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Mitochondrial markers revealed genetic panmixia in the data-deficient yellowfin snapper, *Lutjanus xanthopinnis* (Actinopterygii: Eupercaria: Lutjanidae), from a hotspot of the southern region of the South China Sea

Md Moshiur RAHMAN[1,2], Nur Asma ARIFFIN[1], Ying Giat SEAH[1,3], Siti Azizah Mohd NOR[4], Tun Nurul Aimi MAT JAAFAR[1], Nuralif Fakhrullah Mohd NUR[1], Ahasan HABIB[1]

1 *Faculty of Fisheries and Food Science, Universiti Malaysia Terengganu, Terengganu, Malaysia*

2 *Faculty of Fisheries, Sylhet Agricultural University, Sylhet, Bangladesh*

3 *Fish Division, South China Sea Repository and Reference Centre, Institute of Oceanography and Environment, University Malaysia Terengganu, Terengganu, Malaysia*

4 *Institute of Climate Adaptation and Marine Biotechnology (ICAMB), Universiti Malaysia Terengganu, Terengganu, Malaysia*

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Corresponding authors: Ahasan Habib (a.habib@umt.edu.my); Nur Asma Ariffin (nurasma@umt.edu.my)

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Abstract

Understanding the genetic structure and diversity of marine fish is crucial for a sustainable management program. We examined the genetic diversity and historical demographics of the yellowfin snapper, *Lutjanus xanthopinnis* Iwatsuki, Tanaka et Allen, 2015, in the coastal waters of east Peninsular Malaysia which is bordered by the southern part of the South China Sea using the mitochondrial genes (mtDNA) D-loop and Cytochrome b (*Cyt-b*). A total of 99 (D-loop) and 78 (*Cyt-b*) specimens of *L. xanthopinnis* were successfully sequenced from six locations within the range of species distribution along the Malaysian South China Sea. In the presently reported study, the lack of genetic differentiation among populations can be attributed to historical demographic events, eggs and planktonic larvae' ability to disperse, spawning patterns, and the absence of physical barriers in the geographical landscape. Maximum likelihood gene trees demonstrated that the populations under study had limited structuring and formed a panmictic population that lacks support for internal clades. The AMOVA (Analysis of Molecular Variance) and population pairwise Φ_{ST} values indicated high genetic exchange between the study areas. A high level of haplotype diversity (D-loop: 0.948–1.000; *Cyt-b*: 0.542–0.928), low nucleotide diversity (D-loop: 0.0095–0.0159; *Cyt-b*: 0.0022–0.0049) and starlike haplotype network indicates a recent expansion of *L. xanthopinnis* populations in Malaysian South China Sea. However, neutrality and goodness of fit tests revealed non-significant values. Furthermore, the BSP (Bayesian skyline plot) analysis estimated population expansion events during the late Pleistocene. During this epoch, the fluctuation in sea level may have led to an increase in the abundance of resources and favorable habitats for the yellowfin snapper. The presently reported findings could initiate efficient management strategies for *L. xanthopinnis* along the coastal areas of the Malaysian South China Sea and other nearby nations that share the same waterways.

Keywords

control region, *Cyt-b*, genetic diversity, Malaysia, panmictic population, population expansion

Introduction

Snappers, members of the family Lutjanidae, constitute an abundant and diverse fishery resource. They comprise 17 genera, with 113 documented species in the Atlantic and Indo–Pacific regions of tropical and subtropical waters (Froese and Pauly 2023). Amongst the Lutjanidae family, the genus *Lutjanus* contains the highest number of species, amounting to 73 (Allen 1985). This genus is regarded as a valuable fisheries resource that is both ecologically and commercially significant across its range of distribution (Messias et al. 2019), including Malaysia (Adibah et al. 2018).

The yellowfin snapper, *Lutjanus xanthopinnis* Iwatsuki, Tanaka et Allen, 2015, is a small lutjanid species that was previously mistaken for *Lutjanus madras* (Valenciennes, 1831) widely distributed throughout the western Pacific and Indian Oceans, spanning from Sri Lanka to the Andaman Sea and the Malay Peninsula, towards the southeast to Indonesia, Malaysia, and Brunei, to the Philippines, north to China and Taiwan, and south to Japan (Iwatsuki et al. 2015). Due to its initial taxonomic conundrum with *L. madras*, basic information about the biogeography, ecology, biology, and population stock status of *L. xanthopinnis* is highly limited (Arai et al. 2023). As a result, the present conservation status of *L. xanthopinnis* is classified as Data Deficient (Carpenter et al. 2019). This "*L. xanthopinnis* + *L. madras*" mixed species group is caught using gillnets and trawl nets (Rahman et al. 2023). It is subjected to commercial exploitation and contributes to Malaysia's annual fish landing statistics. Landings of *Lutjanus* species have steadily risen over the last decade (2013–2022) in Malaysia, reaching 15 391 tonnes annually (DOF 2023).

Understanding the genetic population structure of marine fish is crucial, and fisheries management should be based on this knowledge (Gonzalez et al. 2023). Its implementation could mitigate the risk of genetic resource depletion (Laikre et al. 2005). Habib and Sulaiman (2016) reported that identifying stock structure is one of the cornerstones of assessing fisheries stock, particularly for marine fish. Therefore, basic population parameters such as the number and distribution of fish stocks, dispersal pattern, and genetic diversity are needed for a sustainable management and conservation program (Tan et al. 2019; Kasim et al. 2020; Mohd Yusoff et al. 2021). Genetic studies can provide valuable insights into these factors, aiding in determining the optimal management scale for the target species (Ovenden et al. 2015; Alam et al. 2017). Despite its significant contribution to the economy, only a few studies have been conducted on the genetic diversity, population structure, and demographic history of snappers from the biodiverse South China Sea (Guo et al. 2007; Li and Chu-Wu 2007), including Malaysian waters (Halim et al. 2022).

Genetic markers, such as mitochondrial DNA (mtDNA), are highly effective in assessing genetic variation including at species-level population genetics. Furthermore, it is extensively employed in evolutionary genetics and allows the estimation of population history parameters such as divergence time among different groups (Habib and Sulaiman 2017; Tan et al. 2019). Mitochondrial DNA markers are preferred and reliable because they are present in vast quantities in cells and have a mutation rate greater (10–17 times) than nuclear DNA (Allio et al. 2017). The mtDNA D-loop and *Cyt-b* markers were used in the population genetics and demography of the data-deficient *L. xanthopinnis* natural populations in the East Peninsular Malaysian waters of the South China Sea. The non protein-coding D-loop and protein-coding *Cyt-b* regions have been extensively used as population genetic markers in numerous marine fish, including snappers (Silva et al. 2018; Hernández-Álvarez et al. 2020; Veneza et al. 2023).

Currently, there is only one population genetic study of *L. xanthopinnis* based on the *COI* (Cytochrome c oxidase subunit I) gene (Arai et al. 2023), restricting our understanding of this biological resource. Hence, the key objective of the presently reported study was to assess the population genetics and demographic history of this species, *L. xanthopinnis*, in the South China Sea off East Peninsular Malaysia through the analysis of the two mitochondrial regions (D-loop and *Cyt-b*). The findings of this study would be crucial and serve as a point of reference for the management and conservation strategies of this species.

Materials and methods

Sampling and preservation. A total of 120 samples of yellowfin snapper were obtained from fish landing ports at six distinct geographical areas within the range of species distribution along the East Peninsular Malaysian waters of the South China Sea in 2022 (Table 1, Fig. 1). Subsequently, all specimens were identified using several systematic morphological traits described by Iwatsuki et al. (2015) and specimens were randomly validated using a molecular technique based on *COI* genes. This species can be distinguished from other *Lutjanus* species by its yellow stripes, predominantly yellow fins, preopercular flange with several embedded scales, and a pair of small rounded to elliptical nostrils on each side of the snout. A fin clip from each specimen was excised and stored in 95% ethanol. Samples were kept in 1.5 mL centrifuge tubes at 4°C until further analysis.

Table 1. Sampling sites, coordinates, and collection dates of *Lutjanus xanthopinnis* from Malaysian South China Sea.

Sampling site (population)	Coordinates	Date
Kota Bharu, Kelantan	6°08′03.5″N, 102°14′00.8″E	4 May 2022
Tok Bali, Kelantan	5°54′29.5″N, 102°28′08.0″E	7 Oct 2022
Pulau Kambing, Terengganu	5°19′19.4″N, 103°07′44.2″E	13 Aug 2022
Dungun, Terengganu	5°19′19.4″N, 103°07′44.2″E	10 Jul 2022
Kuantan, Pahang	3°47′10.7″N, 103°19′25.4″E	26 Aug 2022
Mersing, Johor	2°26′48.8″N, 103°49′38.5″E	14 Oct 2022

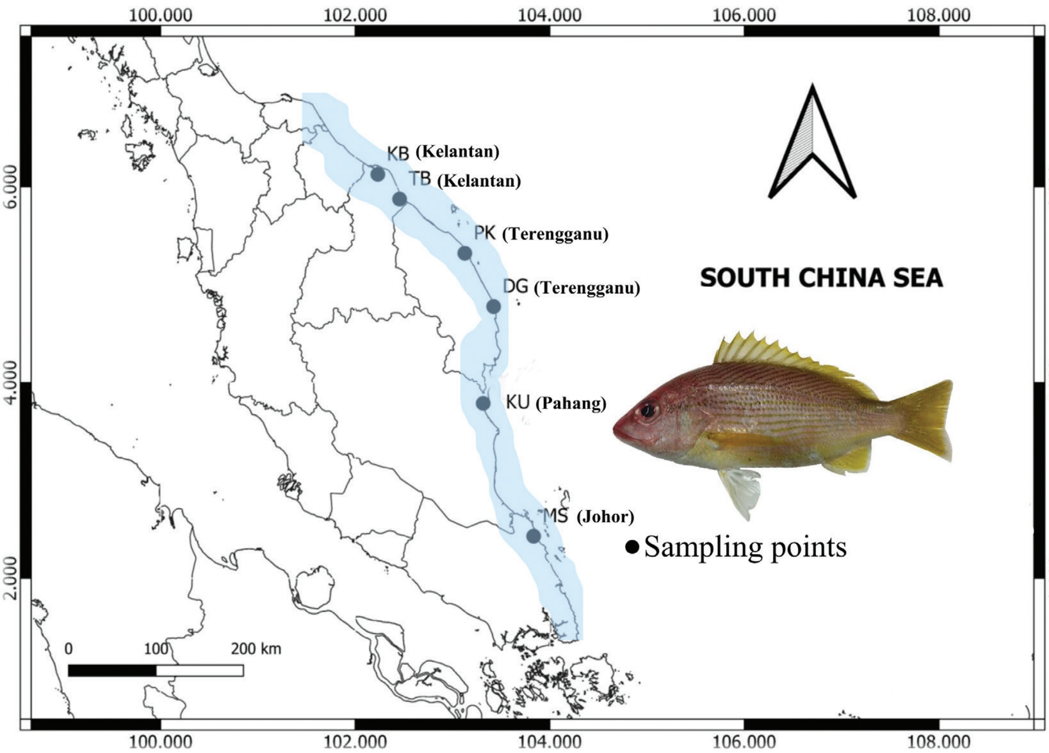

Figure 1. Sampling sites of *Lutjanus xanthopinnis* in the Malaysian waters of the South China Sea. Abbreviations: KB = Kota Bharu, TB = Tok Bali, PK = Pulau Kambing, DG = Dungun, KU = Kuantan, MS = Mersing. The blue-shaded area denotes the natural range of the yellowfin snapper in the area of study.

DNA extraction and quantification. Total genomic DNA was extracted from fin tissue using salt extraction (Aljanabi and Martinez 1997). The extracted DNA samples were assessed for their purities and concentrations using the BioDropand and then kept in 1.5 mL centrifuge tubes at –20°C before amplification.

Polymerase chain reaction (PCR) amplification and sequencing. The preserved DNA samples were PCR amplified using the partial mitochondrial DNA control region (D-loop) and Cytochrome b (*Cyt-b*). The primers used were as follows: (a) D-loop control region A (5′–ATTCCACCTCTAACTCCCAAAGCTAG–3′, forward) and G (5′–CGTCGGATCCCATCT TCAGTGTTATGCTT–3′, reverse) (Lee et al. 1995) (b) *Cyt-b* (forward 5′-GTG ACT TGA AAA ACC ACC GTT G-3′) and (reverse 5′-CTC CAT CTC CGG TTT ACA AGA C-3′) (Song et al. 1998). The final volume of 25 µL PCR reaction solution contained 3 µL of genomic DNA, 0.5 µL of 10 µmol forward primer, 0.5 µL of 10 µmol reverse primer, 12.5 µL of Taq polymerase Bioline red mix, and 8.5 µL of double distilled water (ddH_2O). The thermal protocol for D-loop was: initial denaturation (94°C for 5 min), followed by 35 cycles of reaction, denaturation (95°C for 60 s), annealing (56°C for 90 s), extension at (72°C for 60 s), final extension (72°C for 10 min), and last hold at 4°C. The *Cyt-b* gene was amplified under the following conditions: initial denaturation (94°C for 80 s), 30 cycles of reaction, denaturation at (94°C for 42 s), annealing (47°C for 45 s), extension (72°C for 60 s), final extension (72°C for 5 min), and last hold at 4°C. The PCR results were observed on 1.5% agarose gel stain with SYBR Safe to verify their existence and determine the size of the amplified DNA fragment. All satisfactorily PCR amplified products were later sent to Apical Scientific Sdn Bhd in Selangor, Malaysia, for sequencing. An Applied Biosystem ABI3730×1 capillary-based DNA sequencer was used to perform the sequencing.

Sequence alignment and editing. The ClustalW program incorporated in MEGA 11 software (Tamura et al. 2021) was utilized to verify and align the multiple sequences. Identification of DNA sequences was verified with the Basic Local Alignment Search Tool (BLAST) method available in the National Centre for Biotechnology Information database (NCBI) (http://blast.ncbi.nlm.nih.gov/Blast.cgi) before subsequent processing. The aligned sequence was transformed into a haplotype file in DnaSP 6.0 (Rozas et al. 2017). All haplotypes have been submitted to GenBank and have been assigned accession numbers OR756024–OR756105 (D-loop) and OR764550–OR764577 (*Cyt-b*).

Genetic diversity, phylogenetic, and population structure analyses. The number of haplotypes, polymorphic sites, and genetic diversity indices of haplotype and nucleotide diversity were performed using Arlequin v3.5 (Excoffier and Lischer 2010). The phylogenetic relations of haplotypes were estimated using the Maximum Likelihood (ML) approach employed in MEGA 11. Tamura 3-parameter (Tamura 1992) with Gamma distribution and invariant sites (T92 + G + I) and Hasegawa–Kishino–Yano (Hasegawa et al. 1985) with Gamma distribution (HKY + G) were identified to have the lowest BIC score (Bayesian Information Criterion) for the D-loop and *Cyt-b* sequences, respectively in MEGA 11. The statistical support for the Maximum Likelihood (ML) tree was assessed by 1000 bootstrap replicates (Felsenstein 1985). The brownstripe snapper *Lutjanus vitta* was employed as an outgroup taxon (D-loop sequence, FJ887832) and (*Cyt-b* sequence, DQ900677). A median-joining network (MJN) was accomplished through the utilization of the median-joining approach outlined in the PopART (Population analysis with reticulate trees) software (Leigh and Bryant 2015) for an overview of mutational differences between haplotypes.

The Φ_{ST} (Population pairwise comparisons) for both data sets were calculated by Arlequin v3.5 software, and the statistical significance of the pairwise comparisons was assessed using 10 000 permutations. In addition, AMOVA (Analysis of Molecular Variance) was performed using the Arlequin 3.5 software to evaluate the population partitioning of *L. xanthopinnis* across the South China Sea off East Peninsular Malaysia based on the fixation index F_{ST} values.

Demographic history and population expansion. The historical demographic expansions of the *Lutjanus xanthopinnis* populations were examined. To analyze the deviation from neutrality, Tajima's D (Tajima 1989) and Fu's F_s (Fu 1997) were performed. The population Θ_0 (before expansion), Θ_1 (after expansion), and τ (relative time since population expansion) were calculated as historical demographic variables in Arlequin 3.5. The values of τ were transformed to estimate the T (actual time since population expansion) using the equation

$$T = \tau \cdot 2\mu k^{-1}$$

where μ is the sequence mutation rate per site per generation and k is the length of sequence (Yildirim 2016). In the presently reported study, one mutation rate was used for D-loop (i.e., 3.6% per million years) (Donaldson and Wilson 1999), while a mutation rate of 1% per million years was used for *Cyt-b* (Bowen et al. 2001; Lessios 2008). The Bayesian skyline analysis was conducted using the software BEAST version 2.2.0 (Bouckaert et al. 2019), where the effective population size (N_E) changes were examined over time. Since no population structuring was detected (refer to the "Results" of this study), the analysis was based on a single population model. The data was prepared using the BEAUti, and the subsequent analysis consisted of 108 iterations. A burn-in period of 10^7 iterations was implemented, with sampling occurring every 10^4 iterations. All analyses underwent automatic optimization, and the outcomes were obtained with Tracer version 1.7.1 (Rambaut et al. 2018).

In addition, the goodness of fit test parameters, namely Harpending's raggedness index (H_{RI}) and the sum of squared deviations (SSD), were calculated in Arlequin 3.5 to determine whether the sequence data deviated significantly from the expected outcomes of a population expansion model. Moreover, mismatch distribution analyses were conducted using Arlequin 3.5 software with the graph created using the R tool (R Core Team 2023). The mismatch distribution reveals whether the population of *L. xanthopinnis* was demographically expanding, stable, or declining over time. A population at equilibrium displays a multimodal distribution pattern, whereas a recently expanded population displays a unimodal distribution pattern (Slatkin and Hudson 1991; Rogers and Harpending 1992).

Results

Genetic diversity. A total of 99 and 78 distinct specimens of *Lutjanus xanthopinnis* were successfully sequenced for the mtDNA D-loop and *Cyt-b* fragments, respectively from 120 specimens. The final dataset of D-loop sequences (844 base pairs) revealed 96 polymorphic sites (65 parsimony informative and 31 singletons variable sites), generating 82 haplotypes, of which only four (4.88%) were found in two to six localities. In contrast, the remaining 78 (95.12%) were either singleton haplotypes or exclusive to a single locality. The *Cyt-b* aligned sequences (751 base pairs) revealed 35 polymorphic sites (25 singleton variables and 10 parsimony informative sites), defining 28 haplotypes where 8 (28.58%) were found in two to six localities, and 20 (71.42%) were exclusive to one locality or singleton haplotypes. The D-loop fragment was AT-dominant (62.3%). However, *Cyt-b* gene sequences showed almost similar percentages of AT (50.11%) and CG (49.89%). In all sampled locations, *L. xanthopinnis* revealed a high level of haplotype diversity (D-loop: 0.948–1.000; *Cyt-b*: 0.542–0.928), but the diversity of nucleotide was low (D-loop: 0.0095–0.0159; *Cyt-b*: 0.0022–0.0049) (Table 2).

Phylogenetic and population genetic structure. Based on the phylogenetic analysis derived from the D-loop and *Cyt-b* markers, an ML tree with internal weakly supported clades was revealed (<70%). No geographic partitioning of the haplotype was observed within its haplotypes (Fig. 2A, Suppl. material 1, Fig. 2B). Furthermore, the median-joining network inferred from both genes supported this lack of partitioning among the studied populations (Figs. 3, 4). A complex reticulated network was generated by the 82 D-loop haplotypes (Fig. 3), while 28 *Cyt-b* haplotypes provided a well-defined network pattern (Fig. 4). A single dominant haplotype (Hap_01) was identified in the D-loop sequence followed by Hap_06 and

Table 2. Genetic polymorphisms, neutrality test, mismatch distribution and goodness of fit tests for *Lutjanus xanthopinnis* populations inferred from the mitochondrial DNA D-loop (844 base pairs) and *Cyt-b* (751 base pairs) sequences.

Population	Genetic diversity					Neutrality test				Mismatch distribution			Goodness of fit tests			
	N	N_H	N_{PS}	H	D_N	Tajimas' D		Fu's F_S		Θ_0	Θ_1	τ	SSD		H_{RI}	
						Value	P	Value	P				Value	P	Value	P
D-loop																
TB	18	16	49	0.986	0.013	–0.72	0.24	**–4.69**	0.02	10.07	183.282	3.90	0.0123	0.37	0.0174	0.49
KB	15	14	51	0.990	0.014	–0.94	0.16	**–4.10**	0.03	7.32	58.911	6.65	0.0157	0.38	0.0155	0.81
PK	13	13	49	1.000	0.015	–0.67	0.25	**–4.55**	0.01	8.10	3614.991	7.00	0.0138	0.39	0.0256	0.54
KU	20	19	53	0.994	0.012	–1.26	0.09	**–9.29**	0.001	14.40	6837.57	0.00	0.0127	0.38	0.0159	0.50
MS	18	13	47	0.947	0.010	–1.35	0.07	–1.93	0.18	0.002	15.449	11.00	0.0124	0.74	0.0198	0.79
DG	15	15	41	1.000	0.009	–1.51	0.05	**–8.71**	0.008	5.50	6854.957	2.00	0.0193	0.41	0.0248	0.56
Overall	99	82	96	—	—	—	—	—		—	—	6.639	—		—	
Mean	17			0.986	0.012	–1.08	0.14	**–5.54**	0.04	7.566	2927.527	5.092	0.0144	0.44	0.0198	0.61
Cyt-b																
TB	14	8	13	0.769	0.003	–1.30	0.09	–2.20	0.08	0.00	4.934	4.756	0.0151	0.70	0.0440	0.79
KB	11	8	13	0.927	0.004	–0.71	0.25	–2.31	0.07	0.005	27.363	4.496	0.0061	0.71	0.0290	0.82
PK	10	7	12	0.911	0.004	–1.25	0.11	–1.98	0.07	0.079	16.653	3.461	0.0112	0.61	0.0562	0.49
KU	16	6	10	0.541	0.002	**–1.59**	0.04	–1.09	0.21	0.004	1.743	4.736	0.0801	0.29	0.2888	0.17
MS	15	8	14	0.895	0.003	–1.21	0.11	–1.70	0.16	0.018	8.441	3.844	0.0070	0.77	0.0287	0.83
DG	12	8	12	0.848	0.003	–1.57	0.05	**–3.20**	0.01	0.00	4.221	4.977	0.0307	0.47	0.0835	0.58
Overall	78	28	35	—	—	—	—	—		—	—	4.176	—		—	
Mean	13			0.815	0.003	–1.27	0.11	–2.08	0.1	0.017	10.559	4.378	0.0250	0.59	0.0884	0.61

Bold type denotes significant difference at a level of 5%; N = number of samples, N_H = number of haplotypes, N_{PS} = number of polymorphic sites, H = haplotype diversity, D_N = nucleotide diversity, Θ_0/Θ_1 = Mismatch distribution before/after expansion, τ = relative time since population expansion, SSD = sum of squared deviations, H_{RI} = Harpending's raggedness index; TB = Tok Bali, KB = Kota Bharu, PK = Pulau Kambing, KU = Kuantan, MS = Mersing, DG = Dungun.

Hap_24. Among the *Cyt-b* haplotypes, Hap_03 exhibited the highest level of dominance, followed by Hap_01 and Hap_04. The Hap_03 was observed in all sampling areas and is regarded as the ancestral haplotype based on its dominance and central position where all haplotypes radiate (Clement et al. 2000). A network including an ancestral haplotype often exhibits a star-burst pattern or star-like, with the ancestral haplotype positioned at its center (Ferreri et al. 2011).

The Φ_{ST} (pairwise comparisons) analysis revealed limited and non-significant structuring of *L. xanthopinnis* populations from the Malaysian waters of the South China Sea for both D-loop: −0.0212 to 0.0780) (Table 3) and *Cyt-b*: −0.0359 to 0.1899 (Table 4). Negative Φ_{ST} values indicate higher differences within the sample compared to the variation across different samples. Subsequently, the absence of population partition among the investigated groups was supported by AMOVA. The AMOVA

Table 3. Pairwise Φ_{ST} (below the diagonal) and associated P values (above the diagonal) between sampling sites of *Lutjanus xanthopinnis* inferred by mtDNA D-loop region.

Population	Tok Bali	Pulau Kambing	Kuantan	Kota Bahru	Mersing	Dungun
Tok Bali		0.1335	0.2364	0.0292	0.4735	0.4503
Pulau Kambing	0.0297		0.0345	0.3180	0.0088	0.3150
Kuantan	0.0101	0.0645		0.2594	0.5715	0.0204
Kota Bahru	–0.0061	–0.0045	0.0471		0.7408	0.3000
Mersing	0.0071	0.0780	0.0043	0.0152		0.8005
Dungun	–0.0114	0.0734	–0.0128	0.0132	–0.0212	

Table 4. Pairwise Φ_{ST} (below the diagonal) and associated P values (above the diagonal) between sampling sites of *Lutjanus xanthopinnis* inferred by mtDNA *Cyt-b* region.

Population	Tok Bali	Kota Bahru	Pulau Kambing	Kuantan	Mersing	Dungun
Tok Bali		0.17206	0.74161	0.68112	0.20453	0.00515
Kota Bahru	0.0384		0.06465	0.74111	0.12434	0.24493
Pulau Kambing	–0.03352	–0.03597		0.23978	0.36917	0.02307
Kuantan	0.01387	0.18997	0.08439		0.18642	0.86496
Mersing	–0.02673	0.05859	0.01717	0.01024		0.51678
Dungun	–0.00615	0.13248	0.04497	–0.03304	–0.0113	

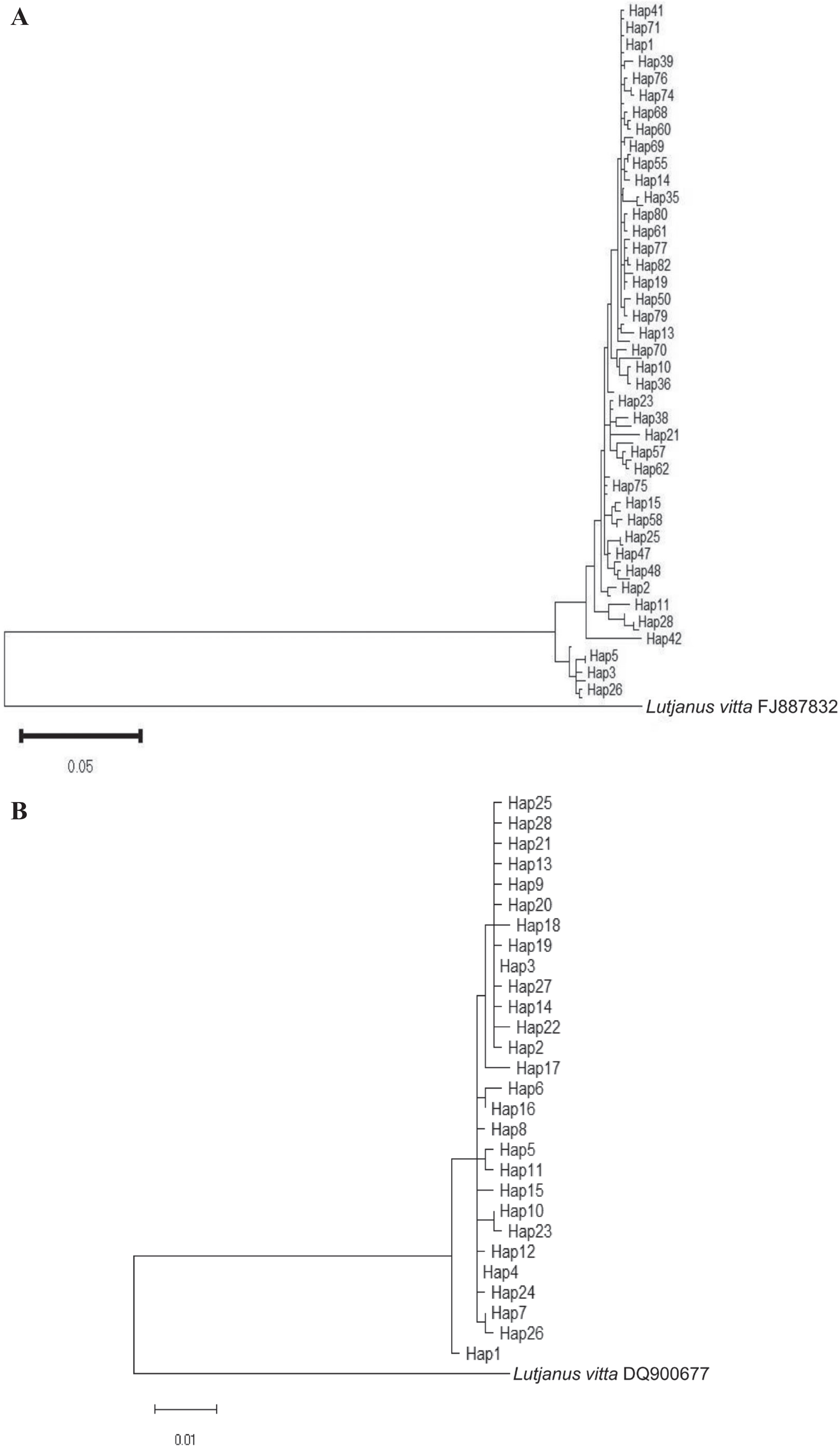

Figure 2. Maximum likelihood (ML) gene trees of *Lutjanus xanthopinnis* haplotypes from the Malaysian waters of the South China Sea inferred from (**A**) D-loop (tree was compressed for a better illustration) (**B**) *Cyt-b* marker. Branches are drawn to scale and bootstrap values <70% are not shown. (The original D-loop ML tree is presented in Suppl. material 1).

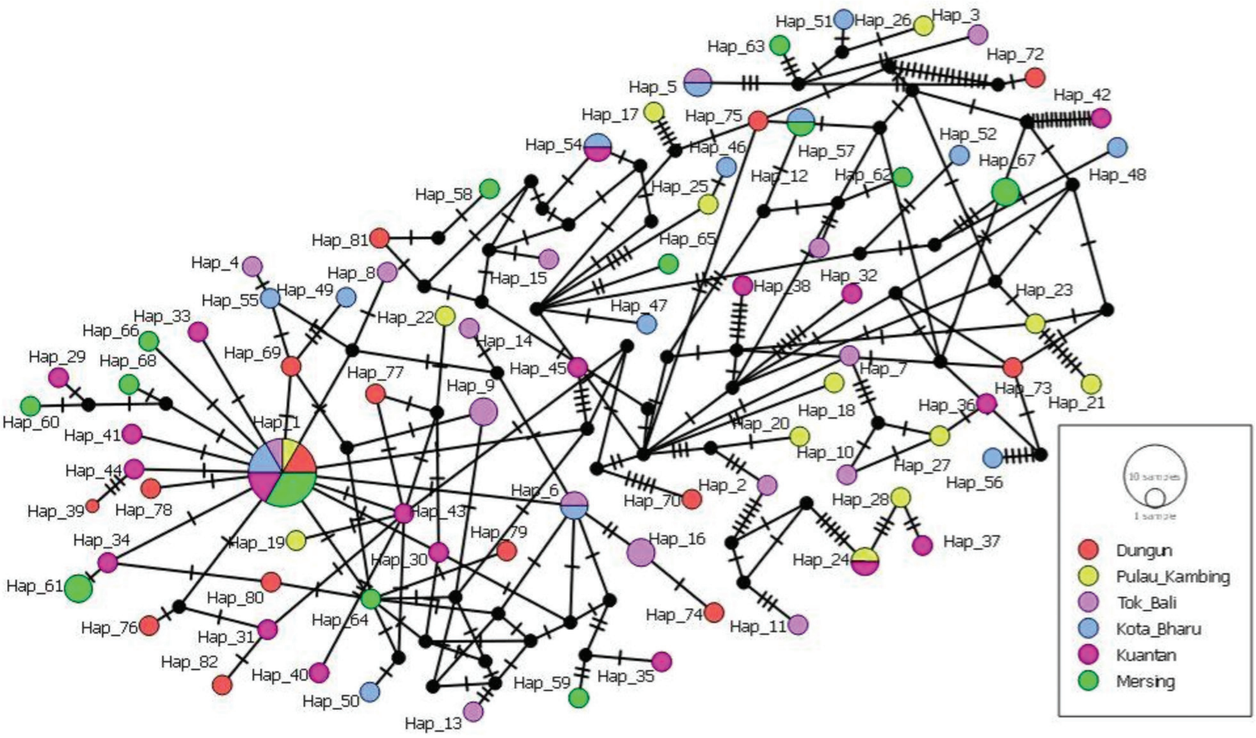

Figure 3. Median-joining haplotypes network diagram of *Lutjanus xanthopinnis* from the Malaysian waters of the South China Sea inferred from D-loop gene. Node size corresponds to the haplotype frequencies; minimum node size is one individual. Black dots indicate median vector. Dashed line is nucleotide mutation.

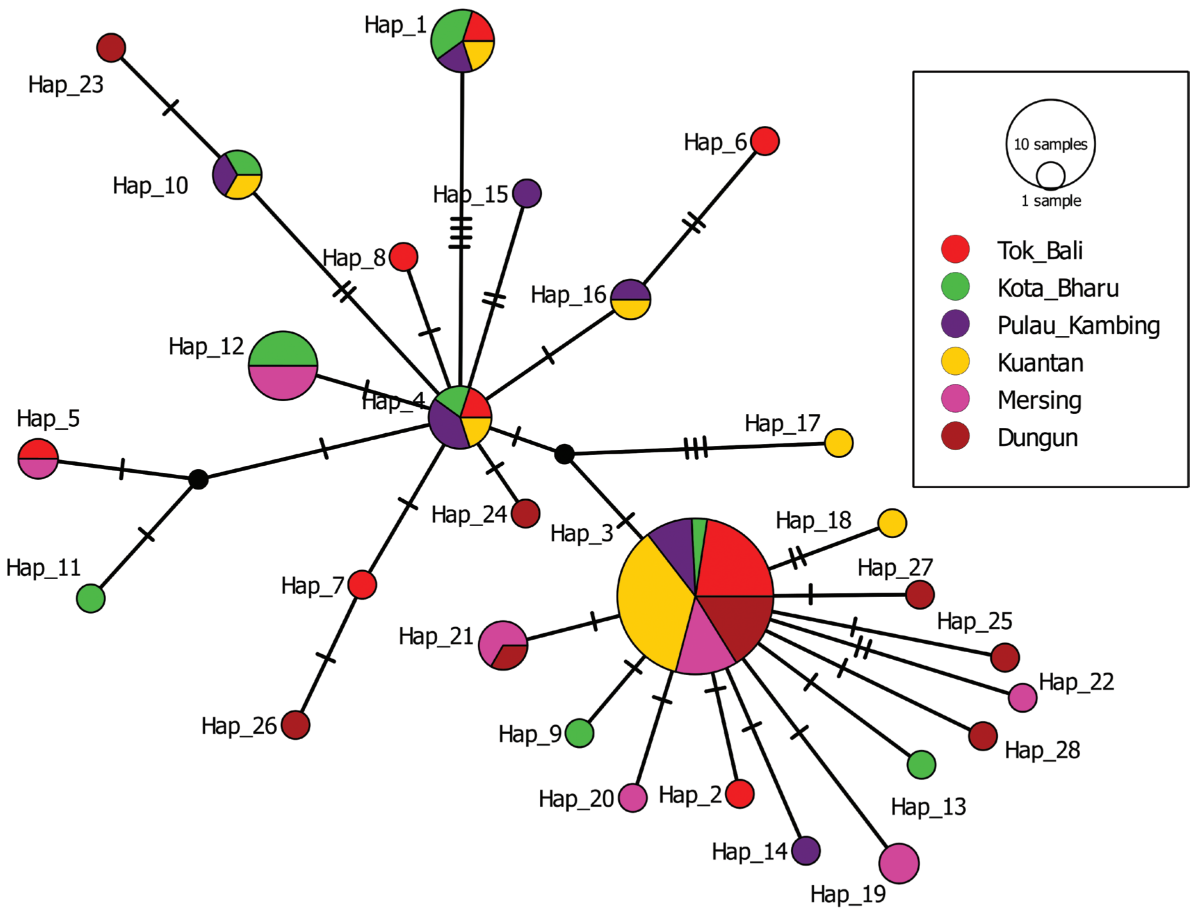

Figure 4. Median-joining haplotypes network diagram of *Lutjanus xanthopinnis* from the Malaysian waters of the South China Sea inferred from *Cyt-b* gene. Node size corresponds to the haplotype frequencies; minimum node size is one individual. Black dots indicate median vector. Dashed line is nucleotide mutation.

results revealed that the intra-population genetic variance was more significant than the inter-population genetic variation for both fragments (Tables 5, 6).

Table 5. Results of AMOVA for *Lutjanus xanthopinnis* inferred by mtDNA D-loop region.

Source of variation	df	Sum of squares	Variance components	Percentage of variation	*P* value
Among populations	5	35.167	0.10395 Va	1.91	0.067
Within populations	93	495.257	5.32534 Vb	98.09	
Total	98	530.424	5.42929		
Fixation Index (F_{ST}) = 0.019					

Table 6. Results of AMOVA for *Lutjanus xanthopinnis* inferred by mtDNA *Cyt-b* region.

Source of variation	df	Sum of squares	Variance components	Percentage of variation	*P* value
Among populations	5	9.688	0.04480 Va	3.19	0.08
Within populations	72	97.812	1.35849 Vb	96.81	
Total	77	107.5	5.42929		
Fixation Index (F_{ST}) = 0.031					

Demographic history. Both neutrality tests (Tajima's *D* and Fu's F_S) showed negative values, and non-significant *P* values at $P > 0.05$ in all studied populations as deduced by the *Cyt-b* and D-loop genes of mtDNA, respectively (Table 2). The disparities in population sizes after (θ_1) and before expansion (θ_0) for the D-loop marker were 7.566 and 2927.52, while 0.017 and 10.559 were estimated from the *Cyt-b* gene (Table 2). The τ value of D-loop was 5.092, while *Cyt-b* was 4.378 (Table 2). The estimated expansion period for *L. xanthopinnis* was 109 246 and 280 254 years ago, inferred by D-loop and *Cyt-b* genes. The Bayesian skyline plot (BSP) analysis indicated that increases in effective population size (N_E) were approximately 87 746 years ago, as inferred from the D-loop (Fig. 5A). In comparison, expansion started 75 244 years ago based on the *Cyt-b* marker (Fig. 5B). For both the total data sets and all sample stations, the Harpending's raggedness index (H_{RI}) and the sum of squared deviations (SSD) showed values that were low and not statistically significant (Table 2). The mismatch distribution (Fig. 6) conformed to the sudden expansion model despite distinct bimodality based on the low and non-significant values in the goodness of fit tests (H_{RI} and SSD).

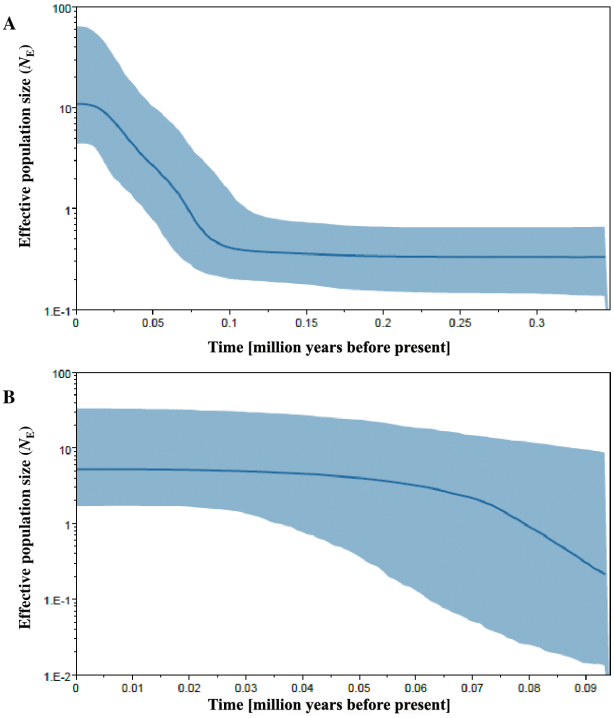

Figure 5. Bayesian Skyline Plots of the mtDNA (**A**) D-loop marker and (**B**) *Cyt-b* gene of *Lutjanus xanthopinnis* populations from Malaysian waters of the South China Sea. The dark blue line represents the mean and the shaded blue band indicates the standard error.

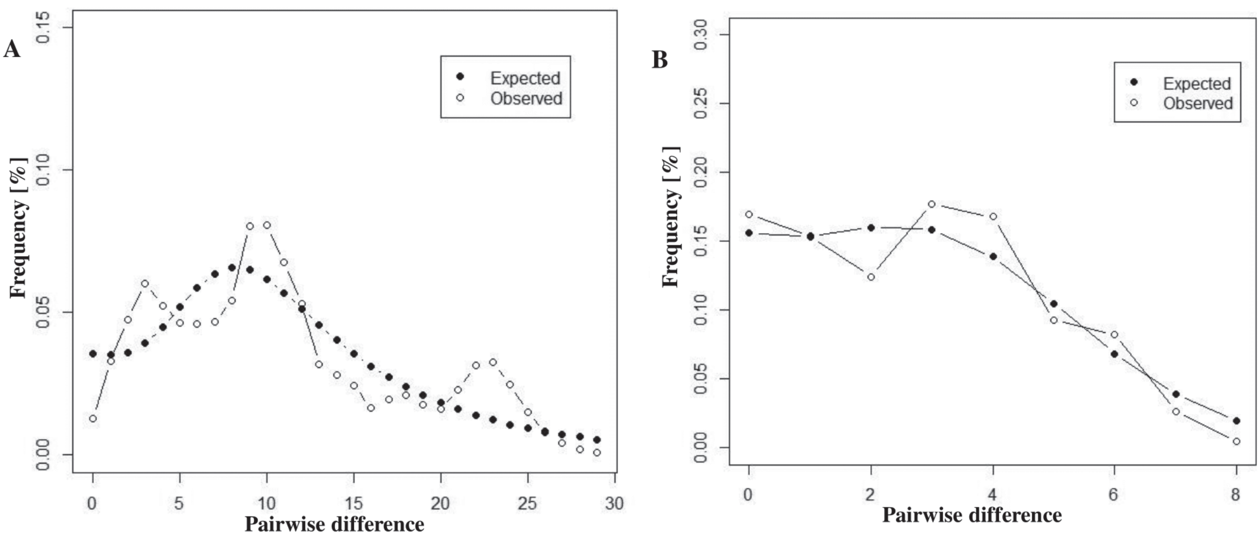

Figure 6. Mismatch distributions (pairwise number of differences) for the mtDNA (**A**) D-loop (**B**) *Cyt-b* genes of *Lutjanus xanthopinnis* from Malaysian waters of the South China Sea.

Discussion

The yellowfin snapper, *Lutjanus xanthopinnis* has only been recognized as a valid species since 2015 (Iwatsuki et al. 2015), although it had been subject to commercial exploitation in a mixed group with *L. madras* with which it had been erroneously synonymized. Thus, it is crucial to investigate the population genetics of this species to implement an efficient management strategy. The presently reported study is the first to investigate the population genetics of *L. xanthopinnis* from the waters of the South China Sea, bordering East Peninsula Malaysia using a combination of two mitochondrial markers.

Genetic diversity. The present levels of nucleotide and haplotype diversity can shed light on the demographic trends of communities in the past (Grant and Bowen 1998). Estimating a population's genetic diversity is based on these two basic metrics (Nei and Li 1979). The presently reported study reveals a high level of haplotype diversity (D-loop: 0.948–1.000; *Cyt-b*: 0.542–0.928) and low nucleotide diversity (D-loop: 0.0095–0.0159; *Cyt-b*: 0.0022–0.0049) observed in all locations where *L. xanthopinnis* was sampled (Table 2). A combination of high haplotype diversity (H) and low nucleotide diversity (D_N) suggests the presence of a large population that has undergone recent expansion, allowing for the persistence of recently generated alleles in the population without sufficient time to gather more nucleotide alternatives within the haplotypes (Grant and Bowen 1998; Delrieu-Trottin et al. 2017; Kasim et al. 2020; Tovar Verba et al. 2023). These findings coincide with earlier studies on several *Lutjanus* species, including the red snapper *Lutjanus campechanus* ($H = 0.946$, $D_N = 0.021$) (Garber et al. 2004), crimson snapper, *Lutjanus erythropterus* ($H = 0.946$, $D_N = 0.03$) (Zhang et al. 2006), southern red snapper, *Lutjanus purpureus* ($H = 0.99$, $D_N = 0.026$) (Gomes et al. 2012), mangrove red snapper *Lutjanus argentimaculatus* ($H = 0.929$, π- 0.003) (Gopalakrishnan et al. 2018), and dog snapper *Lutjanus jocu* ($H = 0.996$, $D_N = 0.036$) (Souza et al. 2019). In addition, the trend in genetic diversity estimates between the two markers in all aligns with the results reported by Silva et al. 2018, with the D-loop region having a greater level of genetic diversity than the *Cyt-b* because of the higher polymorphic sites and mutation rate in the former.

Population genetics structure. The populations of *L. xanthopinnis* from this part of the South China Sea of Malaysian waters showed no geographical structuring based on two mtDNA fragments. All statistical analyses corroborated this: gene trees consisting of a single clade (Fig. 2; Suppl. material 1) and undetermined genetic partition of haplotype networks (Figs. 3, 4), the statistically non-significant value of pairwise Φ_{ST} (Tables 3, 4) as well as lack of genetic differentiation in AMOVA (Tables 5, 6). These findings indicate a significant amount of genetic exchanges between the populations of *L. xanthopinnis* attributed to substantial gene flow. This trend is consistent with earlier research conducted on similar species in different regions of the world (Gomes et al. 2012; Gopalakrishnan et al. 2018; Souza et al. 2019; Veneza et al. 2023), which reflects a common evolutionary pattern among species in this group. A number of factors influence the genetic differentiation and flow of genes among marine organisms, such as planktonic larval stage, extended lifespan, distances and directions of dispersal and spawning pattern (Froukh and Kochzius 2007; Palumbi 2003; Pineda et al. 2007; Haye et al. 2014). The planktonic larval stage is believed to be a crucial determinant of the population genetic patterns of snapper (Tovar Verba et al. 2023). Facilitated by marine currents, the larvae could travel in a long-distance movement, thereby ensuring the continued existence of genetic connectivity. Furthermore, snappers form extensive spawning aggregations across their entire habitat (Claro and Lindeman 2003; Malafaia et al. 2021; Motta et al. 2022). Rahman et al. (2024) reported that *L. xanthopinnis* has a higher tendency to create spawning aggregations in the waters of Malaysia. The vast migration of adult individuals to breeding aggregations also contributes to genetic homogeneity. Typically, marine fishes exhibit minimal genetic differentiation because they can theoretically disperse throughout their life stages as there are no physical barriers preventing passage between basins of the ocean (Mandal et al. 2012).

Demographic history. Our study found that the populations of *L. xanthopinnis* throughout the East Peninsular Malaysian waters had recently undergone a population expansion history. However, the multimodal distribution curve in the mismatch analysis (Fig. 6) suggests population stability. But other lines of evidence such as the median-joining network displayed a star-like pattern, Tajima's D and Fu's F_S show negative values, while H_{RI} and SSD have non-significant values. These findings collectively suggest the presence of a recent demographic expansion. Previous studies on *Lutjanus* have exhibited the same historical demographic pattern. These have been reported in *Lutjanus synagris* (Linnaeus, 1758) (see Silva et al. 2018), *Lutjanus purpureus* (Poey, 1866) (see Gomes et al. 2012), and *Lutjanus argentimaculatus* (Forsskål, 1775) (see Gopalakrishnan et al. 2018). The tau value estimated a population expansion between 109 246 and 280 254 years ago for the mtDNA gene markers, D-loop and *Cyt-b*, respectively.

Additionally, the BSP analysis indicated that the population expansion occurred around 87 746 and 75 244 years ago. These events overlapped with the late Pleistocene, as shown in Fig. 5. The late Pleistocene Epoch is characterized by alternating glaciation and deglaciation periods at approximately 100 000-year intervals (Imbrie et al. 1992). The climatic shifts during the late Pleistocene resulted in alterations in temperature and salinity, consequently affecting the worldwide circulation of the ocean patterns (Bond et al. 1997; Petit et al. 1999). During glaciations, sea levels receded by 120–140 m below the current level, exposing most shallow water habitats. This significantly impacted marine life demographics, including eradication, displacement, recolonization, and population expansion (Hewitt 2000; Lambeck et al. 2002; Liu et al. 2006). Population expansions during the late Pleistocene period have also been previously reported in several other snappers for example in *Lutjanus erythropterus* (see Zhang et al. 2006), *L. purpureus* (see Gomes et al. 2012), *Lutjanus synagris* (Linnaeus, 1758) (see Silva et al. 2018), and *Lutjanus alexandrei* Moura et Lindeman, 2007 (see Veneza et al. 2023).

Based on this preliminary data, the *L. xanthopinnis* populations in the Malaysian waters bordered by the South China Sea could be considered a single stock unit as no population structuring was observed. However, this was based on two maternally inherited mtDNA markers. Furthermore, our work is constrained in its ability to examine other regions of the South China Sea due to the scarcity of specimens from other regions of Malaysian waters and the absence of haplotype sequences in any accessible database. Additional analysis should be conducted with autonomous, genomic nuclear markers, such as a microsatellite marker for a holistic approach to understanding the population genetic pattern in this region. This would also entail examining a broader geographical coverage and increasing the number of samples, particularly from other regions within the South China Sea.

Conclusions

The population structure of *Lutjanus xanthopinnis* still needs to be better understood, particularly in Malaysia. This is a significant challenge from a management perspective. The initial baseline population genetic data on *L. xanthopinnis* populations in the Malaysian South China Sea is crucial for authorities' planning and management strategies. Based on preliminary data, the *L. xanthopinnis* populations in the South China Sea of Malaysia could be considered a single stock unit because the two mtDNA markers revealed no population structure was present. According to their estimated demographic history, populations of *L. xanthopinnis* significantly expanded in the Late Pleistocene. When combined with other relevant data, this genetic information may help create efficient management strategies for Malaysia and other nearby nations that share the same waterways.

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Supplementary material 1

Phylogenetic tree

Authors: Md Moshiur Rahman, Nur Asma Ariffin, Ying Giat Seah, Siti Azizah Mohd Nor, Tun Nurul Aimi Mat Jaafar, Nuralif Fakhrullah Mohd Nur, Ahasan Habib

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