

Genetic diversity of the yellowfin seabream, *Acanthopagrus latus* (Actinopterygii: Perciformes: Sparidae)—An enhancement species in Dongshan Bay

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Abstract

Dongshan Bay is located on the west side of the Taiwan Strait, which had abundant fishery resources in the past. With the increase in fishing pressure, resources have declined. To restore the fishery resources in Dongshan Bay and to increase fishing yield, much enhancement and release work has been carried out in Dongshan Bay. The yellowfin seabream, *Acanthopagrus latus* (Houttuyn, 1782), is an important enhancement species in Dongshan Bay that is also frequently captured. Due to yearly progress in enhancement and release, it is necessary to study the current status of the genetic diversity of yellowfin seabream in Dongshan Bay. The results show that all yellowfin seabream populations have high genetic diversity, which is mainly related to its breeding habits and growth rate, and this ensures a large recruitment stock in the natural seas. The current population has differentiated from the historical population due to a change in genetic structure, and many historical haplotypes have been lost. The results of this study provide a reference for fishery management departments to formulate management measures and conservation policies specifically for yellowfin seabream. In particular, yellowfin seabream is a hermaphroditic and protandrous species. Targeting an older age group as the main fishing subject is not conducive to its breeding protection and resource growth, and therefore, fishing of an older age group should be restricted in fishery production.

Keywords

Dongshan Bay, genetic diversity, resource decline, stock enhancement, yellowfin seabream

Introduction

Located on the west side of the Taiwan Strait, Dongshan Bay is a typical subtropical estuary semi-closed bay. The bay is affected by the offshore water of the South China Sea, by the Taiwan warm current in the summer, and by

the Fujian–Zhejiang coastal current as well as the Taiwan Strait inversion thermocline in the fall. It originally had rich fishery resources and was a good place for various economic species to inhabit, reproduce, and grow. With the rapid development of industry and agriculture since the reform and opening up, the development and

utilization of sea areas and the continuously growing aquaculture industry have aggravated the ecological environment of the sea area in the bay, leading to a significant decline in fishery resources (Lin et al. 2013).

To restore the fishery resources in Dongshan Bay, the government of Dongshan County launched a program for enhancement and release some economically important shellfish and finfish species, *Penaeus japonicus*, *Penaeus penicillatus*, *Pagrus major* (Temminck et Schlegel, 1843); *Acanthopagrus schlegelii* (Bleeker, 1854); and *Acanthopagrus latus* (Houttuyn, 1782). By releasing a large number of artificially bred seedlings into natural seas to restore decreased populations and increase fishing yields, enhancement and release are of great significance for replenishing and restoring the population structure of biological resources, improving the ecological environment of waters, replenishing fishery resources, and increasing fishermen's income. However, the genetic impact of released species on wild resources has also received increasing attention (Helfman 2008). In general, although cultured populations may not be able to adapt well to the changing external environment, they may outperform wild populations in intraspecific competition in natural seas, resulting in a decline in the number of wild populations and a corresponding reduction in their genetic diversity (Tringali and Leber 1999). Moreover, the fishing yield will increase after enhancement and release, which will cause greater fishing pressure on the original wild populations, bringing about a further decline in the number of wild populations and, ultimately, a reduction in the genetic diversity of the species (Helfman 2008).

The yellowfin seabream, *Acanthopagrus latus*, an important economic fishery species in Dongshan Bay, is an important species for enhancement and release in this sea area. It is a warm water shallow coastal fish species that can adapt to rapid changes in salinity and generally does not migrate long distances. It is widely distributed in the East China Sea and South China Sea (Jiang et al. 2012; Iwatsuki 2013). With enhancement and release in Dongshan Bay in the past 10 years, the current status of the genetic diversity of the yellowfin seabream population in the bay is unclear. Has gene flow occurred between the introduced released population and wild populations, thereby changing the composition of the original populations and causing the original stock to become a mixed population consisting of released individuals, wild individuals, and hybrid offspring of the two stocks? Have the genetic diversity and genetic structure of the wild population also changed? It is necessary to evaluate the current status of the genetic diversity

of the yellowfin seabream in Dongshan Bay to propose targeted fishery management measures.

Mitochondrial DNA (mtDNA), as an important genetic information library, has the advantages of maternal inheritance, a fast evolution rate, high copy numbers, and easy amplification. Therefore, it is often employed in research on species diversity and phylogeny with wide applications (Simon et al. 2006; Li et al. 2018, 2019). In this study, the first hypervariable region of the control region (CR) of mtDNA was used to study the genetic diversity and genetic structure of the yellowfin seabream in three populations collected from Dongshan Bay and in one population from Xiamen to evaluate the current status of its genetic resources. This study will provide a reference for the formulation of management measures and conservation policies for yellowfin seabream and the development of enhancement and release work.

Materials and methods

Sample collection

A total of 75 individuals of four yellowfin seabream populations, Dongshan I (DSI; wild individuals, 2009.11), Dongshan II (DSII; wild individuals, 2019.10), Dongshan III (DSIII; cultured individuals, 2019.11), and Xiamen (XM; wild individuals, 2019.10), were collected from November 2009 to November 2019 (Fig. 1, Table 1). Wild individuals were captured in the open waters of Dongshan Bay and Xiamen, and cultured individuals were captured in the farming waters of Dongshan Bay. Yellowfin seabream can be easily identified based on their yellow or pale-yellow ventral fin, anal fin, and lower lobe of the caudal fin. The main morphological identification was based on Nakabo (2013). All samples were accurately identified by morphology, and the dorsal muscles were stored in 95% alcohol for subsequent experiments, or fresh dorsal muscles were collected to directly extract genomic DNA.

Genomic DNA extraction, PCR amplification, and sequencing

A Qiagen DNeasy kit was used to extract the genomic DNA of yellowfin seabream. DNA with a quantified concentration was amplified by PCR. The amplification primers were DL-S (5'-CCCACCACTAACTCCCAAAGC-3') and DL-R (5'-TTAACTTATGCAAGCGTTCGAT-3') (Gao

Table 1. Sampling sites, date, number, number of haplotype and genetic diversity indices for each population of *Acanthopagrus latus*.

Sampling site	ID	Collection date	Sample size	h	π	k	No. of haplotype
Dongshan I	DSI	Nov 2009	20	0.9895 ± 0.0193	0.0163 ± 0.0088	8.9632 ± 4.3104	18
Dongshan II	DSII	Oct 2019	22	0.9957 ± 0.0153	0.0178 ± 0.0095	9.7922 ± 4.6616	21
Dongshan III	DSIII	Nov 2019	14	0.9670 ± 0.0366	0.0129 ± 0.0072	7.0879 ± 3.5401	11
Xiamen	XM	Oct 2019	19	1.0000 ± 0.0171	0.0161 ± 0.0087	8.8246 ± 4.2585	19
Total			75	0.9960 ± 0.0030	0.0196 ± 0.0100	10.8090 ± 4.9731	65

h = haplotype diversity, π = nucleotide diversity, k = mean number of pair-wise differences; DSI = Dongshan I population (wild individuals, 2009.11), DSII = Dongshan II population (wild individuals, 2019.10), DSIII = Dongshan III (cultured individuals, 2019.11), XM = Xiamen (wild individuals, 2019.10).

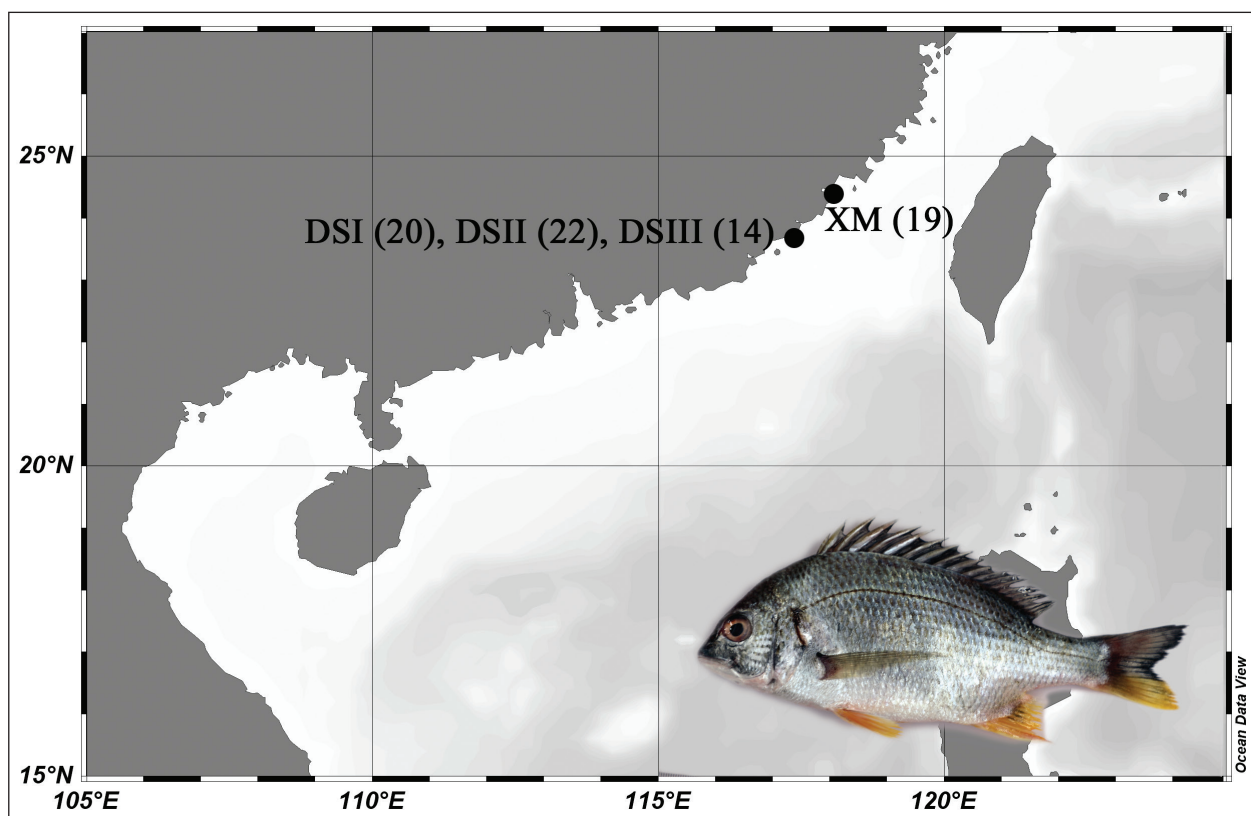


Figure 1. Sampling locations for *Acanthopagrus latus*.

et al. 2019). The PCR system required a total volume of 25 μL , including 17.25 μL of deionized water, 2.5 μL of $10\times$ PCR buffer, 2 μL of dNTPs, 1 μL of each of the forward and reverse primers, 0.25 μL of Taq enzyme, and 1 μL of the DNA template. The PCR conditions were as follows: denaturation at 95°C for 5 min; 30 cycles of denaturation at 95°C for 45 s, annealing at 50°C for 45 s, and extension at 72°C for 45 s; and final extension at 72°C for 10 min. 3 μL of PCR product was used for 1.5% agarose gel electrophoresis. During PCR electrophoresis on agarose gel, different DNA ladder can be distinguished, so the agarose gel electrophoresis was often used to detect the length of PCR products. The qualified products were purified and bidirectional sequenced at the Personal Biotech Co., Ltd. The newly obtained CR haplotype sequences of yellowfin seabream have been submitted to the GenBank database, and the accession numbers are MT312258–MT312282, MT312289, MT312291, MT312298, MT312301, MT312308, MT312310, MT312313, MT312315–MT312321, MT312333–MT312341, MT312343–MT312351, MT312353–MT312358.

Data analysis

The same primers employed for PCR amplification, were used to manually edit and correct the raw sequences for the CR of the yellowfin seabream with SeqMan in the DNASTAR software package. The genetic diversity indexes, such as the mutation sites, haplotype numbers, and

population genetic diversity parameters, were calculated using ARLEQUIN 3.5 (Excoffier et al. 2005). *Acanthopagrus schlegelii* was included as an outgroup. Based on the yellowfin seabream haplotypes and Kimura's two-parameter (K2P) model, MEGA 5.0 software was employed to construct a neighbor-joining tree (NJ). The 1000 nonparametric self-expanding analysis was adopted for repetitive tests and calculation of the confidence of each branch of the phylogenetic tree (Tamura et al. 2011). The F_{ST} values between pairwise groups were calculated with ARLEQUIN 3.0 software (Excoffier et al. 2005), and a significance test was performed using 10 000 replacement tests. Analysis of molecular variation (AMOVA) of the parameters was calculated with ARLEQUIN software to determine the genetic structure of different yellowfin seabream populations, and the significance of covariance at different levels of genetic structure was tested using 5000 replacement tests.

Results

Genetic diversity

A total of 75 sequences were obtained from all populations. After manual alignment, the lengths of the obtained target fragments were 548–550 bp, of which only one sequence was 548 bp in length, 549-bp sequences were dominant (71), and three sequences were 550 bp long. There were 87 mutation sites in all sequences, 54 parsimony informative sites, 33 singleton variable sites, and

three insertions/deletions. The contents of each base were as follows: A, 34.67%; T, 32.04%; G, 13.79%; and C, 19.49%. The A + T content (66.71%) was higher than the G + C content, demonstrating a certain AT preference.

The 75 sequences defined 65 CR haplotypes. The number of haplotypes in each population ranged from 11 to 21. Four (6.15%) haplotypes were shared by two or more populations. There were 61 (93.85%) unique haplotypes. DSIII had a shared haplotype (Hap_11, Hap_17, and Hap_47, respectively) with each of the other three populations, DSI had a shared haplotype (Hap_11 and Hap_17, respectively) with DSIII and XM, and DSII had a shared haplotype (Hap_20) with DSIII; there was no shared haplotype between DSI and DSII (Table 2).

Table 2. Distribution of haplotypes in *Acanthopagrus latus* populations.

	DSI	DSII	DSIII	XM	Total	DSI	DSII	DSIII	XM	Total
Hap_1	1				1	Hap_34	1			1
Hap_2	1				1	Hap_35	1			1
Hap_3	1				1	Hap_36	1			1
Hap_4	1				1	Hap_37	1			1
Hap_5	2				2	Hap_38	1			1
Hap_6	1				1	Hap_39		1		1
Hap_7	1				1	Hap_40		2		2
Hap_8	1				1	Hap_41		1		1
Hap_9	1				1	Hap_42		1		1
Hap_10	2				2	Hap_43		1		1
Hap_11	1		1		2	Hap_44		1		1
Hap_12	1				1	Hap_45		2		2
Hap_13	1				1	Hap_46		1		1
Hap_14	1				1	Hap_47		1	1	2
Hap_15	1				1	Hap_48		1		1
Hap_16	1				1	Hap_49		1		1
Hap_17	1		1		2	Hap_50		1		1
Hap_18		1			1	Hap_51		1		1
Hap_19		1			1	Hap_52		1		1
Hap_20		1	2		3	Hap_53		1		1
Hap_21		1			1	Hap_54		1		1
Hap_22		1			1	Hap_55		1		1
Hap_23		1			1	Hap_56		1		1
Hap_24		1			1	Hap_57		1		1
Hap_25		1			1	Hap_58		1		1
Hap_26		1			1	Hap_59		1		1
Hap_27		2			2	Hap_60		1		1
Hap_28		1			1	Hap_61		1		1
Hap_29		1			1	Hap_62		1		1
Hap_30		1			1	Hap_63		1		1
Hap_31		1			1	Hap_64		1		1
Hap_32		1			1	Hap_65	1			1
Hap_33		1			1					

DSI = Dongshan I population (wild individuals, 2009.11), DSII = Dongshan II population (wild individuals, 2019.10), DSIII = Dongshan III (cultured individuals, 2019.11), XM = Xiamen (wild individuals, 2019.10).

The entire yellowfin seabream population demonstrated high haplotype diversity (0.9960 ± 0.0030) and low nucleotide diversity (0.0196 ± 0.0100). Among them, the wild XM population showed the highest diversity (1.000 ± 0.0171), followed by the current wild Dongshan population (0.9957 ± 0.0153), and the historical wild Dongshan population (0.9895 ± 0.0193); the current cultured Dongshan population showed the lowest diversity (0.9670 ± 0.0366).

Population genetic structure and differentiation

The NJ tree was constructed based on 65 mitochondrial CR haplotypes of yellowfin seabream, showing that two large haplotype lineages existed in the four yellowfin seabream populations, with low confidence. No pedigree structure corresponding to geographic locations was detected (Fig. 2). Lineage 1 consisted of 50 haplotypes (58 individuals), and lineage 2 consisted of 15 haplotypes (17 individuals) (Fig. 2). The haplotype composition of the two lineages was quite different. Thirteen of the 15 haplotypes of lineage

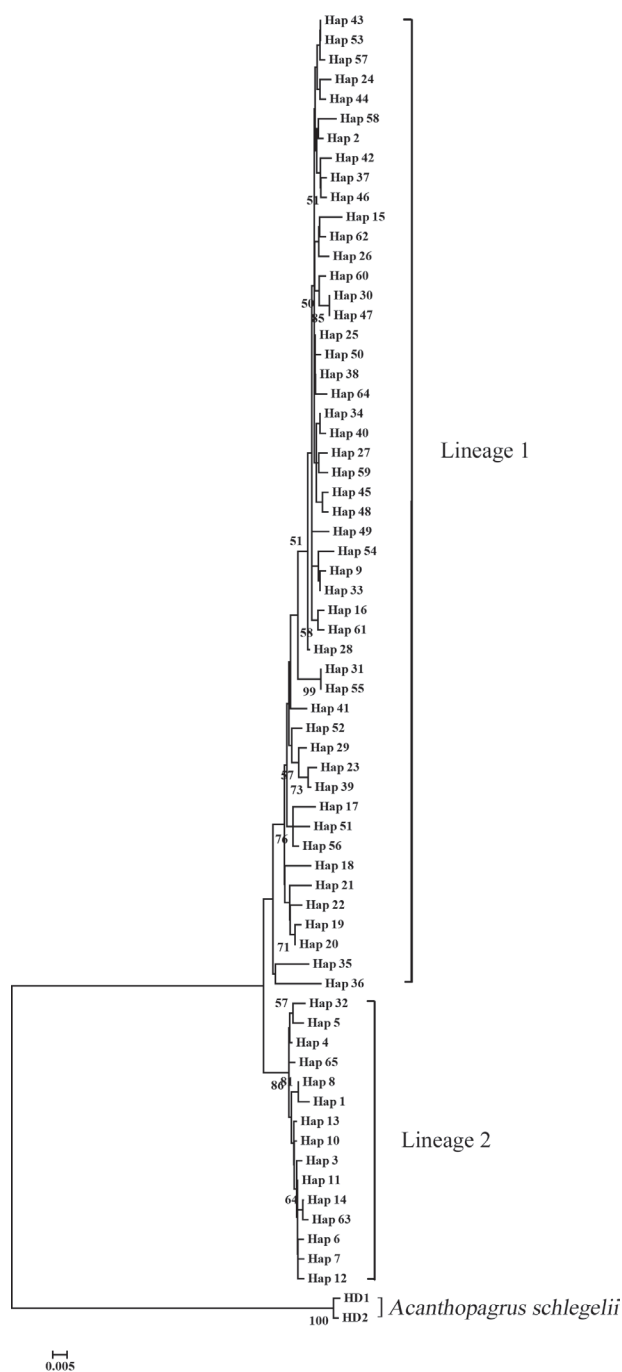


Figure 2. NJ tree of CR haplotypes in *Acanthopagrus latus*. Bootstrap supports > 50 in 1000 replicates are shown.

2 belonged to the DSI population, with one each belonging to the DSII and XM population. Lineage 1 was constituted by the remaining haplotypes of the populations, and there was no specific internal topological structure.

The pairwise F_{ST} values were estimated based on the mtDNA CR sequences, ranging from 0.0005 to 0.4288 (Fig. 3). The F_{ST} values between DSI and the other three populations were large, and statistical tests showed extremely significant differences, indicating significant genetic differentiation between DSI and the other three populations. However, the differences in F_{ST} values among DSII, DSIII, and XM were small, and the statistical tests were not significant, indicating less genetic differentiation among these populations.

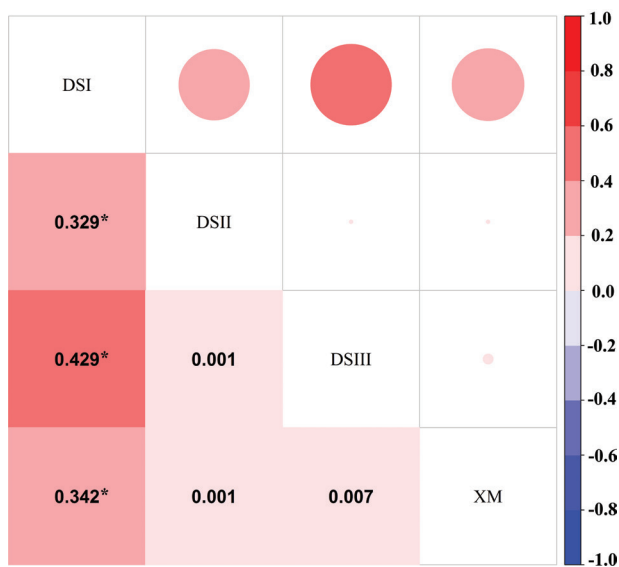


Figure 3. Matrix of pairwise F_{ST} values among four *Acanthopagrus latus* populations. *extremely significant at $P < 0.01$ by the permutation test.

AMOVA was performed to examine the population genetic structure of yellowfin seabream (Table 3). First, all yellowfin seabream populations were analyzed as a single gene pool. The results showed that the genetic differences in the yellowfin seabream populations mainly existed

Table 3. AMOVA of *Acanthopagrus latus* populations based on mtDNA CR sequences.

Source of variation	Percentage variation	F-Statistics	P
One gene pool (DSI, DSII, DSIII, XM)			
Among populations	22.92	0.2292	0.000 ± 0.000
Within populations	77.08		
Two gene pool (DSI, DSII, DSIII), (XM)			
Among groups	-19.17	-0.1917	1.000 ± 0.000
Among populations within groups	34.83	0.2923	0.000 ± 0.000
Within populations	84.34	0.1566	0.000 ± 0.000
Two gene pool (DSI), (DSII, DSIII, XM)			
Among groups	36.27	0.3627	0.253 ± 0.011
Among populations within groups	-0.09	-0.0015	0.420 ± 0.014
Within populations	63.83	0.3617	0.000 ± 0.000

DSI = Dongshan I population (wild individuals, 2009.11), DSII = Dongshan II population (wild individuals, 2019.10), DSIII = Dongshan III (cultured individuals, 2019.11), XM = Xiamen (wild individuals, 2019.10).

inside the population, accounting for 77.08% of all variation, while genetic differences among populations only accounted for 22.92%. To further confirm the population genetic structure of yellowfin seabream, (1) the four populations were grouped into two gene pools according to their geographical distribution, and the results showed that the genetic differences between groups were small with nonsignificant statistical test results ($P > 0.05$), and the genetic differences mainly existed within populations (84.34%) with very significant genetic differentiation ($P < 0.01$); however, the genetic differentiation among populations within groups was small while very significant ($P < 0.01$). (2) According to the F_{ST} values, the four yellowfin seabream populations were divided into two gene pools. The results showed that the genetic differences between groups were small and nonsignificant ($P > 0.05$); genetic differences mainly existed within populations (63.83%), with very significant genetic differentiation ($P < 0.01$), while the genetic differentiation among populations within groups was small and nonsignificant ($P > 0.05$).

Discussion

Due to the impact of ocean currents and climate and its unique geographical location, Dongshan Bay had relatively high biodiversity and rich fishery resources. However, in recent years, with the continuous growth of the human population, the development of surrounding areas and coastal industries, and the increasing development and utilization of sea areas, the impact on the ecology of this sea area has increased, and the habitats and spawning grounds of many economic species have been damaged. Moreover, the fishing pressure of this sea area is overloaded, resulting in a decline in fishery resources (Lin et al. 2013; Ye et al. 2018). To restore the fishery resources in Dongshan Bay, the government of Dongshan County organized the enhancement and release of a variety of economic species, yellowfin seabream is an important economic fish species. After nearly ten years of enhancement and release, to find the changes in the yellowfin seabream of Dongshan Bay, we selected yellowfin seabream samples in 2009 and 2019 for comparative analysis of genetic diversity. Additionally, in order to better reflect the changes in germplasm resources of yellowfin seabream in the past ten years, we also selected yellowfin seabream samples in an adjacent sea area, Xiamen, for reference comparison.

Under normal circumstances, when the number of artificially bred seedlings released into the natural seas is greater than the carrying capacity, an intraspecific competitive relation is formed within the released population, within the wild population, and between the released population and the wild population in which individuals compete for food and living space (Cooney and Brodeur 1998). Additionally, according to the previous study, a higher total allowable catch due to the expansion of coastal development in Dongshan Bay, especially the enhancement and release places more fishing pressure on the wild populations (Ye

et al. 2018). This pressure, to certain extent, further aggravates overfishing and may reduce the size of the wild populations, eventually leading to the loss of genetic and allelic diversity (Helfman 2008), such as *P. major* in the Gulf of Kagoshima, Japan (Hamasaki et al. 2010), and *A. schlegelii* in the Pearl River Estuary, China (Yang and Sun 2019).

However, the results of this study showed that the genetic diversity of yellowfin seabream was high in both wild and cultured populations. The genetic diversity of wild yellowfin seabream in Dongshan Bay in 2009 was largely the same as that in 2019, while that of the cultured population in 2019 was slightly lower (Table 1). The genetic diversity of the wild population in Xiamen in 2019 was basically the same as that in 2008 and slightly higher than that in 2002 (Xia et al. 2008). Such a high level of genetic diversity may be related to the biological reproduction habits of yellowfin seabream, which produce spawn in batches. The individual absolute fecundity of yellowfin seabream reaches as high as 300 000 to 2.38 million, with an average of 1.36 million, and the relative fecundity ranges from 740 to 5,757 spawn \cdot g⁻¹, with an average of 2511 spawn \cdot g⁻¹. Furthermore, its growth rate in natural waters is not lower than that of other fishes (Shi et al. 2012). These favorable characteristics ensure a large recruitment stock of yellowfin seabream in natural seas. Although artificial breeding of yellowfin seabream was successful in 1981, the current breeding seedlings of yellowfin seabream are mainly obtained by sea catch, and the proportion of artificial seedlings is very small (Jiang et al. 2012). Sea-caught seedlings are sold on the market every year from the end of November to December. The continuous seedling supply will ensure that the released population of yellowfin seabream has sufficient parents, avoiding a decline in genetic diversity caused by fewer parents and more offspring, which maintains a high genetic diversity of yellowfin seabream under the current situation of declining fishery resources.

Although the genetic diversity of yellowfin seabream in Dongshan Bay is high, the current fishery resources in Dongshan Bay have been critically overfished (Ye et al. 2018), and the situation is not optimistic. Yellowfin seabream is highly adaptable and can grow in both sea water and fresh water. However, it generally does not migrate long distances, and it is a hermaphroditic male precocious species that can maintain a certain proportion of male and female attributes in its life cycle, which may also be one of the reasons that this species can maintain high genetic diversity under the current situation of declining resources.

To date, many scholars have shown that breeding and release will induce certain genetic impacts on populations in natural seas and have discussed the advantages and dis-

advantages of the breeding and release of fishery resources from the perspective of protecting genetic diversity (Araki and Schmid 2010; Hamasaki et al. 2010). From the genetic structure of yellowfin seabream in this study, significant genetic differentiation can be seen between the 2009 population and the current population, and many historical haplotypes have been lost. Although the sampling strategy and the number of samples may have some impact on the results of this study, these results have revealed certain germplasm resource issues. The breeding and release work of Dongshan Bay placed a large number of seedlings in the natural seas, which restored the fishery resources and at the same time increased the fishing yield, resulting in greater fishing pressure on the yellowfin seabream and further damaged resources, forming a feedback loop. Although this fishing is not the 'sweeping' type, exogenous genetic influences, such as genetic changes caused by the lack of selection pressure and genetic drift, have led to the loss of many haplotypes and genetic and allelic diversity (Helfman 2008).

Campton (1995) proposed that if fisheries were not properly managed, the existing overfishing and continuous breeding and release would change the original population structure and eventually lead to irreversible genetic effects. The results of this study show that the genetic structure of yellowfin seabream in Dongshan Bay has changed. Although it still has high genetic diversity, fishery management of yellowfin seabream resources should attract the attention of management departments to develop specific measures and conservation policies for this species. In particular, yellowfin seabream is a hermaphroditic male precocious species. Targeting older fish as the main fishing subject is not conducive to its breeding protection and resource growth, and therefore, catching older fish should be restricted in fisheries.

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