	a = 92.393	2.964	31.18	0.001		
W% = y0 + a* *CC*	y0 = -21.759	1.387	-15.70	0.004	0.997	21.430
	a = 155.624	4.992	31.18	0.001		

or their abundance in the lagoon has dropped too low to be caught. And the mean body weight of fish in 1998—1999 was significantly larger than that in 2016—2018. Among 32 fish species, there was a significant association between fish loss and economic value, but no association between fish loss and vulnerability and resilience. Economic value was the dominant factor accounting for variations of fish communities in the lagoon of Meiji Reef. In general assumption, fish with high resilience or low vulnerability should be more stable or less likely to disappear when exposed to the same habitat. However, our findings did not support the assumption. We speculated that the true external stress far exceeded resilience limit of fish in the lagoon of Meiji Reef, and

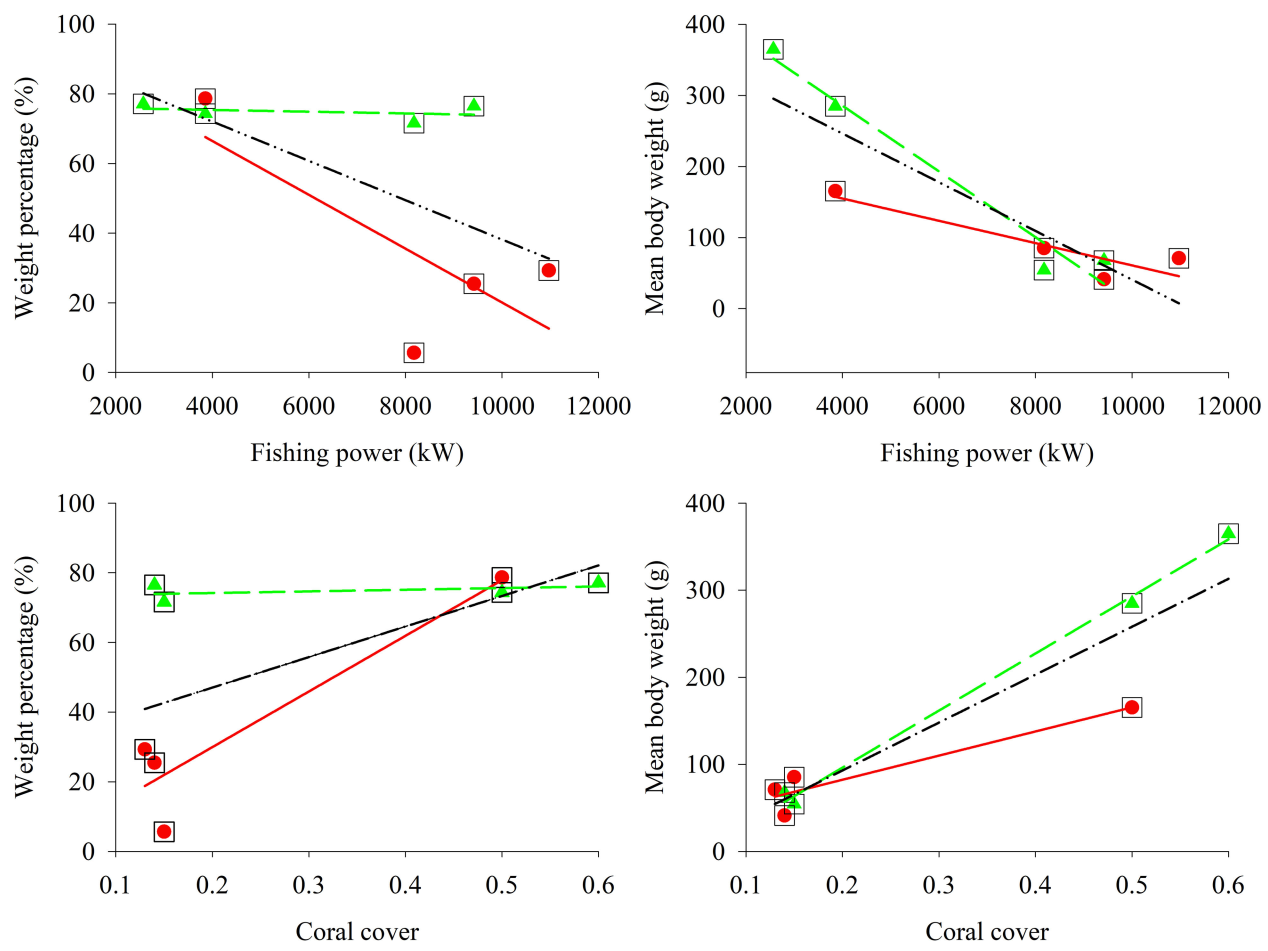

FIGURE 10
Scatter plot and linear fit between weight percentage and mean body weight of very high & high-value fish in the lagoon of in Meiji Reef and fishing power and coral cover in 1998—1999 and 2016—2018. ● and ——: gillnet, ▲ and – – : hand-line, □ and —·· : gillnet & hand-line.

TABLE 5 Linear fit parameters between weight percentage (*W*) and mean body weight (*MBW*) of very high & high-value fish by gillnet and hand-line in the lagoon of in Meiji Reef and fishing power (*F*) and coral cover (*CC*).

Fomular	Coefficient	Std. Error	*t*	*p*	R^2_{adj}	AIC
W% = a**F* + y0 (gillnet)	y0 = 97.378	39.706	2.45	0.134	0.369	3.3012
	a = -0.008	0.005	-1.66	0.239		
W% = a**F* + y0 (hand-line)	y0 = 76.388	3.345	22.83	0.002	0.336	-14.810
	a = -0.0002	0.001	-0.50	0.670		
W% = a**F* + y0 (gillnet & hand-line)	y0 = 94.649	23.384	4.05	0.007	0.256	4.501
	a = -0.006	0.003	-1.85	0.114		
W%=a**CC*+y0 (gillnet)	y0 = -1.989	12.656	-0.16	0.890	0.790	-0.906
	a = 159.747	45.534	3.51	0.073		
W%=a**CC*+y0 (hand-line)	y0 = 28.534	2.678	27.35	0.001	0.270	-15.321
	a = 73.253	6.633	0.711	0.551		
W%=a**CC*+y0 (gillnet&hand-line)	y0 = 29.501	16.230	1.818	0.119	0.264	4.279
	a = 4.717	46.825	1.873	0.110		
MBW = a**F* + y0 (gillnet)	y0 = 217.724	44.788	4.86	0.040	0.725	41.183
	a = -0.016	0.005	-2.98	0.096		
MBW =a**F* + y0 (hand-line)	y0 = 470.594	43.022	10.94	0.008	0.944	43.478
	a = -0.046	0.007	-7.15	0.019		
MBW =a**F*+y0 (gillnet&hand-line)	y0 = 383.4735	53.577	7.16	0.000	0.766	91.502
	a = -0.034	0.007	-4.89	0.003		
MBW =a**CC*+y0 (gillnet)	y0 = 26.852	19.345	1.39	0.300	0.832	39.406
	a = 277.382	69.601	3.99	0.058		
MBW =a**CC*+y0 (hand-line)	y0 = -34.851	12.092	-2.882	0.102	0.994	32.651
	a = 655.492	29.949	21.887	0.002		
MBW =a**CC*+y0 (gillnet&hand-line)	y0 = -17.151	29.983	-0.572	0.588	0.849	88.068
	a = 550.451	86.503	6.363	0.001		

these fishes with different resilience responded similarly when subjected to high external stress.

Fishing and global climate change are the main drivers of the global loss of coral reef fish (Bellwood et al., 2004; Hughes et al., 2013; Allgeier et al., 2016; Hughes et al., 2017). In the northern South China Sea, the ecosystem response was induced by not only anthropogenic activities, but also climate change (Ning et al., 2009). Fishing pressure proved to be the main driver of sharp declines in demersal fish stocks, with high-value species being replaced by low-value ones over time, and fishing effort imposed the most important influence on piscivorous fish (Wang et al., 2019; Zhang et al., 2020; Liu et al., 2021). Our analysis indichated that fishing power and coral cover had greatly effects on variations of fish communities in the lagoon of Meiji Reef, and coral cover had the greater effect on decline of hb fish as compare to fishing power. Significant relationships between reduced mean body weight of high-economy fish in the lagoon of Merji Reef and coral cover and fishing power may reveal the decline and miniaturization of fishes driven by both fishing and coral degradation. To protect fish on Meiji Reef, conservation initiatives (e.g., creating protected areas, prohibiting fishing, and reconstructing habitat) are necessary.

Conclusion

From 1998 to 2018, there were 166 fish species sampled in present study in the lagoon of Meiji Reef, belonging to 33 families.

In 1999, the fish by gillnet was framed by six trophic groups, except there was no pk fish. In contrast, in 2016—2018, some trophic groups disappeared (e.g. hb and pi fish). The species number and weight percentages of hb, pi and dt fish declined significantly from 1998—1999/2016—2018. The hb fish saw the biggest decline. The species number percentages of large-sized fishes in 1998—1999 were significantly larger than that in 2016 —2018.

Thirty-two fish species being found in the lagoon of Meiji Reef during 1998—1999 were not discovered during 2012—2018. There was a significant association between fish loss and economic value, but no association between fish loss and vulnerability and resilience. Economic value was the dominant factor accounting for variations of fish communities in the lagoon of Meiji Reef.

The mean body weight of very high & high-value fish in 1998—1999 was significantly larger than that in 2016—2018. For gillnet, the weight percentage of very high & high-value fish in 1999 was significantly larger than that in 2016—2018. In hand-line surveys, the weight percentage in 1999 has barely changed from the percentages in 2016—2018. Coral cover had the greater effect on percentages of species number and weight of hb fish as compare to fishing power. Both fishing power and coral cover had significant effects on the mean body weight of very high & high-value fish.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Materials, further inquiries can be directed to the corresponding author/s.

Ethics statement

The animal study was reviewed and approved by the South China Sea Fisheries Research Institute Animal welfare committee.

Author contributions

JZ wrote the first draft. JZ, YG, YC, YY and ZC collected fish specimens and performed data analyses. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2023.1122719/full#supplementary-material

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