Population Genetic Structure of Silver Croakers, *Pennahia argentata* (Houttuyn, 1782), in the Gulf of Thailand Based on Cytochrome Oxidase Subunit I Gene Sequences

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Abstract

Genetic information is crucial to manage fish resources, and a good case in point is the population of silver croakers, *Pennahia argentata* (Houttuyn, 1782), which is economically important for Thailand. In the present study, 102 silver croaker samples were collected along the coast of the Gulf of Thailand and analysed for genetic variation based on nucleotide sequences in the cytochrome oxidase subunit I gene (510 bp). Of these, 33 haplotypes were examined, and 21 were singleton haplotypes, indicating a historical pattern of large female effective population sizes (female reproductive success). An analysis of molecular variance (AMOVA) and pairwise F_{ST} analysis showed that the geographic barrier did not affect the genetic structure of the silver croakers in the Gulf of Thailand. The minimum spanning network and phylogenetic tree revealed that the silver croaker population in the Gulf of Thailand separated into two haplogroups. Various methods to examine demographic history showed that the silver croaker population in the Gulf of Thailand had expanded. This study's findings can guide the management of silver croaker populations in the Gulf of Thailand to conserve genetic diversity.

Keywords: demersal fish, genetic diversity, mitochondrial DNA, Thailand waters

Introduction

The silver croaker, *Pennahia argentata* (Houttuyn, 1782), belongs to the family Sciaenidae. It is a demersal fish inhabiting the sandy or muddy bottoms of the coast and is widely distributed along the Asia-Pacific coast (Froese and Pauly, 2019). Silver croakers are commercial demersal fish in the Gulf of Thailand (Yasook, 2008). In Thailand, approximately 7,798 tonnes of silver croakers are fished annually, with an economic value of approximately USD8.35 million. Especially in the Gulf of Thailand's coastal area, catches of the silver croaker fishery reach 6,033 tonnes per year (Fishery Statistics Analysis and Research Group, 2021). Over the years, there have been increasing numbers of silver croaker fisheries due to their higher demand (Yasook, 2008). Therefore, the genetic information of silver croakers in this area should be available for maintaining or increasing silver croaker genetic diversity for conservation management.

The habitats of marine species in the Gulf of Thailand have a scattered pattern. This area was reported to have topographic and hydrographic variations (Panithanarak, 2017). For this reason, the population of marine species in the Gulf of Thailand is fragmented into smaller groups, which may lead to genetic drift (Lourie et al., 2005). The Gulf of Thailand has different currents for each monsoon season (Aschariyaphotha et al., 2008). During the southwest monsoon season (May–August) in the upper Gulf of Thailand, the currents circulate clockwise or counterclockwise depending on the environment. In the middle and lower Gulf of Thailand, there is a clockwise current flow, and it has a sizeable current circle with a clockwise direction in the middle of the gulf. This sea current differs from the water flow pattern during the northeast monsoon season (November–January). In

the upper Gulf of Thailand, the sea current flows counterclockwise. In the lower Gulf of Thailand, a large circle of water flows clockwise (Buranapratheprat, 2008). During each season, the distinct water flows of the upper and lower Gulf of Thailand influence differences in the population structure of various marine species in the Gulf of Thailand, especially those that rely on the influence of water currents in the larval stage. Different flow patterns between the upper and lower Gulf of Thailand act as a geographical barrier, preventing gene flow between silver croakers from the upper and lower Gulf of Thailand (Panithanarak, 2017). Surprisingly, there is no genetic information of silver croakers in this area. Hence, this study aims to uncover whether fragmented habitats along the Gulf of Thailand have generated genetic variation in silver croaker populations. Other studies have reported the genetic structure of marine species in the Gulf of Thailand, including surf clam, *Paphia undulata* (Born, 1778) (Donrung et al., 2011), cobia, *Rachycentron canadum* (Linnaeus, 1766) (Phinchongsakuldit et al., 2013), and blue swimming crab, *Portunus pelagicus* (Linnaeus, 1758) (Supmee, Sawasdee, Sangthong, Suppapan, 2020).

In the present study, the population genetic structure of silver croakers was investigated using nucleotide sequences in mitochondrial DNA. Mitochondrial DNA is suitable for studying genetic diversity because it has a rapid evolutionary rate, lacks recombination and is maternally inherited (Avise, 2000). The present investigation examines nucleotide sequences in the mitochondrial DNA of the cytochrome oxidase subunit I gene (mtDNA *COI*). A nucleotide sequence from mtDNA *COI* has been previously reported in many fish species, such as snow trout, *Schizothorax richardsonii* (Gray, 1832) (Ali et al., 2014); barred knifejaw, *Oplegnathus fasciatus* (Temminck & Schlegel, 1844) (Park et al., 2018); and Asian swamp eel, *Monopterus albus* (Zuiew, 1793) (Zhou et al., 2020). The results from the present study could be used as a guideline for managing the genetic diversity of silver croakers in the Gulf of Thailand.

Materials and Methods

Sample collection, DNA extraction, PCR amplification, and nucleotide sequencing

A total of 102 fresh samples of silver croakers caught by the local fishers from the Gulf of Thailand were collected from the fish landing sites along the coast (Fig. 1; Table 1), placed on ice and transported to the laboratory for DNA extraction.

All samples were identified using the taxonomic keys provided by Nakabo (2002). According to the manufacturer's protocol, DNA extraction from fish meat was performed using a Genomic DNA extraction kit (Tiangen BioTech, China). The primers PA_COI_H1: 5′ CGT CAC AGC CCA TGC CTT T 3′ and PA_COI_L1: 5′ GCT CAT AAG AAT GGG GCT TCT C 3′ were designed

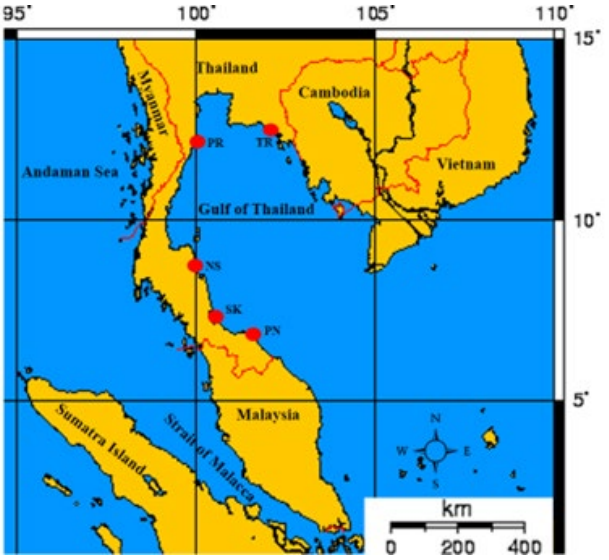

Fig. 1. Map showing the silver croaker, *Pennahia argentata*, sample collection locations from five fish landing sites (red dot) along the Gulf of Thailand coast. PN: Pattani, SK: Songkhla, NS: Nakhon Si Thammarat, PR: Phetchaburi, TR: Trad. (Source: Wikimedia Common; https://commons.wikimedia.org/w/index.php?title=File:Straits_of_%20Malacca.png&oldid=471830265).

using the Primer 3 program to amplify the target DNA from *COI* genes based on the nucleotide sequence of accession number HQ890946.1 in the NCBI database. The target DNA was amplified in a 50 µL PCR tube consisting of 10× Taq buffer (5 µL), 25 mM $MgCl_2$ (7.5 µL), 2 mM dNTP mix (4 µL), 10 mM forward primer (2 µL), 10 mM reverse primer (2 µL), Taq DNA polymerase (0.5 µL, 2.5 units) (RBC Bioscience, USA), DNA template (5 µL, 50–100 ng) and ultrapure water (24 µL). The target DNA was amplified by PCR using a thermocycler (Eppendorf, Germany). The PCR procedure consisted of three steps: (1) 4 min of denaturation at 94 °C for one cycle; (2) 40 sec of denaturation at 94 °C, 1 min of annealing at 55 °C, and 1 min of extension at 72 °C for 35 cycles; and (3) 1 min of final extension at 72 °C for one cycle. Electrophoresis techniques in a 1 % agarose gel were used to determine the correct size of the PCR product. The PCR product was purified using the Gel/PCR Purification Mini Kit (Favorgen Biotech Corporation, Taiwan) and sent to 1st BASE Laboratory (Malaysia) for direct sequencing.

Data analysis and genetic diversity

The nucleotide sequence was validated using the Blastn program and edited. The alignment of multiple sequences was performed using ClustalW ver. 1.83 (Thompson et al., 1994). The genetic diversity was analysed by determining polymorphic sites, nucleotide diversity (π) (Nei and Tajima, 1981), and haplotype diversity (h) (Nei, 1987) using DnaSP version 6.00 (Rozas et al., 2017).

Population genetic structure

The assumption that geographic barriers affected the

genetic structure of silver croaker was investigated. An analysis of molecular variance (AMOVA) was evaluated to compare the levels of genetic diversity within and between populations using ARLEQUIN version 3.5.1.2 (Excoffier and Lischer, 2010). The fixation indices (Φ-statistics), including Φ_{CT}, Φ_{SC}, and Φ_{ST}, were performed at different hierarchical levels using 10,000 permutations. The population genetic structure analysis was grouped into two putative structures. The first putative was divided into five groups according to the sampling provinces (single region), namely, Pattani (PN), Songkhla (SK), Nakhon Si Thammarat (NS), Phetchaburi (PR), and Trad (TR). The second putative was performed on the population groups based on the geography of the lower Gulf of Thailand (PN, SK, NS) and the upper Gulf of Thailand (PR, TR). The pairwise F_{ST} analysed the genetic differences among populations using ARLEQUIN version 3.5.1.2 (Excoffier and Lischer, 2010) with 10,000 permutations.

The evolutionary relationships among haplotypes were examined. The minimum spanning network was constructed based on the mean number of pairwise differences among haplotypes using ARLEQUIN version 3.5.1.2 (Excoffier and Lischer, 2010) and drawn by hand. The neighbour-joining (NJ) method (Saitou and Nei, 1987) is based on the matrix of Kimura 2-parameter distances as implemented in MEGA version 11 (Tamura et al., 2021) using 1,000 bootstrapping replicates to reconstruct a phylogenetic tree.

Demographic history analysis

The historical demography of the silver croakers was examined in three different analyses. First, Tajima's *D* (Tajima, 1989) and Fu's *Fs* (Fu, 1997) were analysed to test the population deviation from neutral evolution based on 10,000 permutations using the Arlequin version 3.5.1.2 program (Excoffier and Lischer, 2010). Second, the mismatch distribution was analysed by using the Harpending raggedness index (Harpending, 1994) and the sum of squared deviations (SSD) to test for goodness-of-fit using 10,000 permutations implemented in Arlequin version 3.5.1.2 (Excoffier and Lischer, 2010). Third, the Bayesian skyline analysis evaluated the effective population size (*Ne*) change using BEAST/BEAUTi ver. 1.7.2 (Drummond et al., 2012), and the result was generated by Tracer ver. 1.6 (Rambaut et al., 2014).

Results

Genetic diversity

The partial nucleotide sequence of mtDNA *COI* (510 bp) from 102 samples showed 41 polymorphic sites, defined as 33 haplotypes. All haplotypes were deposited in GenBank with accession numbers OM056707-OM056739. The haplotype diversity was 0.901 ± 0.019, with a nucleotide diversity of 0.014 ± 0.001 (Table 1). The number of haplotypes shared among the population was 11, and within the population, there was one haplotype. Twenty-one haplotypes were specific populations called "singleton haplotypes" (Table 2). The NS population had the highest number of singleton haplotypes, with seven haplotypes, followed by the SK and PR populations, with four haplotypes each, and the PN and TR populations had three haplotypes each (Table 2).

Table 1. Collection localities, number of individuals per sampling site (*N*), number of polymorphic sites, number of haplotypes, haplotype diversity (*h*) and nucleotide diversity (π) of the silver croaker, *Pennahia argentata*, along the Gulf of Thailand coast.

Collection localities	*N*	No. polymorphic sites	No. haplotypes	Haplotype diversity (*h*) (mean ± SD)	Nucleotide diversity (π) (mean ± SD)
Pattani (PN)	19	24	12	0.936 ± 0.037	0.015 ± 0.003
Songkhla (SK)	19	25	10	0.906 ± 0.045	0.010 ± 0.003
Nakhon Si Thammarat (NS)	21	27	14	0.938 ± 0.036	0.018 ± 0.002
Phetchaburi (PR)	21	26	12	0.914 ± 0.041	0.016 ± 0.002
Trad (TR)	22	28	10	0.848 ± 0.062	0.011 ± 0.003
Total	102	41	33	0.901 ± 0.019	0.014 ± 0.001

Population genetic structure

The results of the genetic differentiation under the assumption that geographic barriers affect the genetic structure of the silver croaker population in the Gulf of Thailand were revealed. First, the AMOVA test results showed that most of the genetic variations of the silver croakers were within-population variations. The Φ-statistical analysis showed no significance in either the putative structure of single groups (Φ_{ST} = 0.011, *P* = 0.273) or 2-separated population groups (Φ_{CT} = 0.015, *P* = 0.601), indicating a lack of genetic structure in the silver croakers across the Gulf of Thailand habitat (Table 3). Second, the population pairwise F_{ST} values among the sampling sites showed no significant differences for most comparisons (Table 4).

The evolutionary relationships among haplotypes revealed two haplogroups. First, the minimum

Table 2. Silver croaker, *Pennahia argentata*, haplotype distributions from five locations along the Gulf of Thailand coast.

Haplotype	PN	SK	NS	PR	TR	Total	Haplotype	PN	SK	NS	PR	TR	Total
HAP_01	4	5	4	5	8	26	HAP_18	-	-	2	-	3	5
HAP_02	1	1	-	1	-	3	HAP_19	-	-	1	-	-	1
HAP_03	1	-	1	-	-	2	HAP_20	-	-	1	-	-	1
HAP_04	2	2	1	2	1	8	HAP_21	-	-	1	-	-	1
HAP_05	1	-	-	-	-	1	HAP_22	-	-	1	-	-	1
HAP_06	3	-	-	-	-	3	HAP_23	-	-	1	-	-	1
HAP_07	1	-	-	-	-	1	HAP_24	-	-	1	-	-	1
HAP_08	1	-	1	-	-	2	HAP_25	-	-	-	1	-	1
HAP_09	1	-	-	-	-	1	HAP_26	-	-	-	1	-	1
HAP_10	1	3	-	1	-	5	HAP_27	-	-	-	1	-	1
HAP_11	2	2	4	4	3	15	HAP_28	-	-	-	2	1	3
HAP_12	1	2	1	1	2	7	HAP_29	-	-	-	1	-	1
HAP_13	-	1	-	-	-	1	HAP_30	-	-	-	1	1	2
HAP_14	-	1	-	-	-	1	HAP_31	-	-	-	-	1	1
HAP_15	-	1	-	-	-	1	HAP_32	-	-	-	-	1	1
HAP_16	-	1	-	-	-	1	HAP_33	-	-	-	-	1	1
HAP_17	-	-	1	-	-	1	TOTAL	19	19	21	21	22	102

PN: Pattani, SK: Songkhla, NS: Nakhon Si Thammarat, PR: Phetchaburi, TR: Trad.

Table 3. Hierarchical analysis of molecular variance (AMOVA) of the silver croaker, *Pennahia argentata*, in the Gulf of Thailand.

Source of variation	df	Sum of squares	Variance components	Percentage of variation	Φ- statistics
1) Single region (PN × SK × NS × PR × TR)					
Among populations	4	18.314	0.041 Va	1.11	Φ_{ST} = 0.011
Within populations	97	361.294	3.724 Vb	98.89	
Total	101	379.608			
2) Lower Gulf of Thailand × upper Gulf of Thailand					
Among groups	1	2.947	0.044 Va	-1.18	Φ_{CT} = 0.015
Among populations within groups	3	15.367	0.068 Vb	1.84	Φ_{SC} = 0.018
Within populations	97	361.294	3.724 Vc	99.34	Φ_{ST} = 0.006
Total	101	379.608	3.749		

*Significant difference ($P < 0.05$).

PN: Pattani, SK: Songkhla, NS: Nakhon Si Thammarat, PR: Phetchaburi, TR: Trad.

Table 4. Population pairwise F_{ST} values of the silver croaker, *Pennahia argentata*, from the Gulf of Thailand.

Population		Lower Gulf of Thailand			Upper Gulf of Thailand	
		PN	SK	NS	PR	TR
Lower Gulf of Thailand	PN	-				
	SK	0.021	-			
	NS	0.031	0.072	-		
Upper Gulf of Thailand	PR	0.025	0.039	0.018	-	
	TR	0.017	0.015	0.040	0.014	-

*Significant difference ($P < 0.05$).

PN: Pattani, SK: Songkhla, NS: Nakhon Si Thammarat, PR: Phetchaburi, TR: Trad.

spanning network showed two distinct groups of haplotypes (haplogroup I and haplogroup II). Haplogroup I consisted of 26 haplotypes, and haplotype HAP_01 was a common haplotype connected with other haplotypes by 1-3 mutation steps. Haplogroup II contained seven haplotypes, and a common haplotype was HAP_11, which was connected to six haplotypes by one mutation step. Both haplogroups were divided by 14 mutation steps (Fig. 2). Second, the phylogenetic tree revealed two distinct lineages of haplotypes (haplogroup I and haplogroup II)(Fig. 3).

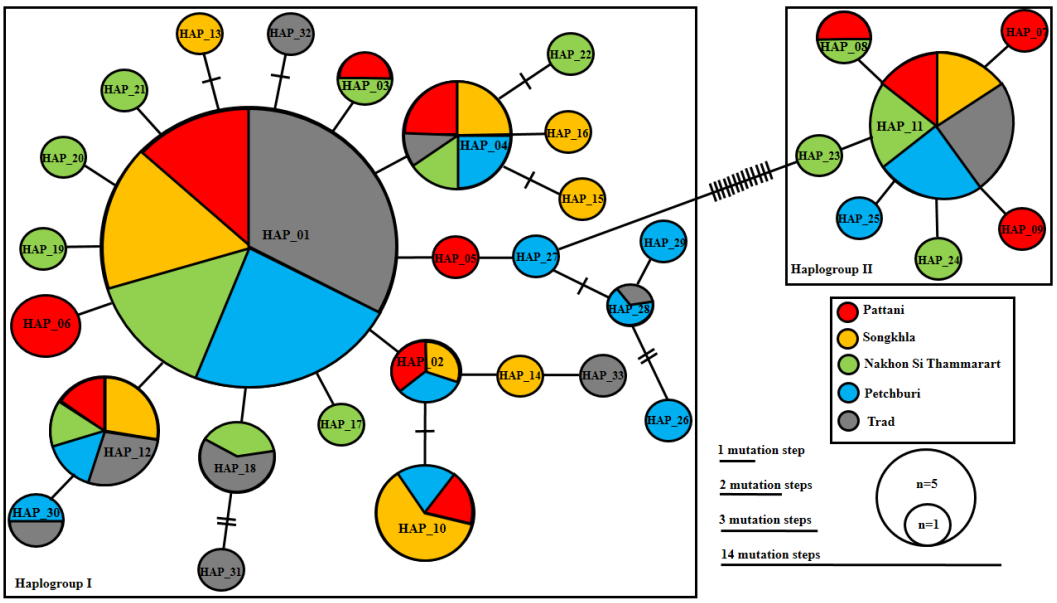

Fig. 2. The minimum spanning network of the 33 mtDNA *COI* haplotypes of the silver croaker, *Pennahia argentata*, from the Gulf of Thailand. The proportional size of the circle is the frequency of the haplotype. The single line connecting directly to the other haplotype represents a single mutation step. The number of vertical bars on the line connecting haplotypes indicates an increasing number of mutation steps.

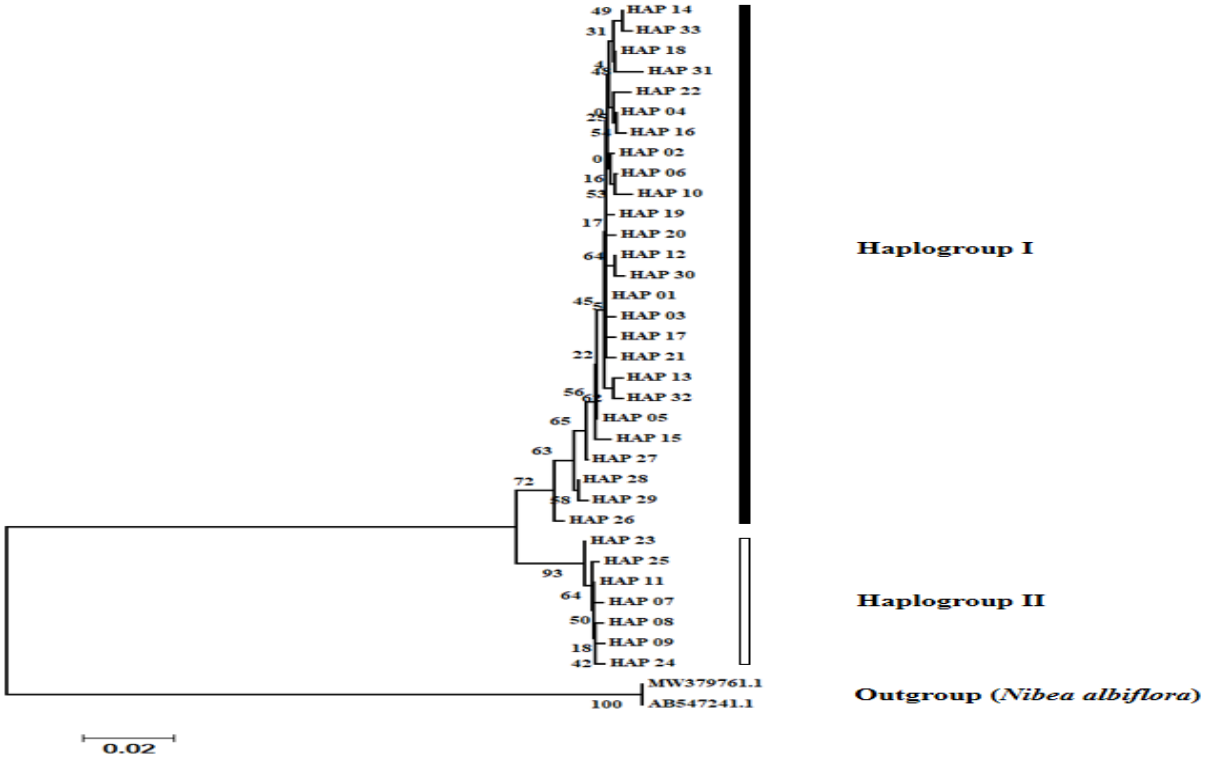

Fig. 3. A neighbour-joining phylogenetic tree based on mtDNA *COI* of the silver croaker, *Pennahia argentata*, from the Gulf of Thailand, constructed under the Kimura 2-parameter model with a bootstrap value of 1,000 replicates and *Nibea albiflora* as an outgroup.

Demographic history

The three independent historical demography analyses showed that the population of silver croakers from the Gulf of Thailand had undergone expansion. First, Fu's *Fs* statistics and Tajima's *D* statistics showed significantly negative values in haplogroup I (*Fs* = -9.174, *P* = 0.024; *D* = -1.021, *P* = 0.018), haplogroup II (*Fs* = -10.423, *P* = 0.034; *D* = -1.356, *P* = 0.018), and the total population (*Fs* = -16.972, *P* = 0.036; *D* = -2.147, *P* = 0.029), which indicates that the population size has expanded before (Table 5). Second, the goodness-of-fit test showed that mismatch distribution was unimodal and fit with a sudden expansion model in haplogroup I (*rg* = 0.039, *P* = 0.482; *SSD* = 0.002, *P* = 0.538), haplogroup II (*rg* = 0.142, *P* = 0.290; *SSD* = 0.012, *P* = 0.206) and the total population (*rg* = 0.131, *P* = 0.457; *SSD* = 0.240, *P* = 0.395) (Table 5; Fig. 4). Third, the Bayesian skyline analysis indicates that the silver croaker population increased approximately 30,000 and 2,000 years ago for haplogroup I and haplogroup II, respectively (Fig. 5).

Table 5. Neutrality test and parameter indices of mismatch distribution analysis of the silver croaker, *Pennahia argentata*, from the Gulf of Thailand.

Collection localities	Fu's *Fs*	Tajima's *D*	*SSD*[a]	Rag[b]
PN	-11.090*	-2.727*	0.181	0.396
SK	-10.785*	-2.945*	0.122	0.432
NS	-11.770*	-1.862*	0.109	0.196
PR	-10.424*	-2.683*	0.234	0.325
TR	-10.042*	-1.877*	0.316	0.228
Haplogroup I	-9.174*	-1.021*	0.002	0.039
Haplogroup II	-10.423*	-1.356*	0.012	0.142
Total	-16.972*	-2.147*	0.240	0.131

*Significant difference (*P* < 0.05); [a]a sum of squared deviations; [b]Raggedness index.
PN: Pattani, SK: Songkhla, NS: Nakhon Si Thammarat, PR: Phetchaburi, TR: Trad.

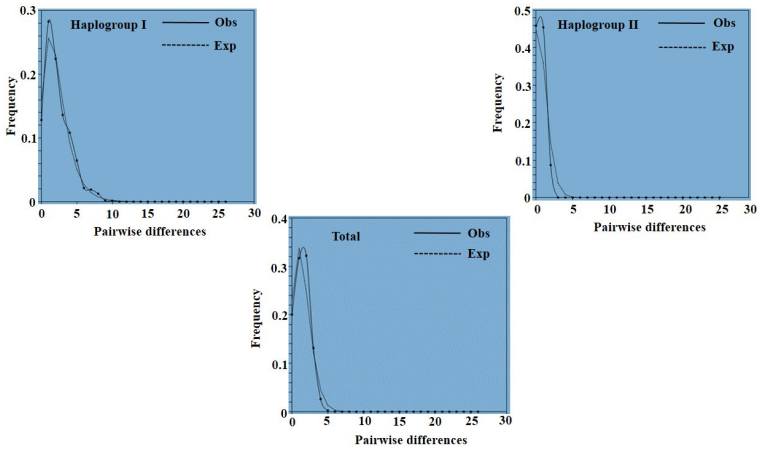

Fig. 4. Mismatch distribution under the sudden silver croaker, (*Pennahia argentata* from the Gulf of Thailand), population expansion model. The expected mismatch distribution is the dotted line, and the observed pairwise differences are the thin line.

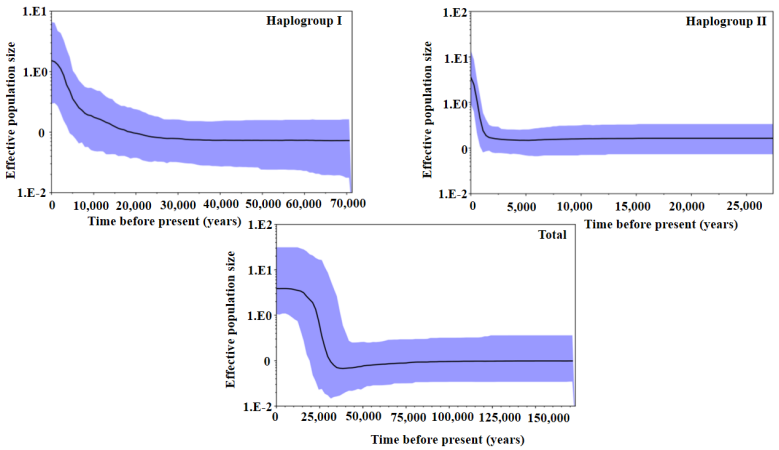

Fig. 5. Bayesian skyline plots show the silver croaker's (*Pennahia argentata*, from the Gulf of Thailand) historical demography in the Gulf of Thailand. The black line is the median estimation, and the blue lines are the limit of a 95 % confidence interval.

Discussion

Genetic diversity

This study analysed 33 mtDNA *COI* haplotypes, and 21 haplotypes were singletons. The presence of many private haplotypes in all silver croaker populations in this study indicated a large female effective population size, which has also been reported in the past in the Gulf of Thailand (Lewontin, 1974; Mbora and McPeek, 2010; Chaves et al. 2011). This haplotype frequency reflects a large effective population size that allows for the retention of numerous unique haplotypes in females. The haplotype diversity of silver croakers in the present study was 0.901. It was high compared with other croaker groups in other areas. For example, the haplotype diversity of the yellow croaker, *Larimichthys polyactis* (Bleeker, 1877) on the coast of the Yellow Sea and the East China Sea was 0.936 (Zhang et al., 2017), and that of the doublewhip threadfin bream, *Nemipterus nematophorus* (Bleeker, 1854) in Peninsular Malaysia was 0.802 (Aimi et al., 2020).

The pattern of a high value of haplotype diversity with a low level of nucleotide diversity was presented within the silver croaker population in the Gulf of Thailand. The variable pattern indicates that silver croakers have experienced a population expansion (Grant and Bowen, 1998). Population growth is responsible for retaining new mutations and helps to maintain high haplotype diversity within a population (Ma et al., 2010). This genetic variation pattern has been reported as a typical molecular characteristic of marine fish, such as yellow croaker (Wang et al., 2013; Zhang et al., 2017) and threadfin bream (Supmee et al., 2021).

Population genetic structure

Silver croakers inhabit coastal inlets and do not migrate for spawning (Yamaguchi et al. (2004); Yamaguchi et al. (2006). In the present study, iced fish specimens were collected along the Gulf of Thailand coastal landing sites. Therefore, the silver croaker samples represent fish from the Gulf of Thailand. In marine fish, there are biological and physical factors that result in genetic differences among populations, such as 1) the buoyancy and swimming ability of a fish in the larval or adult stage, 2) the duration of the planktonic larval stage, and 3) hydrographic and geographic barriers (Ding et al., 2018). In the Gulf of Thailand, the differential flow of the current between the lower and upper Gulf of Thailand is virtually a geographical barrier, preventing gene flow between the two areas. Genetic differences in marine populations due to the upper and lower gulf currents were found in the giant tiger prawn *Penaeus monodon* Fabricius, 1798 (Khamnamtong et al., 2009), blue swimming crabs (Klinbunga et al., 2010), and bivalves (*Donax* spp.) (Manatrinon et al., 2012).

In the present study, the population genetic structure analysis under the assumption of obstruction of the gene flow of silver croakers in the Gulf of Thailand showed a single population. The results revealed that the silver croaker populations in the Gulf of Thailand had high levels of gene flow. The genetic homogeneity of the silver croakers in the Gulf of Thailand may be due to a long planktonic larval stage of up to 30 days, increasing migration ability (Yamaguchi et al., 2006; Zhao et al., 2017). In general, many marine fish release gametes or planktonic larvae into the water mass, and they migrate with the current, which promotes gene flow (Hewitt, 2000; Uthicke and Benzie, 2003). Marine fish with long planktonic larval stages can mix larval populations between subpopulations. The long period of the planktonic larval stage of silver croakers may increase the mixing of planktonic larvae between the upper and lower areas of the central Gulf of Thailand.

Therefore, the gene flow between silver croakers may cover the entire Gulf of Thailand. In addition, the absence of geographical barriers in the Gulf of Thailand promotes gene flow, resulting in no genetic differences in the populations of silver croakers living in the upper and lower Gulf of Thailand. This study concluded that the reproductive barrier caused by the current variation in the Gulf of Thailand did not affect the population genetic structure of silver croakers. Many reports of marine animals in the Gulf of Thailand with long planktonic intervals suggest that population genetic structure does not occur. Examples include the spotted seahorse, *Hippocampus kuda* Bleeker, 1852, (Panithanarak et al., 2010); Asian seabass, *Lates calcarifer* (Bloch, 1790) (Sodsuk et al., 2012); and Asiatic hard clam, *Meretrix meretrix* (Linnaeus, 1758) (Supmee, Sangthong, Songrak, Suppapan, 2020). There have been previous reports on the absence of the population genetic structure of silver croaker and other croaker species from other areas. For example, silver croaker from the Chinese coast (Han et al., 2008); miiuy croaker, *Miichthys miiuy* (Basilewsky, 1855), from the East China Sea (Qin et al., 2014); yellow croaker, *Larimichthys polyactis* (Bleeker, 1877) from the coasts of the Yellow Sea and East China Sea (Zhang et al., 2017); large yellow croaker, *Larimichthys crocea* (Richardson, 1846), along the coast of the mainland China Sea (Liu et al., 2020); and white mouth croaker, *Micropogonias furnieri* (Desmarest, 1823), from the southern Brazilian coast (Puchnick-Legat and Levy, 2006).

In this study, the relationships among the haplotypes of silver croakers revealed two haplogroups. The minimum spanning network and phylogenetic analysis found that the silver croaker population was divided into large and small haplogroups. Both haplogroups showed a star-like topology, indicating a population expanding before. In addition, the demographic history test confirmed the population expansion in the past. The present findings showed that the silver croaker population scaled up in two periods. The large haplogroup was once enlarged approximately 30,000 years ago. Since then, the small haplogroup has been separated from the large haplogroup, and its population expansion took place approximately 2,000 years ago. Such

evolutionary patterns indicate that natural selection may be driving evolution in silver croaker populations in the Gulf of Thailand. This finding found that the small haplogroup was separated from the large haplogroup without being caused by geographic barriers. As a result, the possible explanation for genetic differences in the Gulf of Thailand silver croaker is the evolution of reproductive isolation, which can be caused by specific reproductive behaviours or mismatched spawning intervals in each area. Further studies on silver croaker breeding behaviours and spawning intervals in the Gulf of Thailand be conducted to understand the mechanisms of population isolation.

Based on the coexistence of the two haplogroups within the same geographical range and the possibility of reproductive isolation, silver croaker, the specimens included in the study could be cryptic, subspecies, species complex, or entirely different species. Such assumptions are supported by the high genetic divergence between the haplogroups (96.47 to 96.67 % similarity) based on the mtDNA *COI* gene sequence. Genetic differences in aquatic animals living in the same area, reportedly caused by cryptic species and species complexes, have been reported in the flathead mullet, *Mugil cephalus* (Linnaeus, 1758), along the coast of Taiwan (Shen et al., 2015), and in the Poecilia species complex in southern Mexico (Zimmer et al., 2018). Such assumptions, however, should be investigated further.

According to the present study, the silver croaker population in the Gulf of Thailand has two distinct genetic groups in the same geographical range. The results of this study suggest that the Gulf of Thailand has a high diversity of habitats, which can be both habitats of adult fish and larval nurseries.

Therefore, preserving the area to remain suitable for habitat and preserving the genetic diversity of silver croaker should be planned for fisheries management. The management of this species should prevent overfishing and habitat destruction from jeopardising the survival of existing populations. Such measures should be implemented immediately. Examples include ban fishing during the spawning season, establishing marine reserves to reduce genetic losses, and controlling coastal pollution to increase the number of breeding individuals and larval dispersal. Moreover, gear regulation, habitat monitoring, and restoration may be among the most efficient strategies for maintaining healthy populations. Periodic surveys on genetic diversity and seascape research should be conducted to provide an overall temporal and spatial view of fish populations.

Demographic history

Demographic history studies showed that the silver croaker population in the Gulf of Thailand has expanded based on several test methods. First, the neutrality tests (Tajima's *D* and Fu's *Fs*) showed significantly negative values, indicating that the silver croaker population deviated from the neutral state. The negative Tajima's *D* value indicated that the silver croaker populations were screened for mutations that were inappropriate to discard (purifying selection) or preceding population expansion (Yang, 2006). Furthermore, Fu's *Fs* value (a parameter used to determine the appropriate population expansion of the non-recombination genetic marker) (Ramirez-Soriano et al., 2008) showed a negative value, indicating that the silver croaker population had expanded.

Therefore, it is confirmed that the silver croaker population in the Gulf of Thailand may have grown. Second, the mismatch distribution test revealed that the Harpending Raggedness index accepted the unimodal distribution model, and *SSD* values accepted the sudden expansion model's assumption. Third, the population expansion period estimates showed that the population has been expanding for approximately 30,000 years. The expansion of silver croaker's population in the Gulf of Thailand is likely related to the change in geography during the Pleistocene period, approximately 275,000 to 11,500 years ago. During that time, the Indochina Peninsula was covered with seawater due to the melting of polar ice. After that, the sea level began to recede into the Holocene approximately 30,000 to 10,000 years ago (Gradstein et al., 2004). However, there was still high seawater, and it maintained its level until the middle Holocene and began to recede towards the end Holocene (Horton et al., 2005). After that, the coastal area of the Gulf of Thailand began to accumulate sediment and became a coastal area (Rhodes et al., 2011). The population expansion of silver croaker in the Gulf of Thailand may be correlated with increased fish habitats. Several reports have shown that during this period, there was a population increase of many marine species, such as the threadfin bream, *Nemipterus hexodon* (Quoy & Gaimard 1824), in Thailand (Supmee et al., 2021), and the gazami crab, *Portunus trituberculatus* (Miers, 1876), along the coast of China (Guo et al., 2012).

Conclusion

The genetic structure of the silver croaker, *Pennahia argentata,* in the Gulf of Thailand was studied based on nucleotide sequencing of mtDNA *COI*. The study results revealed that the geographic barrier did not affect the genetic structure of the silver croaker in the Gulf of Thailand. This study found that the silver croaker population in the Gulf of Thailand was divided into two haplogroups. An analysis of population history revealed that the silver croaker in the Gulf of Thailand expanded approximately 30,000 years ago. The results of the present study can be used as information to determine the most effective management strategy for silver croaker populations in the Gulf of Thailand. The use of nuclear DNA genetic markers should be implemented in further studies to provide more explicit information about the genetic information of silver croaker in the Gulf of Thailand.

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