The Mitochondrial COI Gene Reveals the Genetic Diversity of Chub Mackerel (*Scomber japonicus*) in the Taiwan Strait and its Adjacent Waters

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ABSTRACT

The mitochondrial DNA cytochrome c oxidase subunit I (COI) gene was used to evaluate the population genetics and elaborate the historical demography of *Scomber japonicus* collected from four geographical locations in the Taiwan Strait and its adjacent waters. The results of genetic diversity and genetic structure analysis of *S. japonicus* showed that these four populations exhibited moderate genetic diversity across the sampled geographical range of the species. However, no phylogenetic structure corresponding to geographic location was observed from the neighbor-joining (NJ) tree and haplotype network analyses, and gene flow and exact *P* test results revealed that a wide range of gene flow occurred among the four *S. japonicus* populations. Analysis of molecular variance (AMOVA) and F_{st} analysis showed that genetic variation was mainly derived from within populations, and genetic divergence was very weak among populations. The complex hydrologic environment of the Taiwan Strait and its adjacent waters did not block gene flow among different populations, which indicates relatively high genetic homogeneity; thus, the populations should belong to the same fishery management unit. The nucleotide mismatch distribution and neutrality test results indicated that the studied *S. japonicus* populations experienced a recent expansion event during the late Pleistocene. At present, *S. japonicus* resources show recessions and decreased mean ages due to overfishing, emphasizing the need to strengthen the management of corresponding fisheries and to develop and reasonably utilize *S. japonicus* resources to achieve sustainable development.

INTRODUCTION

*S*comber *japonicus*, which belongs to the order Perciformes, family Scombridae, is an oceanic pelagic fish with an oceanic migratory habit. *S. japonicus*, also known as chub mackerel, is widely distributed along the Northwest Pacific coast and is one of the most important pelagic fisheries resources of the East China Sea and the Yellow Sea (Zhu *et al*., 1985; Liu *et al*., 2005). The catches in these regions have been increasing since the development of marine engine purse-seine fishing, and the large-scale utilization of *S. japonicus* resources began in the early 1970s. Moreover, with the decline of large yellow croaker,

small yellow croaker, hairtail, and other economic species resources in the 1980s, the development of *S. japonicus* and other pelagic fish resources has increased, with signs of overfishing since the 1990s (Cheng and Lin, 2004; Liu *et al*., 2006). According to differences in migratory routes and population structure, *S. japonicus* in Fujian coastal water can be divided into two different populations-the East China Sea population and the Minnan-Yuedong population. Individuals from the Minnan fishing ground belong to the Minnan-Yuedong population, which typically does not migrate for long distances, whereas those from the Minzhong-Mindong fishing ground belong to the East China Sea population, which exhibits long-distance migratory characteristics (Yan, 1997).

Population genetic analysis is the most effective tool for evaluating genetic diversity and structure, as well as information regarding conservation genetics, of

a species (Grant and Bowen, 1998; Abbas *et al.*, 2017). Mitochondrial DNA (mtDNA) is frequently used as a marker in population and phylogenetic studies and is useful for elucidating the genetic structure of populations and resolving ambiguous phylogenetic relations among marine species (Wu *et al.*, 2012; Sun *et al.*, 2013, 2017; Yan *et al.*, 2015; Cheng and Sha, 2017). So far, studies on *S. japonicus* in the Taiwan Strait have mainly focused on biology, resource distribution, and stock assessment. In contrast, few molecular genetics studies have been performed and those studies have focused on populations in the coastal waters of Fujian Province (Zhang *et al.*, 2015; Niu *et al.*, 2012). Thus far, no population genetic analyses of *S. japonicus* in the western and eastern waters of the Taiwan Strait have been reported. The Taiwan Strait has undergone many sea-land changes since the Quaternary glaciation, resulting in paleoclimatic and paleogeographic events (such as historical climatic fluctuations and geomorphological changes) taht affect the habitat of marine organisms and combined with other environmental factors, further remodeling their genetic structure (Avise, 2000; Qiu *et al.*, 2016). Therefore, the rise and fall of the sea level in the Taiwan Strait may have influenced the genetic structure of *S. japonicus* in these waters.

In the present study, chub mackerel samples were collected from the Taiwan Strait and its adjacent waters, and sequences of the mtDNA cytochrome coxidase subunit I (COI) gene were used to investigate the genetic diversity and structure of this species in the study area. The results provide an opportunity to assess whether historical processes associated with Pleistocene climatic fluctuations have left genetic signatures in contemporary populations of chub mackerel. Ultimately, we aimed to evaluate how historical and contemporary factors interact to influence variation in the population genetics of this species.

MATERIALS AND METHODS

Sample collection

A total of 120 *S. japonicus* individuals were collected from Ningde (Mindong fishing ground), Pingtan (Minzhong fishing ground), Xiamen (Minnan fishing ground) and Keelung (Taipei fishing ground) in 2015 and 2016 (Fig. 1; Table I). To ensure the accuracy of species identification, all individuals were identified according to Zhu *et al.* (1985). Back-muscle tissues were excised and preserved in 95% alcohol for subsequent experiments.

DNA extraction, amplification and sequencing

Genomic DNA was extracted from muscle tissue using the Qiagen DNeasy Kit, assessed by 1.5% agarose gel electrophoresis and stored at 4°C for polymerase

chain reaction (PCR) amplification. The mtDNA COI fragment was amplified with the primers FishF1, 5′-TCAACCAACCACAAAGACATTGGCAC-3′, and FishR1, 5′- TAGACTTCTGGGTGGCCAAAGAATCA-3′ (Ward *et al.*, 2005). Each reaction was performed in a 25-µL mixture containing 17.5 µL ultrapure water, 2.5 µL 10×PCR buffer, 2 µL deoxynucleotides (dNTPs), 1 µL of each primer (5 µM), 0.15 µL Taq polymerase, and 1 µL DNA template. PCR amplification was performed using a Biometra thermal cycler under the following conditions: 4 min of initial denaturation at 94°C; 35 cycles of 45 s at 94°C for denaturation, 45 s at 52°C for annealing, and 45 s at 72°C for extension; and a final extension at 72°C for 10 min. Successful PCR products were purified, and both strands were sequenced. The newly isolated nucleotide sequences were deposited in GenBank under accession numbers KU302311–KU302319. *Setipinna tenuifilis* was used as an outgroup for the analyses.
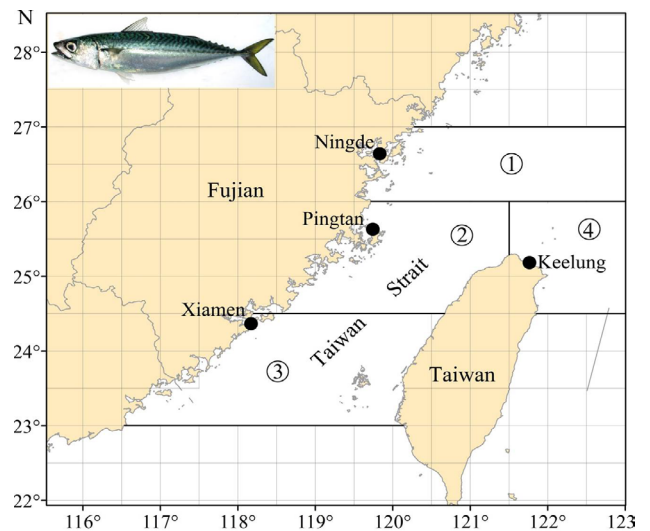

Fig. 1. The four sampling locations of *S. japonicas*. 1, Mindong fishing ground; 2, Minzhong fishing ground; 3, Minnan fishing ground; 4, Taipei fishing ground.

Data analysis

The mitochondrial DNA COI gene sequences were aligned and edited using DNASTAR software. Polymorphic sites, haplotype number and molecular diversity indices for each population were calculated using ARLEQUIN version 3.5 (Excoffier *et al.*, 2005). Genetic relationships among haplotypes were reconstructed using the neighbor-joining (NJ) method implemented with 1000 replicates in MEGA 5.0 (Tamura *et al.*, 2011). Analysis of molecular variance (AMOVA) was performed using ARLEQUIN to investigate the partition of genetic variation among the populations.

Table I.- Information and molecular indices of *S. japonicas.*

Populations	Number	Date	NH	NUH	$h \pm$ SD	$\pi \pm$ SD	$k \pm$ SD
Ningde	30	2015.07	5	0	0.5448±0.0657	0.0019±0.0008	0.5931±0.4882
Pingtan	30	2015.10	4	3	0.7632±0.0505	0.0017±0.0013	1.1333±0.7571
Xiamen	30	2015.07	4	1	0.5402±0.0798	0.0011±0.0009	0.7287±0.5585
Keelung	30	2016.09	6	1	0.6276±0.0628	0.0012±0.0009	0.7655±0.5771
Total	120	-	9	-	0.6203±0.0343	0.0012±0.0010	0.8069±0.5857

NH, number of haplotypes; NUH, number of specific haplotypes; *h*, haplotype diversity; *π*, nucleotide diversity; *k*, average number of pairwise differences.

A minimum spanning tree was constructed via the MINSPN*Et al*gorithm, as implemented in ARLEQUIN, to show the relationship among haplotypes and was subsequently drawn by hand. Historical demography/ spatial expansions were inferred by neutrality testing and mismatch distribution analysis, as implemented in ARLEQUIN. Deviations from neutrality were evaluated using Fu's F_S and Tajima's *D*. Nucleotide mismatch distributions were applied to assess population growth and spatial range expansion. A molecular clock-based time estimate provided an approximate timeframe for evaluating phylogeographical hypotheses. Historical demographic expansions were also investigated via examination of frequency distributions of pair-wise differences between sequences (mismatch distribution) based on three parameters: θ_0, θ_1 (θ before and after population growth) and τ (time since expansion, expressed in units of mutational time) (Rogers and Harpending, 1992). The values of τ were transformed to estimate the time since expansion with the equation $\tau=2\times\mu\times t$, where *μ* is the mutation rate for the entire sequence under study, and *t* is the time since expansion. As no mutation rates have been reported for *S. japonicus*, this uncertainty was taken into account in our analyses in that the mutation rate (0.6% per million years) of COI was used as a prior uniform distribution to obtain a rough estimate of divergence time (1.2% per million years) (Bowen *et al.,* 2001). Bayesian skyline plots were created with BEAST v.8 (Drummond and Rambaut, 2007) to further evaluate the accuracy of the expansion time.

RESULTS

Genetic diversity

After manual correction, the fragment obtained was determined to be 655 bp in length, which corresponds to the 5,567 - 6,221 bp region of the complete mitogenome of *S. japonicus* (AB488405). Nine variable sites and four parsimony-informative sites were detected in the target fragment. In addition, eight transitions and one transversion but no insertions/deletions were found. The ratio of transitions to transversions was found to be

8, indicating that mutations in the mitochondrial COI sequence of *S. japonicus* had not reached saturation. The A+T content (50.13%) was slightly higher than the G+C content, indicating an AT bias.

A total of nine haplotypes were defined among the 120 individuals (Table II).Three haplotypes were shared by four populations, and one haplotype was shared by two populations. The Pingtan population exhibited three specific haplotypes, whereas the Xiamen and Keelung populations each exhibited one haplotype. Moderate levels of haplotype diversity (*h*) and low levels of nucleotide diversity (*π*) were detected in this species. Overall, the average values of *h* and *π* were calculated to be 0.1129±0.0393 and 0.0003±0.0002, respectively (Table I).

Table II.- Distribution of haplotypes in the four *S. japonicus* populations.

Haplotype	Ningde	Pingtan	Xiamen	Keelung	Total
Hap1	9	10	16	5	40
Hap2	1	0	0	0	1
Hap3	5	4	3	2	14
Hap4	13	14	10	19	56
Hap5	2	2	0	0	4
Hap6	0	0	1	0	1
Hap7	0	0	0	1	1
Hap8	0	0	0	1	1
Hap9	0	0	0	2	2

Genetic structure

An NJ tree was constructed based on COI sequences from 120 *S. japonicus* individuals, with *S. tenuifilis* used as the outgroup. However, no phylogenetic structure corresponding to geographic location was detected, and the sequences of all populations were randomly distributed on the NJ tree (Fig. 2). Haplotype network analysis revealed the presence of two main haplotypes without an obvious phylogenetic structure, and the center of each sub-branch contained a shared haplotype with a relatively high distribution frequency. This result was consistent

with the NJ tree, suggesting that the studied *S. japonicus* populations may have undergone a recent expansion event (Fig. 3).
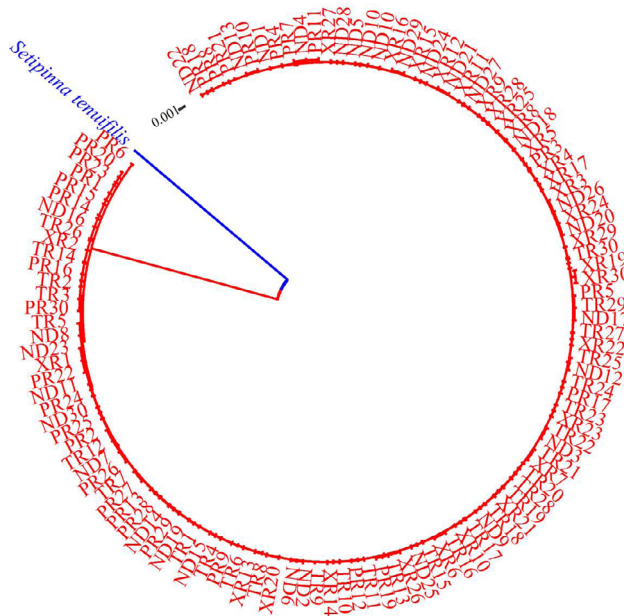

Fig. 2. NJ tree of COI haplotypes of *S. japonicus*. *S. tenuifilis* was used as the outgroup. Bootstrap supports >50 in 1,000 replicates are shown.

Table III.- AMOVA of *S. japonicus* populations based on mitochondrial COI sequences.

Source of variation	Sum of squares	Percentage	*F* statistic	*P*
One gene pool				
Among populations	1.308	0.28		
Within populations	46.700	99.72	F_{ST}= 0.0028	0.000
Two gene pools (Ningde, Pingtan, Xiamen) (Keelung)				
Among groups	0.131	-2.56	F_{CT}=-0.0256	0.346
Among populations within groups	1.178	1.56	F_{SC}=0.0152	0.200
Within populations	46.700	101.00	F_{ST}=-0.0100	0.037

All *S. japonicus* populations were considered one gene pool for AMOVA analysis, and the results showed that the divergence was attributable to 99.72% of the genetic variation among the populations with statistical significance. To further investigate the possible effects, four populations were assigned to two pools, the western waters of the Taiwan Strait (Ningde, Pingtan and Xiamen) and the eastern waters of the Taiwan Strait (Keelung), and the results showed that 101% of genetic variation was derived from within populations and -2.56% from among

groups (*P*<0.05) (Table III). Therefore, the divergence among populations was very weak with no statistical significance (F_{CT}=-0.026, *P*>0.05) (Table III). In all cases, no significant genetic structure was identified across the sampled geographical range of this species.
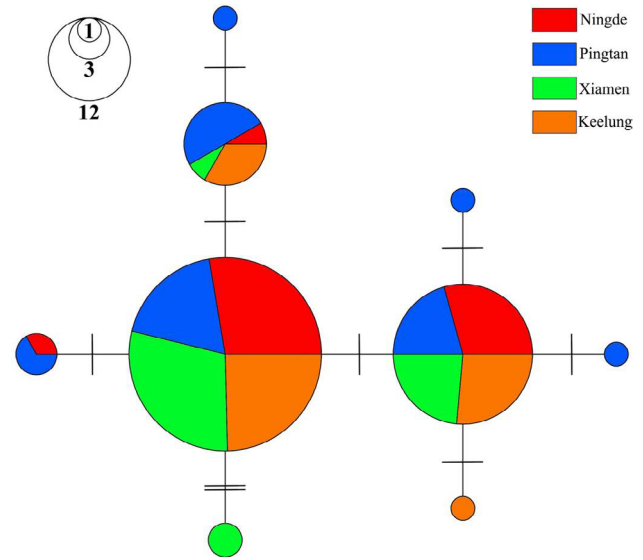

Fig. 3. Unrooted minimum spanning tree depicting the genetic relationship among *S. japonicus* COI haplotypes. Circle sizes are proportional to the haplotype frequency. Perpendicular tick marks on the lines joining the haplotypes represent the number of nucleotide substitutions.

Table IV.- Matrix of pairwise *F*$_{ST}$ (below diagonal) and gene flow (above diagonal) between *S. japonicus* populations.

	Ningde	Pingtan	Xiamen	Keelung
Ningde		12.91	20.58	15.38
Pingtan	0.019		8.68	20.58
Xiamen	-0.012	0.028		22.48
Keelung	-0.016	-0.012	-0.001	

The F_{ST} values between the four populations were very low (0.001~0.028), and all the observed population pairwise F_{ST} statistics were statistically non-significant after the sequential Bonferroni correction (*P*>0.05; Table IV), suggesting a pattern of overall mitochondrial COI homogeneity of *S. japonicus*. Negative F_{ST} values were found between Ningde and Xiamen and between Keelung and other populations, which suggests that the genetic differentiation among individuals was higher than that within populations. The gene flow among the four populations ranged from 8.68 to 22.48, suggesting frequent gene flow (Table IV). Exact *P* tests for population

differentiation (test of haplotype frequencies) were also non-significant ($P>0.05$), indicating very weak genetic differentiation and supporting the null hypothesis of panmixia.

Historical demographics

The nucleotide mismatch distribution showed a unimodal pattern that was similar to a normal distribution and consistent with the expected distribution in the population expansion model (Fig. 4). Both Tajima's *D* value and Fu's *Fs* value were negative and statistically significant (Table V). In addition, both *SSD* and *HRI* tests were not statistically significant ($P>0.05$).

All results indicated that the *S. japonicus* evolutionary model significantly deviated from neutrality and coincided with the null hypothesis of the sudden expansion model. The value of τ was calculated to be 0.918, and the time since expansion for *S. japonicus* was roughly estimated to be in the late Pleistocene. The Bayesian skyline plots revealed a detailed demographic history of changes in population size, from which we could see that *S. japonicus* underwent population expansion in the late Pleistocene. The effective population size increased slowly after the

last glacial maximum (LGM) approximately 8.9×10^4 years before the present (Fig. 5), which is consistent with the results of Cheng *et al*. (2018).
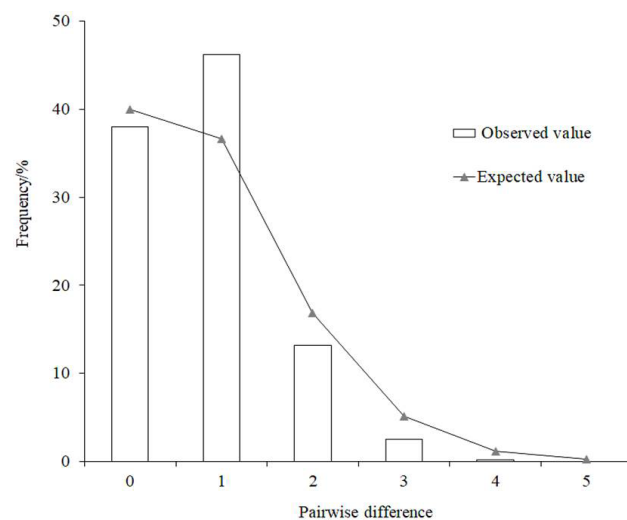

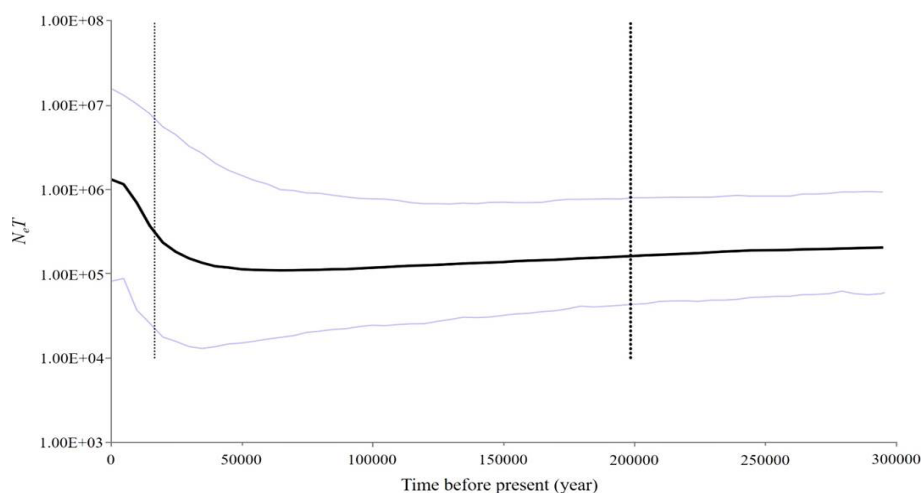Fig. 4. The mismatch distribution of COI haplotypes of *S. japonicas.*

Fig. 5. Bayesian skyline plots showing N_{ef}T (N_{ef} is effective population size and T is generation time) changes in *S. japonicus* over time based on COI sequences. The upper and lower limits of the blue line represent the 95% confidence intervals of highest posterior densities (HPD) analysis. The black line represents median estimates of N_{ef}T.

Table V.- Results of neutral tests and goodness-of-fit tests.

Populations	Tajiam's *D*		Fu's F_S		Goodness-of-fit tests			
	D	*P*	*Fs*	*P*	*SSD*	*P*	*HRI*	*P*
Ningde	-0.510	0.035	-0.822	0.023	0.028	0.060	0.205	0.051
Pingtan	-0.718	0.026	-2.297	0.045	0.015	0.120	0.134	0.062
Xiamen	-0.714	0.030	-0.351	0.038	0.002	0.670	0.093	0.540
Keelung	-0.026	0.058	-0.236	0.040	0.022	0.070	0.172	0.070
Total	-1.263	0.041	-3.747	0.054	0.012	0.060	0.128	0.051

DISCUSSION

Due to the characteristics of rapid rate of evolution, maternal inheritance, and easy-to-detect interpopulation genetic differences, mitochondrial genes are considered efficient genetic markers for assessing genetic variation and distinguishing different populations (Aquadro and Greenberg, 1983). Indeed, such markers have been applied in studies on many species (Wu *et al*., 2012; Sun *et al*., 2013, 2017; Yan *et al*., 2015; Cheng and Sha, 2017).

Genetic diversity

Over the long course of evolution, the level of genetic diversity is closely related to the survival and evolutionary potential of a species, and it can be evaluated by two important indicators: h and π. Analyzing the genetic diversity and genetic structure of a species can help to both understand its evolutionary history and provide an important basis for analyzing its evolutionary potential and predicting its direction of development (Soltis and Soltis, 1991). The h of *S. japonicus* was moderate, whereas the π was low, which was similar to the results for *S. tenuifilis* (Zhang *et al*., 2015), *Pampus argenteus* (Peng *et al*., 2009; Wu *et al*., 2012), and other ocean fishes distributed in the same waters. The reason for this phenomenon may be that the populations of each generation highly overlap with each other, and the fluctuation in the effective population size is small, resulting in relatively consistent contributions by breeding populations. Such a phenomenon is common in marine fishes with a pelagic stage (Grant and Bowen, 1998). The h and π pattern of *S. japonicus* was in line with the second population rapid growth hypothesis of marine fishes proposed by Grant and Bowen (1998). Overall, this species may have undergone a population expansion event after experiencing a period with a small effective population size; this speculation was also confirmed by our subsequent historical dynamic analysis.

Such genetic diversity characteristics of *S. japonicus* in the Taiwan Strait and its adjacent waters are mainly associated with the following aspects: (1) In general, widespread species have higher genetic diversity than those distributed in a small region (Hamrick *et al*., 1991). As an important commercial fish species, *S. japonicus* is widely distributed in the coastal areas of the northwest Pacific, such as China, Japan, and the Korean peninsula. The broad habitat range indicates that these species face relatively low natural selection pressure and can accumulate more genetic variation. (2) *S. japonicus* has a short life cycle with characteristics of rapid growth, early sexual maturity, quick generation alternation, and strong ability for resource recruitment and restock (Yan *et al*., 1986; Li *et al*., 2014). These characteristics allow *S.*

japonicus resources to be maintained in a good condition and be less prone to genetic bottleneck, thereby preserving their rich genetic diversity. (3) The sex ratio of the *S. japonicus* population in the Taiwan Strait and its coastal waters is nearly 1:1, which ensures an effective population size (Wang *et al*., 1983; Yan, 1997) and reduces genetic diversity loss (Chopelet *et al*., 2009).

Genetic structure

According to the gene flow theory by Hartl and Clark (1989) and considering the AMOVA, the F_{ST} value and the exact P test results, the studied *S. japonicus* populations appear to belong to a panmictic population with nonsignificant genetic differentiation and no genetic structure. As few geographical barriers are present in an open ocean environment, genetic differentiation between various geographic populations of marine fish that can migrate long distances or engage in pelagic life is low, which could lead to frequent gene flow among different populations. This is mainly attributed to the substantial dispersal and high connectivity of pelagic eggs, juveniles and adult fish (Grant and Bowen, 1998).

In fact, *S. japonicus* eggs are pelagic. Fertilized eggs hatch into larvae within 56h at a water temperature of 19°C, and the pelagic period of the larvae is 16 (22.1°C) to 24 (16.8°C) days (Hunter and Kimbrell, 1980; Zhu *et al*., 1985), suggesting that the eggs and the larvae of this species have a strong dispersal capacity. The Taiwan warm current, the South China Sea monsoon drift, the northward current along the Taiwan Strait, the Zhemin coastal current converge at the study area, and the ocean circulation favors dispersion of eggs and larvae in these waters (Fu, 1997). Some populations of *S. japonicus* at the juvenile fish stage in the Minnan-Taiwan bank fishing ground can reach the coastal waters of the Minnan and Mindong in summer, becoming recruit populations in the Mindong fishing ground. This may occur under the combined effect of the Taiwan warm current and the northward current along the Taiwan Strait. In addition, *S. japonicus* exhibits an obvious seasonal migration. The *S. japonicus* Minnan population inhabits the Minnan-Yuedong fishing ground for almost their entire life cycle and only migrates for short distances, with a spawning period from December to June of the following year. The *S. japonicus* Mindong population has two overwintering grounds: one near the100 meters isobath north of Taiwan and the other in the south-central water of the Taiwan Strait (co-occurring with the Minnan population) (Yan, 1997). Every March to May, *S. japonicus* arrives at the Minzhong and Mindong fishing grounds from these two overwintering grounds for spawning and feeding migration, with a spawning period from April to July (Yan, 1997). The overlap of the overwintering ground and the

spawning period can provide a platform for gene flow among different populations of this species. In summary, the strong dispersal ability and migratory characteristics, as well as the marine circulation, may explain the high genetic homogeneity between the *S. japonicus* populations in the Taiwan Strait. In addition, the time for population expansion of *S. japonicus* in the waters was relatively late (117,000 years ago), and insufficient time has accumulated to attain migration-drift equilibrium (Avise, 2000; Liu *et al.*, 2007).

Historical demographics

Both the nucleotide mismatch distribution and neutrality test results suggested that the species experienced a population expansion event in the late Pleistocene. After the expansion, the effective population size increased dramatically (Slatkin and Hudson, 1991; Rogers and Harpenfing, 1992). Furthermore, some recent studies have suggested that the Pleistocene underwent a series of changes in glacial-interglacial periods, which led to corresponding changes in climate, sea level, salinity, temperature, and ocean current patterns that had crucial impacts on the biological distribution and the number of populations (Avise, 2000; Liu *et al.*, 2007; Wu *et al.*, 2012; Cheng *et al.*, 2018). It can be speculated that the distribution of *S. japonicus* was likely drastically affected by glacial periods, and its distribution was narrowed to the refuge of the East China Sea Basin during the middle Pleistocene. Along with the rise in sea level, a recolonization event and gene flow may have occurred from this refuge after the last glaciation. In this context, the spatial distribution of *S. japonicus* haplotypes is probably indicative of secondary contact during interglacial periods of global warming.

The results of nucleotide mismatch distribution and neutrality test indicated a strong deviation from neutrality and verified that the *S. japonicus* population experienced a population expansion event. Similar results from historical dynamic analyses have been obtained in *P. argenteus* (Wu *et al.*, 2012; Sun *et al.*, 2013), *P. chinensis* (Sun *et al.*, 2017), *Oratosquilla oratoria* (Cheng and Sha, 2017), and *Chelon haematocheilus* (Liu *et al.*, 2007), whose distribution overlaps with that of *S. japonicus.*

The complex hydrologic environment of the Taiwan Strait and its adjacent waters did not prevent gene flow among *S. japonicus* populations. Therefore, genetic differentiation among the different populations is quite weak, so these populations should belong to the same fishery management unit. To avoid the disaster that has fallen on small yellow croaker and other traditional commercial fish resources, the fisheries resources of *S. japonicus* should be utilized and developed more rationally. For example, more measures should be taken to limit the mesh size, reduce the fishing intensity, and enforce fish ban. Traditional fish population management considers a single fish species as the starting point, recognizing that the overexploitation and utilization of a single species (especially a low-trophic-level species) will cause drastic fluctuations in other species resources. Therefore, we should monitor the sensitive fisheries resources from the perspective of sustainable utilization to generate a reasonable and scientific marine development system and to promote the sustainable development of fisheries resources.

Statement of conflict of interest

The authors declare that they have no conflicts of interest related to the implementation of the experiments or the writing of this manuscript.

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