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Variations in Fish Community Structure at the Lagoon of Yongshu Reef, South China Sea between 1999 and 2016–2019

Xuejiao Dai [1,2], Yuanjie Li [1], Yancong Cai [1], Yuyan Gong [1], Jun Zhang [1,3,*] and Zuozhi Chen [1,3,*]

[1] Key Laboratory of Open-Sea Fishery Development, Ministry of Agriculture and Rural Affairs, South China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Guangzhou 510300, China
[2] Guangdong Provincial Academy of Environmental Science, Guangzhou 510045, China
[3] Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou), Guangzhou 510301, China
* Correspondence: zhangjun@scsfri.ac.cn (J.Z.); zzchen2000@163.com (Z.C.)

Abstract: Owing to climate change and anthropogenic stressors, the abundance and diversity of reef fishes have globally decreased. However, we know little about the long-term change in reef fishes in the South China Sea (SCS). To reveal the response of reef fishes to these threats in the SCS, based on the fish specimens at Yongshu Reef lagoon collected in 1999 and 2016–2019, this study investigated variations in fish composition and community structure. Additionally, we inferred the changes in the coral cover of Yongshu Reef based on the change of the coral cover of near Meiji Reef in the SCS, sea surface temperature (SST) in Yongshu Reef, and total annual catch of Epinephelinae from China in the SCS. We found that compared with 1999, the number of dominant species in 2016–2019 decreased. The relative dominance of the first dominant species increased from 24.46 in 1999 to 39.44 in 2016–2019. Indices of catch per unit effort, species diversity and richness declined from 1999 to 2016–2019. Community pattern changed with some species with a higher trophic level (3.7–4.5) decreased, while those with lower trophic level (2.2–4.1) increased greatly. Some species with high economic value and important ecological functions decreased or disappeared locally. Correlation analysis indicated that declining coral cover, increasing fishing and rising SST were clearly associated with changes in fish community structure at Yongshu Reef. We speculated that declining coral cover and increasing fishing had a direct impact on the degradation of fish communities at Yongshu Reef lagoon, but increasing SST had an indirect impact on that. To conserve coral reef fish, it is recommended to take rigorous measures for improving habitat and protecting resource.

Keywords: coral reef fish; species composition; biodiversity; dominant species; coral cover

Citation: Dai, X.; Li, Y.; Cai, Y.; Gong, Y.; Zhang, J.; Chen, Z. Variations in Fish Community Structure at the Lagoon of Yongshu Reef, South China Sea between 1999 and 2016–2019. *Diversity* **2022**, *14*, 763. https://doi.org/10.3390/d14090763

Academic Editor: Stuart Kininmonth

Received: 16 August 2022
Accepted: 13 September 2022
Published: 15 September 2022

1. Introduction

Coral reefs are ecosystems with some of the highest biodiversity that supports a range of vital recreational and commercial fisheries operating in the region [1]. Available data showed that the annual catch of the coral reef fishery reached millions of tons valued at USD 6.8 billion [2]. Some coral reef fishes ecologically function as top predators, which helps to regulate the balance of coral reef ecosystems [3], while herbivorous species restrain the establishment and growth of microalgae, which is beneficial for the restoration of degraded coral reefs [4,5]. In recent years, the abundance, species diversity, and biomass of coral reef fishes have evidently decreased owing to the combined impact of climate change and human activities [2,6,7]. These declines not only threaten the livelihoods of coastal fishers but also weaken the health of coral reef ecosystems [8–10]. Researchers have long focused on how to maintain a balance between the social and economic benefits of the coral reef fishery and the stability of the ecosystem. This requires investigations of the evolving process and driving mechanisms that determine the community composition and structure of coral reef fish.

To protect and restore coral reef ecosystems and promote sustainable coral reef fishery, it is essential to investigate the response of coral reef fishes to long-term climate change and fishing pressure. Thus far, numerous studies have compared the species composition and structure of reef fishes before and after coral bleaching events driven by global warming [8,11,12]. The results showed that changes under deteriorating climate change decreases in fish biomass, richness and fatness, and length at sexual maturation.

The South China Sea (SCS) in the tropical and subtropical region is the largest marginal sea in the west Pacific Ocean. The densely populated in mainland China and Taiwan province, the Philippines, and Great Sunda Islands, and the Indo China Peninsula geographically surrounding the SCS. There are thousands of fish species with high species diversity and low taxonomic diversity in the SCS [13,14]. These fishes include rich pelagic commercial fishes (such as tuna), continental shelf demersal fishes (such as Priacanthidae and Nemipteridae), and many coral reef fishes (such as parrotfish and Epinephelus) [15,16]. These lucrative fisheries are crucial for the food security and employment of millions of people around the SCS. Coral reefs in the SCS are close to the global center of marine biodiversity known as the Coral Triangle [17], with a high diversity of corals and associated reef fishes. Although coral reef fishes are not as abundant as pelagic fishes and shelf demersal fishes, they are highly valued and well loved. However, they are also vulnerable to uncontrolled human activity. In the coral reefs of SCS, commercial fisheries are far more valuable than recreational fisheries, and gain more attention [14,18,19]. For coral reef fishes in the region, artisanal fisheries mainly include fishing by diving and fishing by hand-line, and there are also some destructive fishing activities, such as overfishing, poison fishing and blast fishing [18,20,21].

Under the dual influence of human activities and climate change, live coral coverage on reefs in the SCS have decreased by ~80% over three decades [18,22], and associated reef fish density and the quantity of large fish have likewise significantly decreased [19,23,24]. This situation endangers the sustainable use of fishery resources and ecological security in the SCS [23–25]. Notably, long-term data of associated reef fish in this area can be difficult to acquire owing to the remoteness of voyages, rough seas, and a complex political environment, thus relevant research has been performed only within a time span of less than 10 years [23,24]. Whereas short-term assessments are inadequate for revealing changes of associated reef fish communities under long-term threats. Hence, constraints to field research of associated reef fish in the SCS have limited our understanding of the response of coral reef fish community to natural and anthropogenic threats, which in turn has hindered science-based fishery management in the region.

Yongshu Reef is located in the southwest of the Nansha Islands, SCS (Figure 1). It is about 450 km to the western border of the Coral Triangle, a global center of marine biodiversity. Available data indicate that Yongshu Reef has rich fish resources, although fishing activity is frequent [15,26]. Regular surveys of associated reef fishes at Yongshu Reef lagoon of the SCS conducted since the 1990s provided us with long-term data for studying variation in reef fish community under external threats. This study begins with a description of the study area and the data sources. The data were normalized and used to calculate indices of similarity and biodiversity. With these data, we also analyzed the species composition and main dominant species. The findings reveal long-term changes in the associated reef fish community at Yongshu Reef, and provide some valued information for conservation and management of associated reef fish in the SCS.

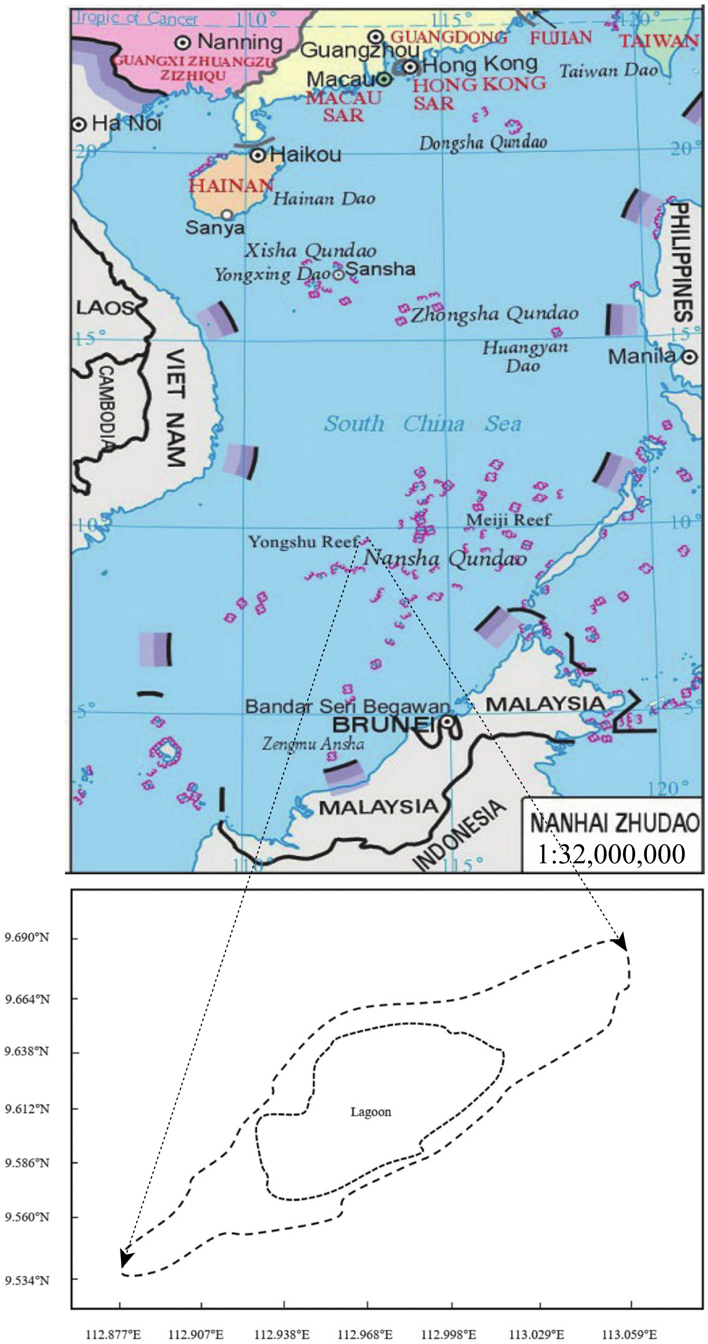

Figure 1. Study area: Yongshu Reef in the South China Sea.

2. Materials and Methods

2.1. Study Area

Yongshu Reef is a semi-open atoll located in the Nansha Islands of the SCS (9°32′–9°42′ N, 112°52′–113°04′ E); it is ~25 km long in the NE–SW direction and ~6 km wide in the NW–SE direction, and covers an area of approximately 110 km^2 [27] (Figure 1). Most of the reef top is submerged at depths of just 0.5–1 m. Reef flats in the southwest, northeast, and northwest intermittently appear during low tide. The lagoon of Yongshu Reef has a depth of 8–40 m [28].

Yongshu Reef experiences a tropical monsoon climate, with a mean temperature of 25–29°C and abundant rainfall. It supports various fish species and is one of the largest tropical fishing grounds within Chinese marine waters.

2.2. Data Collection

This study used fish samples from Yongshu Reef collected in 1999 and from 2016 to 2019, during surveys conducted by the South China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences. The fish were sampled by hand fishing in depths of 10–30 m; specifications of the hand line gears were 26.0 mm length, 10.0 mm width, 1.0 mm thickness, and 0.33 mm diameter nylon wire. Eight surveys stations in the reef were set to cover the area of the lagoon [25]. At each station, four fishers used four hooks and sampled synchronously for 3 h (07:00–08:00, 13:00–14:00, 19:00–20:00) with fresh shrimp as bait. The sites selected for each survey were as close as possible in space. This study does not investigate the entire fish community but only species caught by hand fishing.

The fish specimens were identified to species level based on morphological characteristics [29–32]. The number of species collected as well as individual body length (mm) and wet weight (g) were recorded. The wet body mass was measured using electronic scales to the nearest 0.01 g (Sunny Hengping Instrument, Shanghai, China).

In May 1999, the survey was undertaken onboard the commercial fishing vessel *F/V* Yueyu 730 (98 GT, 26.5 m length, 5.3 m width). During 2016–2019, the surveys were undertaken onboard *R/V* Nanfeng (1537 t GT, 66.66 m length, and 12.40 m width) equipped with a motorboat, and fish were collected onboard the motorboat (1 GT, 7.85 m length, 1.50 m width) with a compression–ignition internal combustion engine.

2.3. Data Analysis

2.3.1. Species Similarity

The degree of species similarity among surveys was assessed based on the Jaccard similarity coefficient (I) [33], calculated as follows:

$$I = c/(a + b - c) \tag{1}$$

where a is the number of fish species recorded in the ith survey; b represents the number of species recorded in the jth survey; and c represents the number of shared species in the two surveys. The values of I were divided into four levels of similarity between surveys: extremely dissimilar ($0 \leq I \leq 0.25$); moderately dissimilar ($0.25 < I \leq 0.5$); moderately similar ($0.5 < I \leq 0.75$); and extremely similar ($0.75 < I \leq 1$).

2.3.2. Catch per Unit Effort and Species per Unit Effort

In this study, catch per unit effort (CPUE) was estimated based on individuals ($CPUE_I$) and weight ($CPUE_B$), respectively [19]. The equations are expressed as:

$$CPUE_I = \frac{N}{n \times T} \times 100 \tag{2}$$

$$CPUE_B = \frac{W}{n \times T} \times 100 \tag{3}$$

where $CPUE_I$ [individuals/(100·hooks·h)] and $CPUE_B$ [kg/(100·hooks·h)] are the CPUE based on the number and weight of specimens, respectively. N (individuals) and W (kg) are the number and weight of specimens, respectively; n is the number of fishing lines, T (h) is fishing hours.

To measure the relative changes in fish species richness, we defined species per unit effort (SPUE) for each survey as follows:

$$SPUE = \frac{N_{species}}{n \times T} \tag{4}$$

where $N_{species}$ is fish species richness based on hand-line. The n and T (h) are # of lines and working time, respectively. We used t-test to test differences in CPUE and SPUE between 1999 and 2016–2019 (significance = 0.05).

2.3.3. Index of Relative Importance

The IRI and its percentage (pIRI) were applied to analyze the status of fish in the coral reef fish community [34], calculated by the equations:

$$\mathrm{IRI}_i = 100(N_i + W_i) \times 100F_i \tag{5}$$

$$\mathrm{pIRI}_i = \mathrm{IRI}_i / \sum \mathrm{IRI} \tag{6}$$

where N_i is the proportion of individuals of the ith species to the total individuals of all sampled fish; W_i is the proportion of wet weight of the species to total wet weight of all sampled fish; F_i represents the occurrence of the ith species, that is the proportion of sites where the species was collected among all sites sampled. In this study, F_i was set at 1 because we sampled only in the lagoon. The pIRI_i represents the percentage of IRI_i to the total IRI for all species in a survey. Subsequently we calculated the mean IRI (mIRI) of all dominant species in each survey. Individual species were designated as dominant (IRI $\geq$ 1000), important (500 $\leq$ IRI < 1000), common (100 $\leq$ IRI < 500), uncommon (10 $\leq$ IRI < 100), or rare (IRI < 10).

2.3.4. Species Diversity Indices

Indices of species diversity were used to characterize the degree of biological resource richness in a certain area. The Shannon–Weiner diversity index (H') was used as a measure of heterogeneity (i.e., comprehensive evenness and richness) to evaluate the species diversity and long-term changes in the fish community at Yongshu Reef [35]. Pielou's evenness index (J') were used to measure species richness and evenness [36]. The calculations are expressed as:

$$H' = -\sum_{i=1}^{S} P_i \times \ln P_i \tag{7}$$

$$J' = H' / \ln S \tag{8}$$

where S is the total number of species and individuals in the catches of a survey, and P_i is the proportion of standardized individuals of the ith species in the survey to the total individuals of all sampled fish.

2.4. Effects of Coral Cover, SST, and Fishing on Fish Community

Until now, information on live coral cover in Yongshu Reef has been lacking and has not been reported. Here, we inferred the change in the coral cover of Yongshu Reef based on the change in the coral cover of Meiji Reef in the Nansha Islands. Meiji Reef (9°55′ N, 115°32′ E) is an atoll similar to Yongshu Reef and is approximately 9 km wide and 6 km long, with a total area of 56.6 km^2. The straight-line distance of Meiji Reef and Yongshu Reef is nearly 293 km. According to the study of Hughes et al. [18], live coral cover declined from an average of around 65% to around 20% during 1998–2007 in the major atolls of Nansha Islands. Zhao et al.reported that the mean coral cover of Meiji Reef in 2007 was 28.31% [37]. To estimate variation in coral cover in the survey area, this study assumed that the cover exponentially declined with constant loss is as follows:

$$\frac{C_{i+1}}{C_i} = q = (1 - p) \tag{9}$$

where C_i and C_{i+1} were the cover in year i and (i + 1), respectively, and q and p (p < 1) were the retention rate and loss rate of coral in adjacent years, respectively. Here, we assumed that the cover in 1998 was 65% and that in 2007 was 28.3%. The relationship between cover in 1998 (C_{1998}) and that in 2007 (C_{2007}) was determined as follows:

$$\frac{C_{2007}}{C_{1998}} = \frac{28.3\%}{65\%} = (1 - p)^9 \tag{10}$$

where *p* was approximately 0.0883. According to published literature [18,38], we used the actual data of a coral survey in the adjacent Xisha Islands of SCS (approximately 70% in 1998 and approximately 20% in 2007) to test the exponential hypothesis. The cover estimated in Xisha Islands in 2016 was approximately 5.48%, which was close to the amount of cover determined in the actual survey (5.44%). According to our assessment, the mean coral cover in Meiji Reef in 2016–2019 was ~10.78%, equivalent to 17.36% in 1998–1999.

In Yongshu Reef, sea surface temperature (SST) derived from MODIS satellite measurements was obtained from the Ocean Color website (http://oceancolor.gsfc.nasa.gov/ accessed on 1 January 2022). We downloaded level three (4 km) monthly data corresponding to the geographic scope of specimens collected from 1999 and 2019. We used the May datasets to analyze the SST change.

The total catches coral reef fish in the SCS including Yongshu Reef were not counted. Thus, we tried to use the total catch data of Epinephelinae (a typical reef fish) from annual catch statistics for three south China provinces: Guangdong, Hainan, and Guangxi to estimate changes in the relative fishing pressure of coral reef fish in the SCS (Bureau of Fisheries of the Ministry of Agriculture and Rural Affairs PRC, 1998–2019). Although this treatment had some limitations and might not accurately reflect the actual fishing pressure on Yongshu Reef, it might be helpful to understand the trends in human fishing on reef fish. In this study, we analyzed the time series data of Epinephelinae catch from 1998 to 2019.

We used Pearson correlation analysis to test the effects of cover, SST, and fishing intensity on fish community (significance = 0.05).

3. Results

3.1. Composition and Similarity of Community

Across six surveys spanning 1998 to 2019, 1897 fish individuals were collected, representing 4 orders, 23 families, 54 genera and 112 species (Table A1). Fish composition differed significantly among the surveys. Four species each appeared in all five surveys (*Lutjanus kasmira*, *Cephalopholis urodeta*, *Balistapus undulatus* and *Melichthys vidua*), whereas 76 of the species each occurred in only one of the surveys. Nine species of fish collected in May 1999, such as *Chaetodon melannotus*, *Acanthurus mata*, and *Scarus forsteni*, did not appear in 2016–2019 (Table 1). These disappearing fish belong to six families, and their food habits include detritivores (dt), invertebrate feeder and piscivores (ip), invertebrate feeders (iv), planktivores (pk), and herbivores (hb). They have low to medium vulnerability, medium to high resilience, and medium to very high economic value. These fish are at least used by fisheries or aquariums. Fish composition among all surveys presented as extremely dissimilar to each other (Table 2).

Table 1. Ecological and economic property of fishes that were found in Yongshu Reef in 1999 but not in 2016–2019.

Species	Diet	Human Use	Resilience	Vulnerability	Economic Value
Acanthurus olivaceus	dt	F and A	H	L	M
Sphyraena forsteri	ip	F	M	M	M
Chaetodon melannotus	iv	A	L	M–H	unknown
Cephalopholis boenak	ip	F and A	M	L–M	VH
Balistoides conspicillum	iv	F and A	M	M	M
Acanthurus mata	pk	F and A	L	M	M
Scarus forsteni	hb	F	H	L	H
Chaetodon wiebeli	hb	A	H	L	unknown
Chaetodon auriga	iv	F and A	H	L	unknown

Note: The dt, ip, iv, pk, and hb mean detritivores, invertebrate feeder and piscivores, invertebrate feeders, planktivores and herbivores, respectively. The F means fisheries. The A means Aquarium. The VH, H, M, and L mean very high, high, medium, and low, respectively. The M–H and L–M mean medium to high and low to medium, respectively, refer to FishBase website (https://www.fishbase.se/search.php accessed on 25 April 2022).

Table 2. Share species number and Jaccard's similarity coefficient of fish communities at Yongshu Reef for different surveys.

Month Year	Month Year				
	May 1999	**May 2016**	**May 2017**	**May 2018**	**May 2019**
May 1999		15	9	5	11
May 2016	0.20		15	5	17
May 2017	0.17	0.21		4	9
May 2018	0.12	0.08	0.11		7
May 2019	0.17	0.21	0.15	0.15	
Number of species	33	57	28	13	42

Note: The values above diagonal are the share species number. The values below diagonal are the Jaccard's similarity coefficient.

3.2. Catch per Unit Effort and Species per Unit Effort

During 1999 and 2016–2019, the $CPUE_I$ values ranged from 170 to 343 individuals/(100·hooks·h), with maximum in 2016 and minimum in 2019. The $CPUE_B$ values ranged from 16.73 to 73.20 kg/(100·hooks·h), with maximum in 1999 and minimum in 2018. The average $CPUE_I$ in 1999 was higher in 2016–2019. The $CPUE_B$ continued to decline from 1999 to 2018 and slightly increased in 2019. Compared with that in 1999, The $CPUE_B$ declined significantly in 2016–2019 (*t*-test, $p < 0.05$). The decline in $CPUE_B$ was much greater than that of $CPUE_I$ (Figure 2).

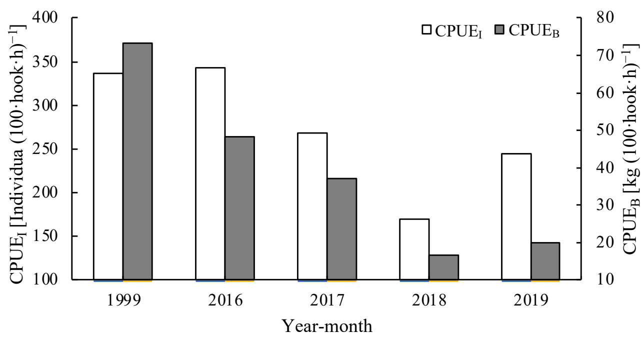

Figure 2. CPUE of fish at Yongshu Reef lagoon during 1999–2019.

The SPUE of the fish community at Yongshu Reef lagoon in 1999 was 1.81 times that in 2016–2019 (Figure 3). The SPUE in 1999 was significantly higher than that in 2016–2019 (*t*-test, $p < 0.05$), indicating that some fish appeared significantly less often, making them more difficult to catch.

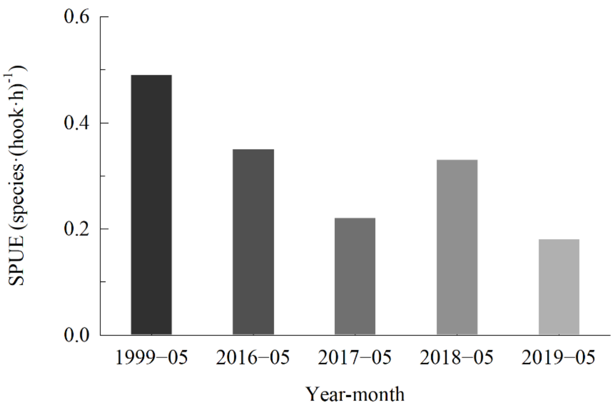

Figure 3. SPUE of fish at Yongshu Reef lagoon during 1999–2019.

3.3. Dominant Fish Species

In all surveys from 1999 to 2019, there were 14 dominant species. Four species appeared on the dominant species list in more than two surveys, and the other ten species appeared dominant in only one survey (Table 3). The most frequent occurrence was *L. kasmira*, which had a dominant position in four surveys except 2019. From 1999 to 2017, the IRI and pIRI of *L. kasmira* continued to rise when the IRI and pIRI peaked at 9307.90 and 46.54%, and dropped sharply in 2018, then fell out of the dominant species list in 2019. *Gnathodentex aureolineatus* and *C. urodeta* occupied a dominant position in three surveys. In 1999 and 2016, the dominance of *G. aureolineatus* was not high (IRI < 2000, pIRI < 10), and it lost the dominant position in 2017–2018, but it jumped to the first dominant species in 2019. *C. urodeta* was the dominant species in 1999, lost its dominant position in 2016–2017, and reappeared in the list of dominant species in 2018–2019. *Melichthys vidua* occurred twice on the dominant species list. Both *Gymnosarda unicolor* and *Oxycheilinus orientalis* were dominant species in 1999, but lost their dominant position in 2016–2019.

Table 3. Dominant fish species at Yongshu Reef lagoon for different surveys during 1999 and 2016–2019.

Month Year	Species	IRI	pIRI	mIRI	Trophic Level
May 1999	*Gymnosarda unicolor*	4892.14	24.46	2164.90	4.5 ± 0.75 se
	Cephalopholis urodeta	3103.57	15.52		4.0 ± 0.69 se
	Gnathodentex aureolineatus	1520.02	7.60		3.7 ± 0.57 se
	Epinephelus fasciatus	1239.11	6.20		3.7 ± 0.4 se
	Oxycheilinus orientalis	1181.69	5.91		3.8 ± 0.62 se
	Lutjanus kasmira	1052.84	5.26		3.9 ± 0.3 se
May 2016	*Lutjanus kasmira*	6072.87	30.36	3682.19	3.9 ± 0.3 se
	Odonus niger	3264.13	16.32		3.2 ± 0.32 se
	Gnathodentex aureolineatus	1709.58	8.55		3.7 ± 0.57 se
May 2017	*Lutjanus kasmira*	9307.90	46.54	4128.95	3.9 ± 0.3 se
	Euthynnus alletteratus	2014.07	10.07		4.0 ± 0.0 se
	Aphareus furca	1064.89	5.32		4.1 ± 0.73 se
May 2018	*Melichthys vidua*	7610.84	38.05	2694.47	3.4 ± 0.39 se
	Lutjanus kasmira	2848.68	14.24		3.9 ± 0.3 se
	Malacanthus brevirostris	1720.68	8.60		3.5 ± 0.37 se
	Cephalopholis urodeta	1606.89	8.03		4.0 ± 0.69 se
	Sufflamen chrysopterum	1245.88	6.23		3.5 ± 0.41 se
	Naso vlamingii	1133.85	5.67		2.2 ± 0.11 se
May 2019	*Gnathodentex aureolineatus*	8557.39	42.79	3477.16	3.7 ± 0.57 se
	Melichthys vidua	2598.03	12.99		3.4 ± 0.39 se
	Cephalopholis spiloparaea	1724.59	8.62		4.1 ± 0.7 se
	Cephalopholis urodeta	1028.62	5.14		4.0 ± 0.69 se

Note: The trophic level refer to FishBase website (https://www.fishbase.se/search.php accessed on 25 April 2022).

The number of dominant species was six in 1999, with an average of four in 2016—2019 (Figure 4). The average pIRI of the most-dominant species in 2016—2019 was significantly higher than that in 1999 (*t*-test, $p < 0.05$). The mIRI of all dominant species was 3496 in 2016—2019 and significantly higher than that in 1999 (*t*-test, $p < 0.05$).

3.4. Species Diversity

In 1999 and 2016–2019, the range of H' was 1.65–2.74 (Figure 5). H' was the highest in 1999 and the lowest in 2017, and showed a significant decline between 1999 and 2016–2019 (*t*-test, $p < 0.05$). J' in 1999 was 0.78, higher than that in 2016–2017 and 2019, but lower than that in 2018 (Figure 5). The mean J' in 2016–2019 was 83.01% of that in 1999, but there were no significant difference in J' between 1999 and 2016–2019 (*t*-test, $p > 0.05$).

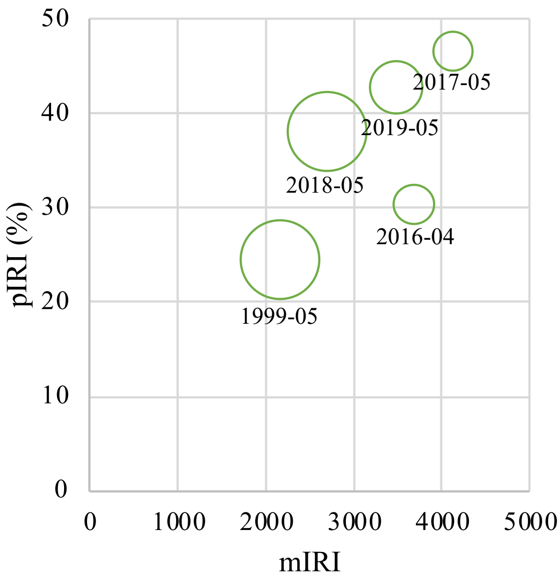

Figure 4. Quantity and dominance degree of the dominant fish at Yongshu Reef lagoon for each survey during 1999 and 2016—2019. The larger the bubble, the more the dominant species.

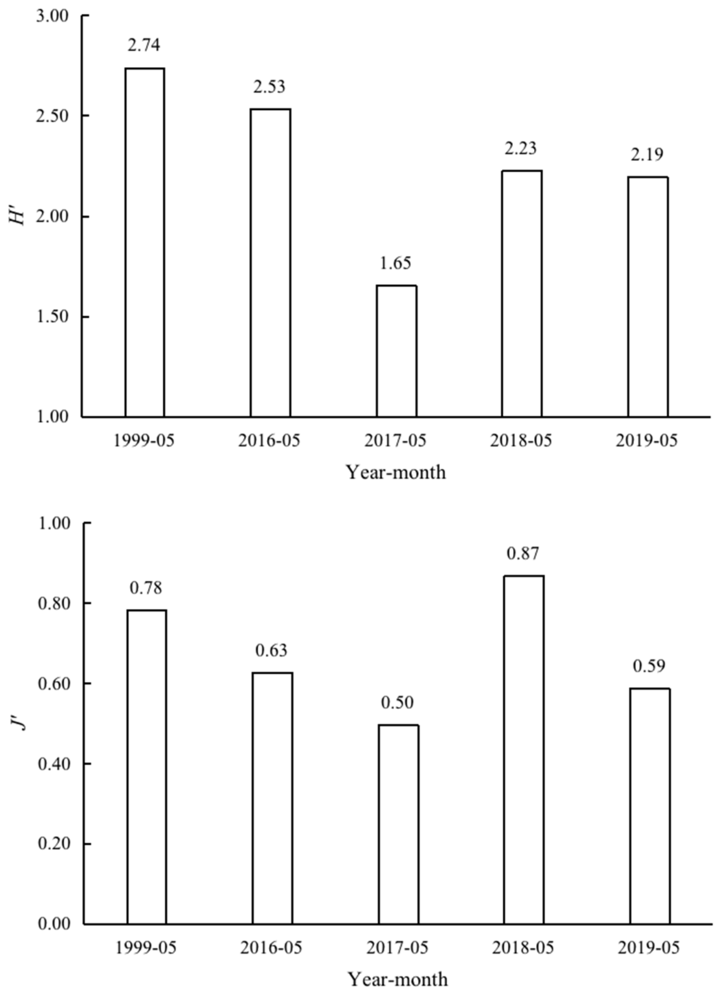

Figure 5. Changes of species diversity index H' and Pielou's evenness index J' of fish community at Yongshu Reef during 1999–2019.

3.5. Correlation between External Pressure and Fish Community Decline

In Meiji Reef, the coral cover in 1999 was ~59.26%, and decreased to 10.78% in 2016–2019, equivalent to 18.19% in 1999 (Figure 6). We speculated that the changing trend of coral cover in Yongshu Reef was similar to Meiji Reef.

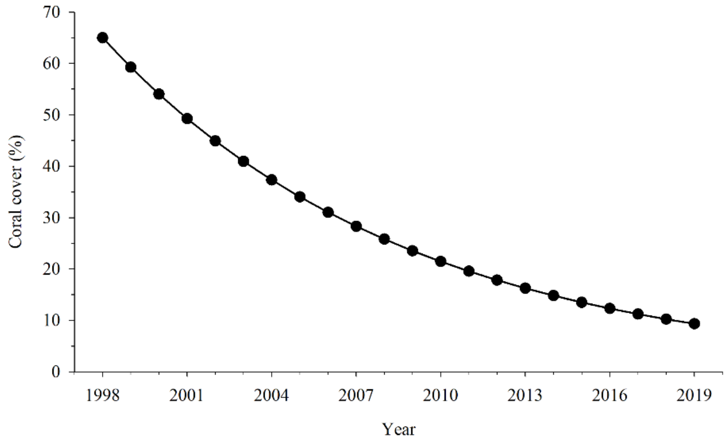

Figure 6. Variation in coral cover in the Meiji Reef of South China Sea from 1998 to 2019 based on exponential loss assumption and published literature [18,37,38]. N_{1998} = 65% and p = 0.0883 represented coral cover of 65% in 1998 and an annual loss rate of 0.0883.

The mean SST in annual May in Yongshu Reef has been rising significantly since 2013 (Figure 7), and the mean SST in 2016–2019 was significantly higher than that in 1999 (*t*-test, $p < 0.05$). In addition, two El Niño events with higher SST occurred in 1998 and 2015 in the SCS, causing massive coral bleaching and death.

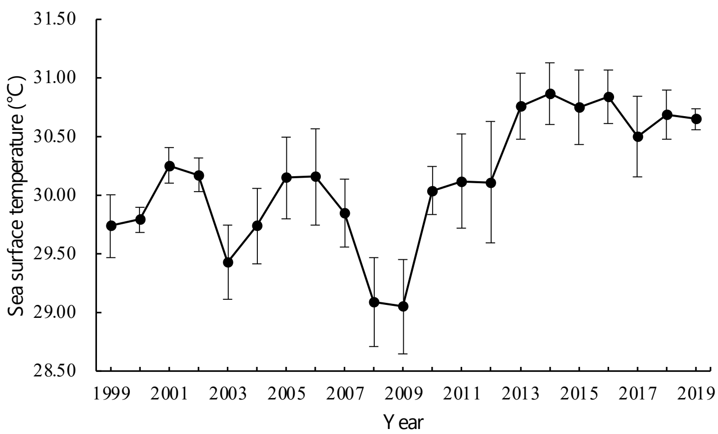

Figure 7. Variation in mean sea surface temperature in May from 1999 to 2019 in the Yongshu Reef, South China Sea.

From 1999–2019, the total annual catch of Epinephelinae from China in the SCS experienced an increase and then a decrease, and the peak catch was 104,697 t in 2016 (Figure 8). Although catch has declined since 2016, the mean catch in 2016–2019 was still 2.80 times higher than that in 1999.

Pearson correlation analysis showed that declining coral cover, increasing fishing, and rising SST had a noticeable relationship with a decline of fish community (Table 4). Overall, SST had the least correlation with the change in fish communities. However, none of the correlations between cover, fishing, SST and fish communities were significant ($p > 0.05$).

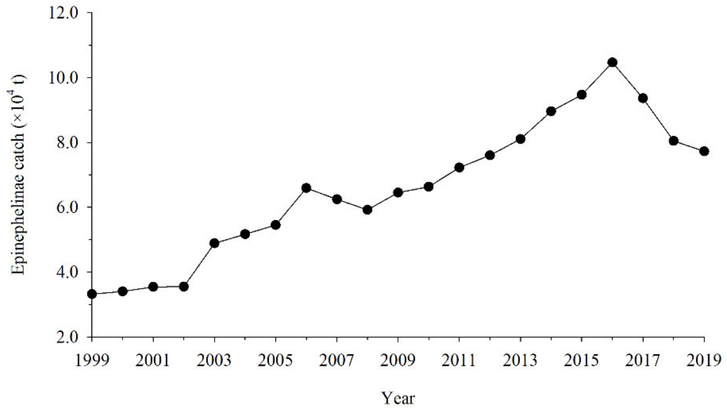

Figure 8. Annual catch of Epinephelinae from China1999–2019 in the South China Sea.

Table 4. Pearson correlation coefficients between fish community indicators and coral cover, fishing, and sea surface temperature (SST) at Yongshu Reef lagoon during 1999 and 2016–2019.

Factor	$CPUE_B$	SPUE	mIRI	pIRI	H'	J'
Cover	0.805	0.826	−0.738	−0.760	0.645	0.387
Fishing	−0.468	−0.622	0.840	0.540	−0.530	−0.498
SST	−0.709	−0.657	0.657	0.531	−0.404	−0.274

4. Discussion

The fish community composition and the dominant fish species at Yongshu Reef have greatly changed since 1999. Some fish species collected in May 1999 did not appear again in 2016–2019. Considering that the fishing effort in 2106–2019 far exceeded that in 1999, it might indicate that the distribution scope and abundance of these species have dropped dramatically, or have moved out from Yongshu Reef. Compared to 1999, the number of dominant fish species at Yongshu Reef has decreased, while the relative dominance of those species has increased, suggesting that some highly competitive fishes occupy dominant positions in the community. These species would exclusively exploit the limited resources and force out other fishes from the habitat, which would weaken the ability of the coral reef ecosystem to resist further disturbances [39,40]. This finding is similar to the reports at Meiji Reef [19,25]. When compared with that in 1999, the number of dominant fish species at Meiji Reef decreased by nearly half in 2017 to 2018.

IRI analysis showed that the relative richness of *G. unicolor*, *E. fasciatus*, and *C. urodeta* was relatively high in 1999, but *G. unicolor* did not appear after 2016. Although *E. fasciatus* and *C. urodeta* were caught during 2016–2019, their individuals and biomass were very low. On the contrary, *G. aureolineatus*, *L. kasmira*, and *Odonus niger* were not or were rarely caught in 1999, but appeared in large numbers in 2016–2019. Our study showed that the trophic level of species with high relative richness in 1999 (3.7–4.5) was higher than that in 2016–2019 (2.2–4.1). The healthy coral reefs often form a "concave" trophic structure pattern [41], in which biomass accumulated at the base and peak of the trophic pyramid. Therefore, we speculated that the fish community of Yongshu Reef in 2016–2019 was greatly degraded compared with 1999.

In addition, the CPUE of fishes at Yongshu Reef decreased, as well as species diversity. We found that the survey with the highest J' value is also the survey with the lowest species. Excluding the influence of the lowest number of species in this survey (May 2018), the species evenness in 2016–2019 was also significantly lower than that in 1999. These changes indicated a continuous decline in the fish biomass at Yongshu Reef. This conclusion was further supported by the finding that nearly half of the fish species collected in May 1999 were not recorded by the surveys from 2016 to 2019, especially some large economic species (such as parrotfish). This is consistent with the findings of Zhang et al. [25] who investigated the long-term changes in the dominant species and diversity of associated reef fish at Meiji Reef in the SCS. Significantly, the decline in $CPUE_B$ was much greater than in $CPUE_I$, which might suggest miniaturization of fish community [25].

We know that the dynamics of fish populations are ubiquitous, movement patterns of some coral reef fishes change with natural cycles (e.g., tidal, lunar and seasonal), resulting in term shifts in fish communities [42]. When the external conditions remain relatively stable, the coral reef fish community can maintain a relatively stable structure. However, this relative stability can be disrupted by abnormal external disturbances, especially powerful natural disturbances, and human activities. Under these conditions, fish communities may exhibit extraordinary negative changes, such as rapid declines in biomass and diversity [3,5,9,11]. In our study, we found that the decline of fish community at the Yongshu Reef lagoon was obvious, far beyond the scope of the natural cycle changes of fish. Therefore, we speculated that habitat degradation (reduced coral cover) and human fishing have played an important driving role in fish community changes.

According to our analysis and assumption, the decline in coral cover at Yongshu Reef was extremely severe, which seriously threatened the health of associated reef fishes. Coral bleaching induced by abnormal increases in sea temperature and the subsequent change in habitat structure are considered the most serious threats to coral reef fishes [9,43]. Coral reef structures tend to collapse following mass bleaching; the loss of habitat complexity not only directly threatens the survival of coral-feeding fish, but also fails to provide suitable fish habitat and shelter [44], eventually leading to massive loss of the reef fishes [45]. For instance, the disappearance of coral-feeding fishes (such as species of *Chaetodon*) will ensue from coral bleaching [46]. The presence of *Chaetodon* species is commonly considered to be an indicator of coral reef ecosystem health [47], thus their disappearance may indicate that Yongshu Reef ecosystem has been seriously damaged. The SST at the coral reef in the Nansha Islands were measured and have risen overall, increasing at an intensity of 0.096°C every 10 years over the period 1982–2015 [48]. Moreover, two El Niño events, in 1998 and 2015–2016, caused abnormally high SSTs in the SCS, leading to widespread bleaching and the death of corals in the region [48]. Increasing temperature is of particular concern among climate changes damaging coral reef systems [9]. Overall, the average May SST at Yongshu Reef increased from 1999 to 2019, especially from 2013 to 2019. In addition, two El Niño events in the SCS in 1998 and 2015 caused widespread coral bleaching and death [22]. It is generally believed that increasing sea temperature primarily disturbed reef fish indirectly by damaging coral rather than directly damaging reef fish [18,22]. Thus, we speculated that increasing temperature was less directly associated with declines in fish communities at the Yongshu Reef.

Hughes et al. found that the impact of climate change on coral reefs in the SCS was far less than human activities such as pollution, overfishing and destructive fishing [18]. Overfishing and destructive fishing are the main human activities leading to the reduction or loss of moderate to large fish in coral reefs [49–51]. Similar conclusions can be drawn from Table 4. The fish that have disappeared since 2016 have low vulnerability and good resilience. They have medium to very high economic value and are widely used by fisheries and/or aquariums. It is not difficult to infer that their decline is closely related to human activities. Presently, a majority of coral reefs in the SCS are under threat from destructive fishing practices [20,21]. Several studies in the Xisha Islands demonstrated that fishing activities and habitat destruction were the direct causes of decreases in coral reef fish density and large fish [23]. Partly as a consequence of historically weak awareness of fishery management, intensive fishing activities have greatly impacted coral reef fish communities in the SCS. However, that impact is difficult to quantify because of an extreme lack of fishery production data, which mainly resulted from restrictions such as disputes over the occupation of coral reef atolls.

This study is the first long-term investigation of variations in the coral reef fish community at Yongshu Reef. The results showed that there were clear decreases in species diversity and the number of dominant species between 1999 and 2016–2019; the community structure pattern changed accordingly. These findings have critical relevance for fishery management and coral reef protection in the SCS. Furthermore, we believe that continuous surveys are vital to document changes in the naturally rich coral reef fishes in the SCS.

5. Conclusions

There was relative dissimilarity in the fish community composition at Yongshu Reef between surveys over a 20-year period. Notably, the density of some species with important ecological functions or high economic value decreased or even disappeared locally.

The number of dominant reef fish species decreased but their dominance increased. The overall fish biomass declined, and individuals showed a trend of fish miniaturization. Since 1999, the species diversity and evenness of the fish community at Yongshu Reef have declined. Declining coral cover, increasing fishing and rising SST were clearly associated with changes in fish community structure at Yongshu Reef.

Author Contributions: Conceptualization, X.D. and J.Z.; methodology, X.D. and J.Z.; software, X.D. and J.Z.; investigation, Y.C., J.Z., Y.G., and Y.L.; writing—original draft preparation, X.D. and J.Z.; writing—review and editing, all authors; supervision, Z.C.; project administration, J.Z. and Z.C. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the National Natural Science Foundation of China, grant number 31902374; the Natural Science Foundation of Guangdong Province, grant number 2021A1515011025; the Key Special Project for Introduced Talents Team of Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou), grant number GML2019ZD0605; the Special Agricultural Finance Project, grant number NFZX2021; the Central Public-interest Scientific Institution Basal Research Fund, CAFS, grant number 2020TD05; and the Central Public Interest Scientific Institution Basal Research Fund, South China Sea Fisheries Research Institute, CAFS, grant number 2021SD01.

Institutional Review Board Statement: This study was reviewed and approved by the South China Sea Fisheries Research Institute animal welfare committee.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are available on request from the corresponding author.

Acknowledgments: We thank Cynthia Kulongowski who assisted with editing the language of the final version of this manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Fish species at Yongshu Reef for each survey during 1999 and 2016–2019.

Taxon	Year-Month					SUM
	1999-05	2016-04	2017-05	2018-05	2019-05	
Holocentridae						
Sargocentron rubrum		+				1
Sargocentron diadema	+	+			+	3
Sargocentron caudimaculatum		+	+			2
Sargocentron ittodai		+				1
Sargocentron microstoma					+	1
Myripristis murdjan	+	+	+		+	4
Myripristis botche		+				1
Myripristis vittata		+				1
Neoniphon sammara					+	1
Acanthuridae						
Naso brevirostris					+	1
Naso lituratus		+			+	2
Naso vlamingii				+		1
Acanthurus olivaceus	+					1
Acanthurus mata	+					1
Paracanthurus hepatus		+				1

Table A1. *Cont.*

Taxon	Year-Month					SUM
	1999-05	2016-04	2017-05	2018-05	2019-05	
Priacanthidae						
Priacanthus sagittarius					+	1
Priacanthus blochii		+				1
Priacanthus hamrur					+	1
Heteropriacanthus cruentatus				+		1
Lutjanidae						
Aphareus furca		+	+			2
Aphareus rutilans		+				1
Lutjanus bohar	+	+	+			3
Lutjanus sanguineus			+			1
Lutjanus gibbus		+	+			2
Lutjanus kasmira	+	+	+	+		4
Lutjanus argentimaculatus		+				1
prion virescens		+				1
Pristipomoides multidens			+			1
Pristipomoides typus			+			1
Pristipomoides auricilla			+			1
Pristipomoides filamentosus	+	+				2
Paracaesio sordida		+	+			2
Paracaesio xanthura		+				1
Macolor niger			+			1
Sparidae						
Acanthopagrus latus		+				1
Haemulidae						
Plectorhinchus flavomaculatus		+				1
Chaetodontidae						
Chaetodon melannotus	+					1
Chaetodon wiebeli	+					1
Chaetodon auriga	+					1
Pinguipedidae						
Parapercis muronis		+				1
Parapercis decemfasciata			+			1
Parapercis clathrata		+		+		2
Parapercis millepunctata					+	1
Parapercis hexophtalma					+	1
Nemipteridae						
Parascolopsis inermis		+				1
Pentapodus aureofasciatus					+	1
Pentapodus caninus		+			+	2
Siganidae						
Siganus canaliculatus	+	+				2
Siganus argenteus		+			+	2
Labridae						
Cheilinus fasciatus		+				1
Cheilinus oxycephalus					+	1
Halichoeres hartzfeldii	+	+		+		3
Halichoeres trimaculatus					+	1
Oxycheilinus unifasciatus		+	+		+	3
Oxycheilinus orientalis	+				+	2
Oxycheilinus digramma					+	1
Hologymnosus annulatus	+					1
Hologymnosus doliatus		+				1
Iniistius pavo		+				1
Lethrinidae						
Gnathodentex aureolineatus	+	+	+		+	4
Monotaxis grandoculis	+	+			+	3
Gymnocranius griseus		+	+			2
Lethrinus semicinctus					+	1
Lethrinus harak		+				1
Lethrinus rubrioperculatus		+			+	2
Lethrinus xanthochilus	+					1
Lethrinus erythracanthus		+				1

Table A1. *Cont.*

Taxon	Year-Month					SUM
	1999-05	2016-04	2017-05	2018-05	2019-05	
Lethrinus microdon		+				1
Lethrinus variegatus	+					1
Lethrinus miniatus	+	+				2
Serranidae						
Variola albimarginata		+				1
Variola louti	+		+		+	3
Cephalopholis leopardus					+	1
Cephalopholis spiloparaea		+			+	2
Cephalopholis boenak	+					1
Cephalopholis sonnerati			+			1
Cephalopholis urodeta	+	+	+	+	+	5
Plectropomus oligacanthus			+			1
Epinephelus quoyanus	+					1
Epinephelus merra					+	1
Epinephelus fasciatus	+	+			+	3
Epinephelus sexfasciatus	+					1
Epinephelus chlorostigma			+			1
Epinephelus miliaris					+	1
Scombridae						
Euthynnus alletteratus			+			1
Gymnosarda unicolor	+					1
Pomacentridae						
Neoglyphidodon melas		+				1
Amphiprion clarkii					+	1
Malacanthidae						
Malacanthus brevirostris				+	+	2
Carangidae						
Elagatis bipinnulata		+				1
Carangoides orthogrammus		+				1
Apogonidae						
Nectamia fusca				+		1
Pristiapogon fraenatus		+				1
Pristiapogon kallopterus				+	+	2
Mullidae						
Parupeneus multifasciatus			+			1
Parupeneus pleurostigma				+	+	2
Parupeneus trifasciatus	+	+			+	3
Mulloidichthys vanicolensis					+	1
Scaridae						
Scarus forsteni	+					1
Scarus ghobban		+				1
Sphyraenidae						
Sphyraena forsteri	+					1
Balistidae						
Sufflamen chrysopterum				+	+	2
Sufflamen fraenatum		+	+		+	3
Pseudobalistes flavimarginatus		+				1
Balistapus undulatus	+	+	+	+	+	5
Odonus niger		+	+		+	3
Melichthys vidua	+	+	+	+	+	5
Melichthys niger	+					1
Balistoides conspicillum	+		+			2
Balistoides viridescens					+	1
Synodontidae						
Synodus ulae		+				1
Synodus variegatus					+	1
SUM	33	57	28	13	42	

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