African Journal of Biotechnology Vol. 8 (18), pp. 4308-4315, 15 September, 2009
Available online at http://www.academicjournals.org/AJB
ISSN 1684–5315 © 2009 Academic Journals

Full Length Research Paper

Analysis of genetic structure of white croaker using amplified fragment length polymorphism (AFLP) markers

Zhi Qiang Han[1], Bo Nian Shui[1], Zhi Yong Wang[2], Zhen Qing Miao[1] and Tian Xiang Gao[1,3]*

[1]Fishery College, Zhejiang Ocean University, Zhoushan, 316004 P. R. China.
[2]Fisheries College, Jimei University, Xiamen 361021 P. R. China.
[3]The Key Laboratory of Mariculture, Ministry of Education, Ocean University of China, Qingdao 266003 P. R. China.

Accepted 20 July, 2009

The genetic structure of 4 populations of white croaker *Pennahia argentata* was analyzed by amplified fragment length polymorphism (AFLP) technology. A total of 304 putative loci were detected by the 5 primer combinations, of which 200 were polymorphic. The proportion of polymorphic loci among four populations varied from 47.13 to 57.63%. The population with the highest Nei's genetic diversity and Shannon diversity index was Ariake Sea population, the lowest Nei's genetic diversity and Shannon diversity index was found in Ise Bay population. Two geographic clades (Chinese clade and Japanese clade) were detected among 70 individuals of white croaker by AFLP markers; molecular variance analysis and pairwise F_{ST} also supported the separation of Chinese and Japanese populations of *P. argentata*. The Pleistocene isolation and biological characteristics of species may be responsible for the genetic differentiation of *P. argentata* between China and Japan coastal waters. Our result also revealed that white croaker might choose the retention larval strategy within coastal waters to minimize the offshore dispersal.

Key words: White croaker, *Pennahia argentata*, amplified fragment length polymorphism (AFLP), genetic structure.

INTRODUCTION

Representatives of the family Sciaenidae (croakers or drums) are widely distributed in shelf waters of the tropical and subtropical Indian, Pacific and Atlantic oceans and are important components of fisheries in several countries (Fischer and Bianchi, 1984). *Pennahia argentata*, a member of this family, commonly called white croaker, is one of the important economically sciaenid species and widely distributed in northwestern Pacific, ranging from Tohoku, Japan to Guangdong, China (Zhu et al., 1963; Yamada et al., 2000). It is a demersal fish that inhabits sandy or muddy bottoms in coastal inlets to a depth of 140 m and is a major component of demersal fish assemblages off the coasts of China and Japan, supporting an important commercial fishery (Taki, 2000).

*Corresponding author. E-mail: gaozhang@ouc.edu.cn

However, over-fishing, heavy marine pollution and deterioration of marine ecosystem have brought risk of exhaustion to the resource of white croaker (Seikai National Fisheries Research Institute, 2001). In recent years, the commercial catch in the East China Sea has dramatically decreased from more than 20,000 tones (the highest level in history) to 22 tones in year 2000 (Yamaguchi et al., 2004).

Previous studies mainly focused on the biological characteristics (Chen et al., 2005; Lan and Luo, 1995, Yamaguchi et al., 2004, 2006) and little information related to the genetic structures of white croaker is available (Menezes et al., 1990). Larval dispersal plays a fundamental role in the ecology and evolution of marine organisms (Caley et al., 1996; Strathmann et al., 2002). Marine organisms with high dispersal potential generally show low levels of genetic differentiation over large geographical distances (Palumbi, 1994). White croaker is

a multiple spawner with pelagic eggs and larva. Spawning occurs inshore in shallow waters and eggs hatch in about 22-33 h at 22-24℃ (Seikai National Fisheries Research Institute, 2001). In the close relatives *Nibea albiflora* and *N. miichthioides,* the length of the pelagic larval stage are about 25 to 32 days (Lei and Fan, 1981; Takita, 1974). The length of larval stage in white croaker might be long. Such a species with long planktonic larval stage of about a month may be expected to have high dispersal potential, causing a decrease in the genetic or demographic differentiations among local populations. However, several distinguishable local stocks of white croaker around China and Japan coastal waters have been identified by different spawning grounds, migration routes and overwintering grounds (Seikai National Fisheries Research Institute, 2001). Whether these stocks of white croaker in China and Japan coastal waters are independent biological units has not been recently investigated by DNA markers.

An accurate definition of population structure is important for the management of commercial marine fishes. The conservation of genetic diversity is also important for the long-term interest in any species. Determination of population genetic structure is essential information to underpin resource recovery and to aid delineating and monitoring populations for fishery management. Failure to detect population units can lead to local over fishing and ultimately to severe declines (Zhang et al., 2006). In order to effective conservation and use of white croaker, it is first necessary to obtain knowledge of its genetic background.

Molecular markers have been very useful for analysis of genetic structure and genetic diversity. Among the several marker systems, amplified fragment length polymorphism (AFLP) (Vos et al., 1995) is highly reliable for the assessment of genetic variation among and within populations. AFLP is a PCR-based, multi-locus fingerprinting technique that combines the strengths and overcomes the weaknesses of the RFLP and RAPD methods. The major strengths of the AFLP method include large (over 100) numbers of revealed polymorphisms, high reproducibility due to high PCR annealing temperatures and requiring no prior sequence knowledge of species. It has been widely used in the field of population genetics and often cast light on population structure and gave useful information for the management of resources (Liu and Cordes, 2004). AFLP has been successfully applied in many marine fish species such as large yellow croaker (*Pseudosciaena crocea*), Yellowback sea bream (*Dentex tumifrons*) and *Paralichthys olivaceus* (Wang et al., 2002; Xia and Jiang, 2006). Some researchers have simplified, optimized and improved the AFLP protocol so that it was easily performed and had higher resolution to polymorphic loci (Habu et al., 1997; Suazo and Hall, 1999). In this study, 4 geographic populations of white croaker collected from China and Japan were analyzed using AFLP. This study provides insight into the genetic structure of this species and assesses the gene flow between China and Japan coastal waters.

MATERIALS AND METHODS

Sample collection

Seventy specimens were collected from four geographic locations (A170, B21, Ariake Sea and Ise Bay) across the East China Sea and Japan coastal waters from 2003 to 2005 (Figure 1, Table 2). The whole fish was frozen and shipped to the Ocean University of China. Muscle samples were obtained and preserved in 95% ethanol or frozen for DNA extraction after specimen identification and morphological measure.

AFLP analysis

Genomic DNA was isolated from muscle tissue by proteinase K digestion followed by a standard phenol–chloroform method. DNA was subsequently resuspended in 100 µL of TE buffer (10 mmol/L Tris-Cl, 1 mmol/L EDTA, PH = 8.0). Procedures of AFLP were essentially based on Vos et al. (1995) and Wang et al. (2000). About 100 ng genomic DNA was digested with 1unit of *Eco*R I and *Mse* I (NEB) at 37°C for 6 h. Double-stranded adapters were ligated to the restriction fragments at 20°C overnight after adding 1 µL 10 × ligation buffer, 5 pmol E*co*R I adapter (E*co*R I-1/E*co*R I - 2; Table 1), 50 pmol *Mse* I adapter (*Mse*I-1/*Mse*I-2; Table 1), 0.3 unit of T4 DNA ligase (Promega) with a final volume of 10 µL. Preamplification PCR reaction was conducted using an Eppendorf thermocycler (Mastercycler 5334) with a pair of primers containing a single selective nucleotide. Amplification was performed at an annealing temperature of 53°C for 30 s. The 20 µL PCR product mixture was diluted 10 fold with distilled water and used as templates for the subsequent selective PCR amplification. The selective amplifications were carried out in 20 µL PCR reaction volume containing 1 µL productions of preamplifications, 1 × PCR reaction buffer, 150 µM of each dNTP, 30 ng of each selective primer and 0.5 unit of Taq DNA polymerase on a gradient thermal cycler (Mastercycler 5334) with a touchdown cycling profile of nine cycles of 30 s at 94℃, 30 s at 65℃ (–1℃ at each cycle) and 30 s at 72℃ followed by the cycling profile of 28 cycles of 30 s at 94℃, 30 s at 56℃ and 1 min at 72℃. The final step was a prolonged extension of 7 min at 72℃. PCR products were run on 6.0% denaturing polyacrylamide gel electrophoresis (PAGE) for 2.5 h at 50℃ on the Sequi-Gen GT sequencing cell (Bio-Rad, USA) and finally detected using the silver staining technique modified from Merril et al. (1979). Sequences of AFLP adapters and primers are listed in Table 1. Five primer combinations (E-AGG/M-CAC, E-AGG/M-CTC, E-AGG/M-CAT, E-AAG/M-CAT and E-AAG/M-CTA) were chosen for AFLP analysis (Table 1).

Data analysis

AFLP bands were scored for presence (1) or absent (0) and transformed into 0/1 binary character matrix. Proportion of polymorphic loci, Nei's genetic diversity and Shannon diversity index were calculated by POPGEN. Similarity indices were calculated using the formula $S = 2N_{ab}/(N_a+N_b)$ (Nei and Li, 1979), where N_a and N_b are the number of bands in individuals a and b, respectively and N_{ab} is the number of sharing bands. Genetic distances between individuals were computed using the formula $D = -\ln S$ (Nei and Li, 1979). Genetic relationships among populations were estimated by constructing UPGMA tree based on Nei's standard genetic distance (Nei, 1972) in Mega 3.0. Population structure of white croaker was investigated using the molecular variance software package (AMOVA) and *F*-statistics in ARLEQUIN 2.000 (Schneider et al., 2000).

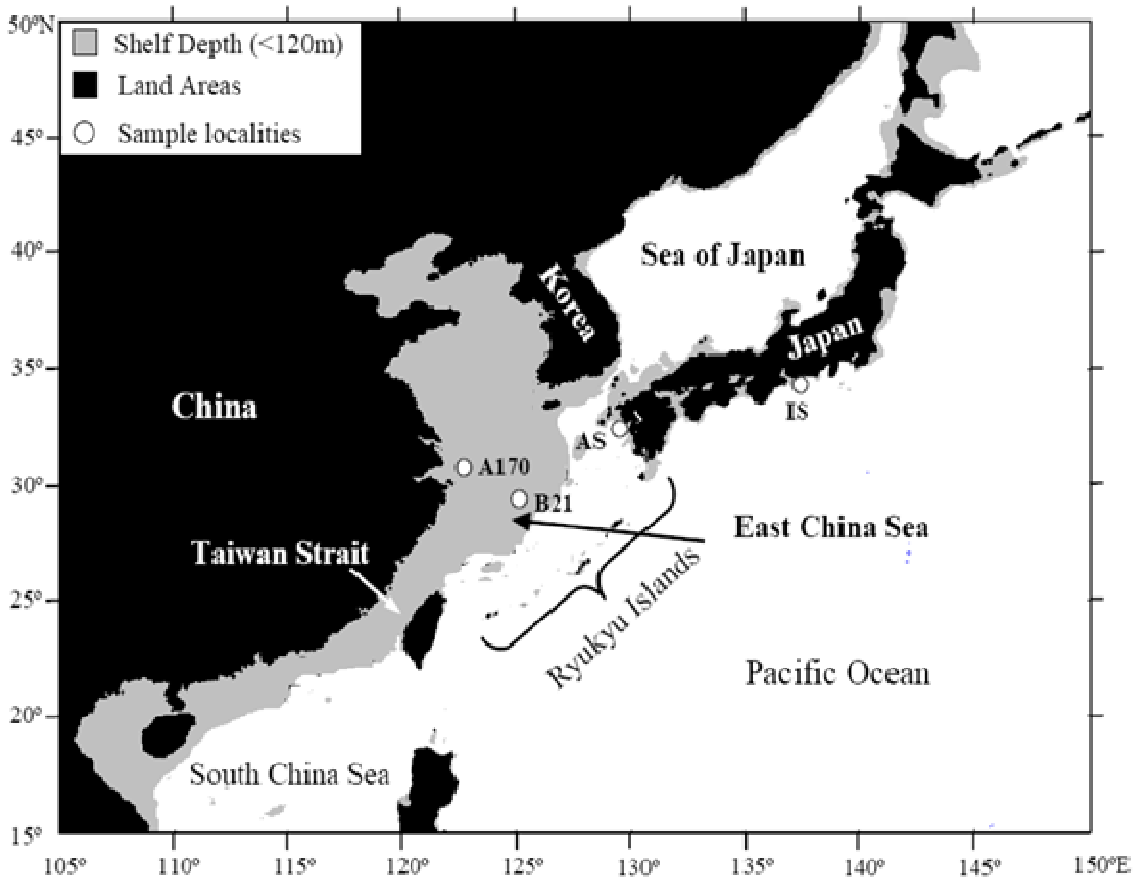

Figure 1. Sample locations of *Pennahia argentata*.

Table 1. Adaptor and primer sequences used in AFLP analysis.

Primer	Sequence
Adapters	
*Eco*RI-adapter	5'-CTCGTAGACTGCGTACC-3' 5'-AATTGGTACGCAGTCTAC-3'
*Mse*I-adapter	5'-GACGTGAGTCCTGAG-3' 5'-TACTCAGGACTCAT-3'
Pre-amplification primer	
*Eco*RI	5'-GACTGCGTACCAATTC-3'
*Mse*I	5'-GATGAGTCCTGAGTAA-3'
Selective amplification primer	
E-AGG/M-CAC	5'-GACTGCGTACCAATTCAGG-3' 5'-GATGAGTCCTGAGTAACAC-3'
E-AGG/M-CTC	5'-GACTGCGTACCAATTCAGG-3' 5'-GATGAGTCCTGAGTAACTC-3'
E-AGG/M-CAT	5'-GACTGCGTACCAATTCAGG-3' 5'-GATGAGTCCTGAGTAACAT-3'
E-AAG/M-CAT	5'-GACTGCGTACCAATTCAAG-3' 5'-GATGAGTCCTGAGTAACAT-3'
E-AAG/M-CTA	5'-GACTGCGTACCAATTCAAG-3' 5'-GATGAGTCCTGAGTAACTA-3'

Table 2. Parameters of genetic diversity for populations of white croaker.

Populations	n	Date of collection	Number of loci	Number of polymorphic loci	Proportion of polymorphic loci	Nei's genetic diversity	Shannon diversity index
A170	9	Apr 2004	227	107	47.13%	0.0949	0.1496
B21	13	Apr 2004	229	112	48.91%	0.0941	0.1490
Ariake Sea	24	Mar 2005	262	151	57.63%	0.0956	0.1594
Ise Bay	24	Sep 2005	245	131	53.47%	0.0738	0.1262

Table 3. Number of bands generated by primer combinations.

Locus	E-AGG/ M-CAC	E-AGG/ M-CTC	E-AGG / M-CAT	E-AAG/ M-CAT	E-AAG/ M-CTA	Total
Number of loci	60	64	60	62	58	304
Number of polymorphic loci	42	37	49	33	39	200
Proportion of polymorphic loci	70.00%	57.81%	81.67%	53.22%	67.24%	65.79%

RESULTS

In the range between 50 - 500 base pairs, a total of 304 putative loci were detected by the 5 primer combinations, of which 200 were polymorphic (Table 3). The number of polymorphic loci amplified by each primer combination over all populations ranged from 33 to 49, with the average of 40 polymorphic loci per prime combination. Figure 2 showed the AFLP fingerprints generated by primer combination E-AGG/M-CAT.

The population with the highest proportion of polymorphic loci and number of polymorphic loci was Ariake Sea, whereas that with the lowest values was A170. The population with the highest Nei's genetic diversity and Shannon diversity index was Ariake Sea population, the lowest Nei's genetic diversity and Shannon diversity index was found in Ise Bay population (Table 2).

Nei's genetic distances among four populations were from 0.1291 to 0.1749. The greatest genetic distance was between the populations B21 and Ise Bay. Based on the UPGMA tree (Figure 3), the 4 populations were clustered into 2 groups. The Chinese group, included populations A170 and B21, was from locations in the East China Sea shelf. The populations Ariake Sea and Ise Bay from the Japan Islands were clustered as the Japanese group. Two specific bands had been amplified by primer combination E-AGG/M-CAT, which supported the genetic break between China and Japan populations (Figure 2). The UPGMA tree of all individuals also revealed 2 reciprocal monophyly clades (Figure 4). In Chinese clade, all individuals from A170 and B21 clustered together; Japanese clade contained all individuals from Ariake Sea and Ise Bay.

The significant separation of the 2 groups was supported by AMOVA, with 19.21% of all variance being partitioned between the 2 groups (F_{CT} = 0.1921, P < 0.001). AMOVA analysis also revealed the significant genetic differentiation between populations within 2 groups (F_{SC} = 0.0799, P < 0.001), suggesting significant population structures in both groups. Among 4 populations, all pairwise F_{ST} values especially the F_{ST} values between the 2 groups were high and significant (P < 0.05), supporting significant genetic differentiation among populations and high limited gene flow between the two groups (Table 4).

DISCUSSION

Marine fishes generally show low levels of genetic differentiation among geographic regions due to higher dispersal potential during planktonic egg, larval, or adult history stages coupled with an absence of physical barriers to movement between ocean basins or adjacent continental margins (Grant and Bowen, 1998; Hewitt, 2000). White croaker with long planktonic larval stage might confirm to this pattern. Preliminary allozyme analysis of white croaker in the same area showed a similar trend with weak genetic differentiation (Pairwise F_{ST} values between populations calculated from allozyme data were not significant) between the East China Sea and the Japan coastal waters (Menezes at al., 1990). However, contracting to this hypothesis, significant genetic differentiation between China and Japan groups has been revealed by AFLP markers. The topology of UPGMA tree based on AFLP marker revealed 2 clades. The pairwise F_{ST} values between populations within the East China Sea and Japan groups were all significant, indicating significant population structures within both groups and limited gene flow between populations. These results suggested several distinct stocks in white croaker.

The causes of differentiation in marine organisms are not well understood. In marine environments, the geo-

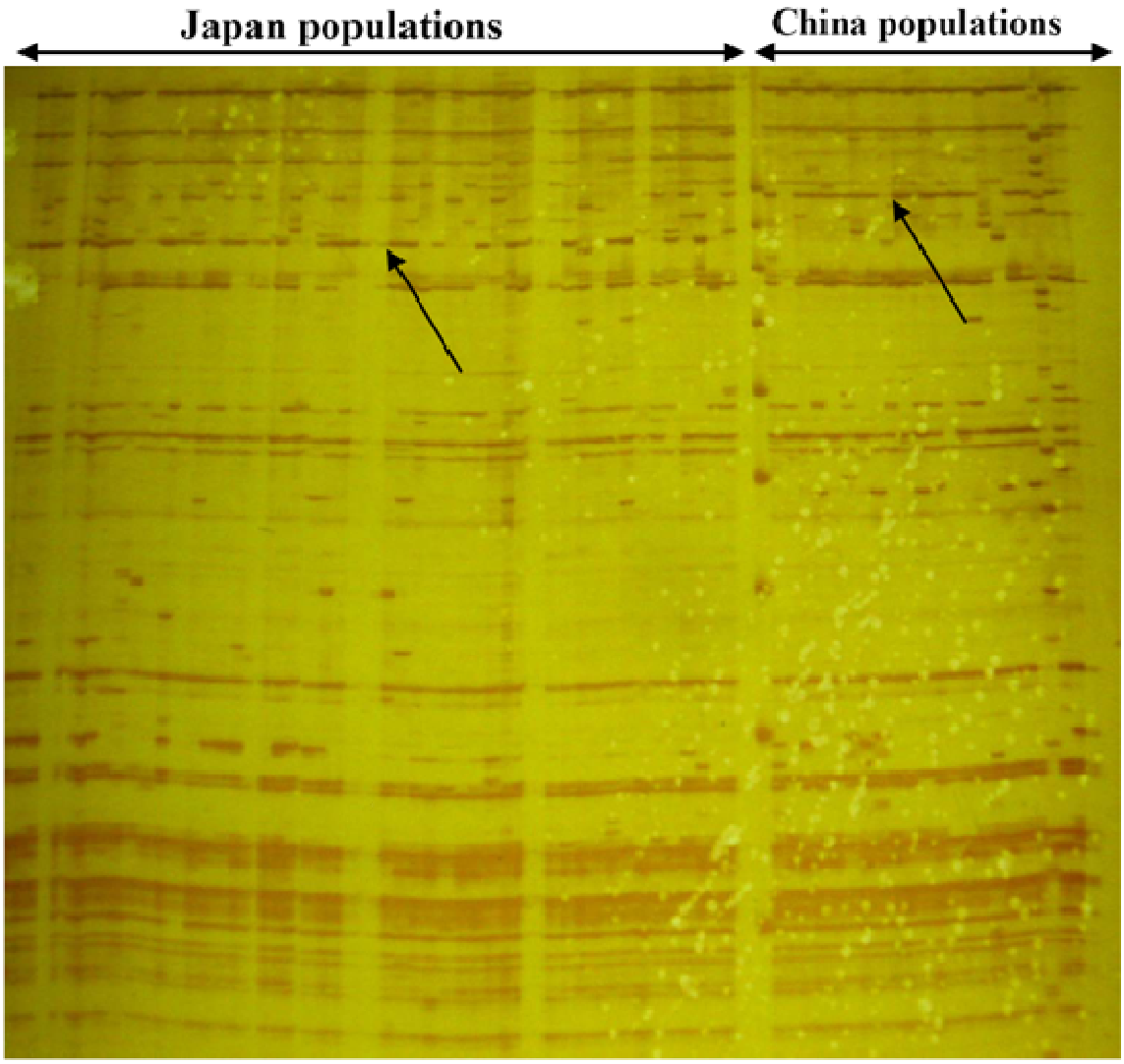

Figure 2. AFLP fingerprints generated by primer combination E-AGG/M-CAT. Arrows showed the specific bands in China populations and Japan populations.

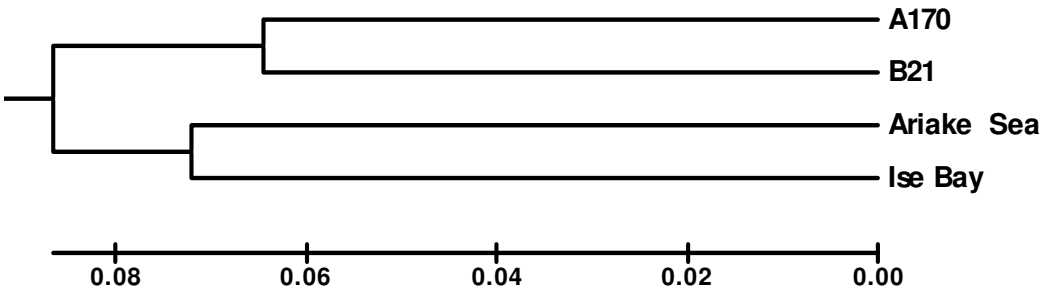

Figure 3. The UPGMA tree based on the Nei's genetic distances.

graphic structure of populations may be influenced by local environmental conditions and the life history of the species. The geographical structure of a species is not only due to present factors, but also more important to historical factors (Santos et al., 2003). The significant geographic structures of white croaker suggested that the dispersal of species is limited by some historical and present local factors, or species biological characteristics.

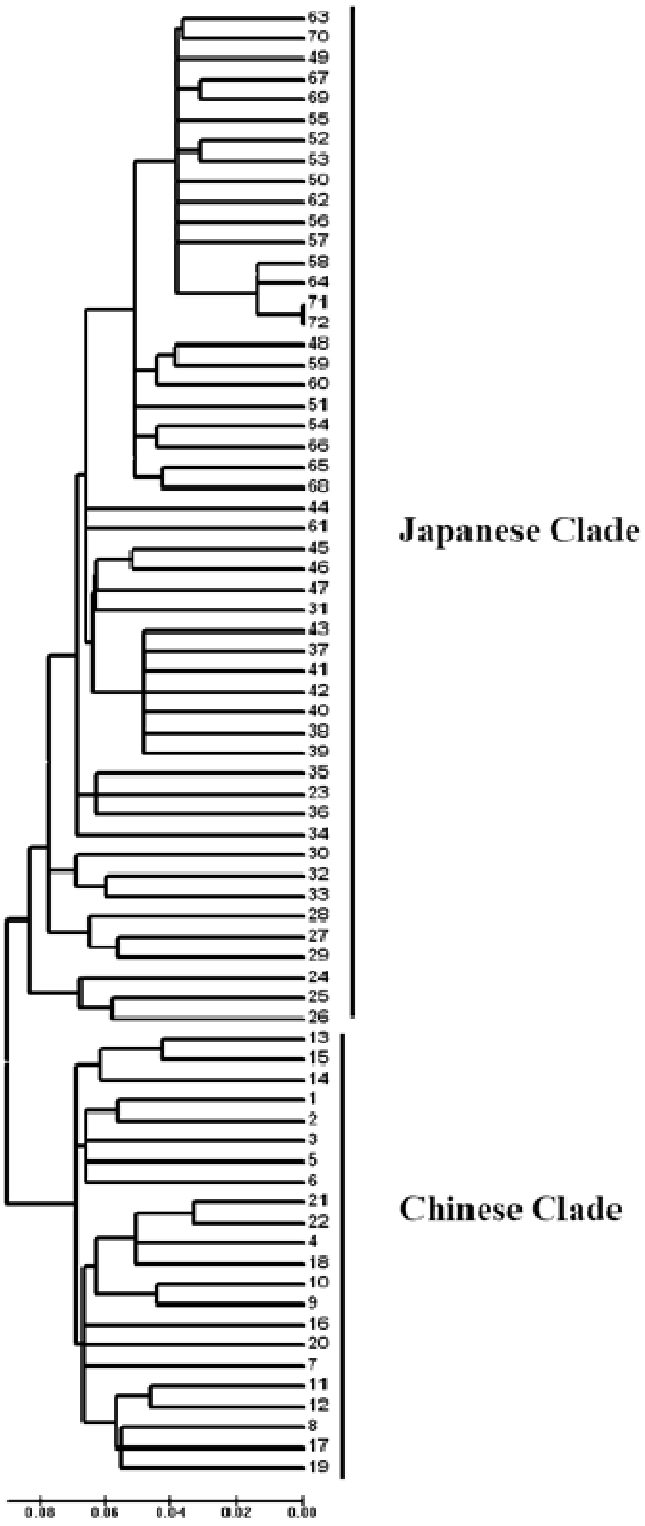

Figure 4. UPGMA tree of all individuals based on the Nei and Li (1979) distance (1-9: A170; 10-22: B21; 23-46: Ariake Sea; 47-70: Ise Bay).

Previous genetic studies in northwestern Pacific demonstrated that Pleistocene ice ages had greatly influenced the genetic structures of marine organisms (Liu et al., 2006, 2007). During late quaternary glacial cycles, the sea-level-induced environmental signal was amplified in the marginal seas of the western Pacific (Wang, 1999), giving rise to drastic changes in areas and configurations of these seas and causing populations isolation and species speciation between the East China Sea and Pacific ocean. The gene flow between the East China Sea and Pacific ocean was interrupted by the land bridge, which extended from eastern China to Taiwan, the Ryukyus and probably to the main islands of Japan during the ice ages in late Pleistocene. The significant genetic differentiation between the 2 groups of white croaker might be caused by this historical physical barrier. This historical physical barrier was also respon-sible for the strong genetic break in redlip mullet *Chelon haematocheilus* and the divergence of 2 sea bass species (Liu et al., 2006, 2007). Our result also supported that the land bridge formed in Pleistocene was the major factor to cause significant differentiation between the East China Sea and Japan populations.

The biological characteristics of white croaker may also be responsible for the genetic differentiation of the 2 groups. Ecology studies on white croaker revealed different over-wintering grounds, spawning grounds, spawning period and spawning migration routes in China and Japan coastal waters (Seikai National Fisheries Research Institute, 2001). In the East China Sea, white croaker does not migrate with long distance, only migrates in south and north within short distance and spawns eggs along the East China Sea coast. In the Japanese coastal waters, no long distance migration was also observed. The primary spawning grounds in Japan are in the coastal waters of Ariake Sea and Ise Bay. Yamaguchi et al. (2006) reported geographic variation in spawning season and age at sexual maturity of females among the yellow sea, East China Sea and Ariake Sea. As these biological characteristics coupled with different migration routes, different mating periods and specific spawning grounds may predispose white croaker to genetic structuring along its geographical distribution.

Besides above factors, another reason for genetic differentiation among populations of white croaker could be that dispersal is prevented by behavioural mechanisms that act to prevent transport of larvae between populations (Planes et al., 2001). Coastal marine fishes utilize near-shore or estuarine habitat as nursery grounds for larvae and juveniles. In contrast to pelagic or reef-based species, where reproduction often involves long-distance transport of larvae, such coastal species have developed strategies to minimize offshore transplant of larvae (Checkley et al., 1988; Liu et al., 2007). The pelagic larvae of white croaker are typically found in near-shore waters and post-larvae migrate to inshore waters and shallow estuaries, indicating limited offshore dispersal for this species. The AFLP marker revealed genetic break between China and Japan groups and significant differentiation within groups, supporting that white croaker choose the

Table 4. Nei's genetic distance (above) and pairwise F_{ST} (below) between populations.

	A170	B21	Ariake Sea	Ise Bay
A170		0.1292	0.1749	0.1727
B21	0.0283*		0.1729	0.1716
Ariake Sea	0.1918**	0.2012**		0.1440
Ise Bay	0.3081**	0.3139**	0.1014**	

*Significant P < 0.05; ** significant P values after Bonferroni correction.

larval dispersal strategy to retain larvae within the coastal waters and minimize offshore trans-plant of larvae between China and Japan coastal waters.

In conclusion, our results showed that white croaker experienced limited gene flow between China and Japan groups, suggesting existence of different stocks. The AFLP marker was consistent with the previous allozyme results (Han et al., 2008). However, only 22 individuals were analyzed in the East China Sea, this is not a sufficient number of individuals in population genetics using variable markers. It is necessary to increase the individuals and use different molecular markers for assessing the genetic structures of white croaker.

ACKNOWLEDGMENTS

The present study could not have been carried out without the willing help of those listed below in collecting white croaker specimens: Dr. Koji Yokogawa, Mr. Minoru Tomiyama, Dr. Long-Shan Lin, Mr. Dian-Rong Sun. Prof. Nobuhiko Taniguchi provided technical assistance with species identification. This work was supported by the National Natural Science Foundation of China (30471329), State 863 High-Technology R&D Project of China (2006AA09Z418), the National Key Basic Research Program from the Ministry of Science and Technology, P.R. China (Grant no. 2005CB422306) and the Key Grant of Science and Technology Department of Zhejiang Province (2006C23051).

REFERENCES

Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996). Recruitment and the local dynamics of open marine populations. Ann. Rev. Ecol. Syst. 27: 477-500.

Checkley DM, Raman S, Maillet GL, Mason KM (1988). Winter storm effects on the spawning and larval drift of a pelagic fish. Nature, 335: 346-348.

Fischer W, Bianchi G (1984). FAO Species Identification Sheets for Fishery Purposes-Western Indian Ocean. Vol. IV. FAO, Rome.

Grant WS, Bowen BW (1998). Shallow population histories in deep evolutionary lineages of marine fishes: insights from sardines and anchovies and lessons for conservation. J. Hered. 89: 415-426.

Hewitt GM (2000). The genetic legacy of the Quaternary ice ages. Nature, 405: 907-913.

Habu Y, Fukada-Tanaka S, Hisatomi Y, Iida S (1997). Amplified restriction fragment length polymorphism-based mRNA fingerprinting using a single restriction enzyme that recognizes a 4-bp sequence. Biochem. Biophys. Res. Commun. 234:516–521.

Han ZQ, Gao TX, Zhuang ZM, Tang QS (2008). Genetic variation among white croaker populations. J. Ocean Univ. China. 7:25-30.

Lan YL, Luo BZ (1995). Age and growth of six sciaenid fishes (Sciaendae) in the East China Sea. Oceanol. Limnol. Sin. 26: 108-114.

Lei JL, Fan NC (1981). A preliminary observation on the morphological characteristics of mbryos, larvae and juveniles of *Nibea albiflora* (Richardson). Mar. Fish. Res. 2: 77-84.

Liu JZ, Cordes JF (2004). DNA marker technologies and their applications in aquaculture genetic. Aquaculture, 238: 1-37.

Liu JX, Gao TX, Yokogawa K, Zhang YP (2006). Differential population structuring and demographic history of two closely related fish species, Japanese sea bass (*Lateolabrax japonicus*) and spotted sea bass (*Lateolabrax maculatus*) in Northwestern Pacific. Mol. Phylogenet. Evol. 39: 799-811.

Liu JX, Gao TX, Wu SF, Zhang YP (2007). Pleistocene isolation in the marginal ocean basins and limited dispersal in a marine fish, *Chelon haematocheila* (Temminck & Schlegel, 1845). Mol. Ecol. 16: 275-288.

Menezes MR, Taniguchi N, Seki S (1990). Degree of intraspecific genetic divergence and variability in three sciaenid species. Jpn. J. Ichtyol. 37: 39-48.

Merril CR, Switzer RC, Van Keuren ML (1979). Trace polypeptides in cellular extracts and human body fluid detected by two-dimensional electrophoresis and a highly sensitive silver stain. Proc. Natl. Acad. Sci. USA, 76: 4335-4339.

Nei M (1972). Genetic distance between populations. Am. Nat. 106: 283-292.

Nei M, Li WH (1979). Mathematical model for studying genetic variation in terms of restriction endonucleases. Proc. Natl. Acad. Sci. USA, 76: 5269-5273

Planes S, Doherty PJ, Bernardi G (2001). Strong genetic divergence among populations of a marine fish with limited dispersal, *Acanthochromis polyacanthus*, within the great barrier reef and the coral sea. Evolution, 55: 2263-2273.

Palumbi SR (1994). Genetic divergence, reproductive isolation, and marine speciation. Annu. Rev. Ecol. Syst. 25: 547-572.

Santos S, Scheider H, Sampaio I (2003). Genetic differentiation of *Macrodon ancylodon* (Sciaenidae, Perciformes) populations in Atlantic coastal waters of South America as revealed by mtDNA analysis. Genet. Mol. Biol. 26: 151-161.

Schneider S, Roessli D, Excoffier L (2000). ARLEQUIN, version 2.0: A software for population genetic data analysis. University of Geneva, Geneva.

Seikai National Fisheries Research Institute (2001). Biological and ecological characteristics of valuable fisheries resources from the East China Sea and the Yellow sea-comparison between the Chinese and Japanese knowledges. Seikai National Fisheries Research Institute, Nagasaki.

Strathmann RR, Hughes TP, Kuris AM, Lindeman KC, Morgan SG, Pandolfi JM, Warner RR (2002). Evolution of local recruitment and its consequences for marine populations. B. Mar. Sci. 70: S377-S396.

Suazo A, Hall HG (1999). Modification of the AFLP protocol applied to honey bee (*Apis mellifera* L.). DNA Biotechniques 26:704–705, 708–709.

Taki Y (2004). Fish. In: Shitanaka N (eds). The Encyclopedia of Fish and Seafood. Heibonsha, Tokyo. pp. 47-163.

Takita T (1974). Studies on the early life history of *Nibea albiflora* Richardson) in Ariake Sound. Bull. Fac. Fish. Nagasaki Univ. 38:1-55.

Vos P, Hogers R, Bleeker M, Reijans M, Lee T, Hornes M, Friters A, Pot J, Paleman J, Kuiper M, Zabeau M" instead of "Vos P, Hogers R, Bleeker M, Reijans M (1995). AFLP: a new technique for DNA fingerprinting. Nucleos. Acids. Res. 23: 4407- 4414.

Wang Z, Jayasankar P, Khoo SK (2000). AFLP fingerprinting reveals genetic variability in common carp stocks from Indonesia. Asian Fish. Sci. 13: 139-147.

Wang PX (1999). Response of Western Pacific marginal seas to glacial cycles: paleoceanographic and sedimentological features. Mar. Geol. 156: 5-39.

Xia JH, Jiang SG (2006). Genetic structure of yellowback sea bream *Dentex tumifrons* in China inferred from AFLP data. Fish. Sci. 72: 829-834.

Yamada U (2000). Sciaenidae. In: Nakabo T (eds). Fishes of Japan with Pictorial Keys to the Species. Tokai University Press, Tokyo. pp. 867-870.

Yamaguchi A, Kume G, Higuchi T, Takita T (2004). Geographic variation in the growth of white croaker, *Pennahia argentata*, off the coast of northwest Kyushu, Japanese. Environ. Biol. Fish. 71: 179-188.

Yamaguchi A, Todoroki T, Kume G (2006). Reproductive cycle, sexual maturity and diel-reproductive periodicity of white croaker, *Pennahia argentata* (Sciaenidae), in Ariake Sound, Jpn. Fish. Res. 82: 95-100.

Zhang JB, Cai ZP, Huang LM (2006). Population genetic structure of crimson snapper *Lutjanus erythropterus* in East Asia, revealed by analysis of the mitochondrial control region. ICES J. Mar. Sci. 63: 693-704.

Zhu YD, Luo YL, Wu HL (1963). A Study on the Classification of the Sciaenoid Fishes of China, with Description of New Genera and Species. Shanghai Sci. Tech. Pub. Shanghai.