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ORIGINAL PAPER

Genetic polymorphism and phylogenetic relationships of the brushtooth lizardfish (*Saurida undosquamis*) (Aulopiformes: Synodontidae) based on mitochondrial DNA markers

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Abstract
The brushtooth lizardfish (*Saurida undosquamis*) is an economically important demersal fishery resource, yet several aspects critical for its conservation are poorly studied. This study examined the genetic variability and structure of *S. undosquamis* from the east coast of Peninsular Malaysia (ECPM), Malaysia, and its broad-scale phylogenetic relationships inferred from the mitochondrial 16S rRNA and COI gene markers, respectively. Results showed that *S. undosquamis* from the ECPM was characterized by a moderate haplotype diversity and a low nucleotide diversity. These characteristics coupled with historical demography analyses suggest a recent population expansion during the Late Pleistocene epoch. A significantly higher nucleotide polymorphism of *S. undosquamis* inhabiting near shore and shallower waters was observed, suggesting a better habitat quality for survival and/or less fishing pressure at these areas. Protecting these areas is critical to maintain these genetically healthy populations. Genetic homogeneity within the ECPM (panmixia) was observed, attributed to its dispersal ability, water currents, absence of physical barrier to gene flow, and/or range expansion. This recommends for a single-stock management regime for *S. undosquamis* in this region. *Saurida undosquamis* from the ECPM, South China Sea, and Japan (East China Sea) were genetically closer with individuals from the Mediterranean coast of Turkey, as evident from all relevant analyses despite being more distant than the Indian Ocean populations.

Keywords Marine fish · COI · 16S · Genetic diversity · Panmixia · South China Sea

Introduction

The marine environment comprises a very high biodiversity that forms the fundamental element of the marine ecosystems (Cochrane et al. 2016). The status or condition of the biodiversity can be assessed from the genetic variability to the species, populations, communities, and ecosystems. Specifically, population genetic study that provides valuable information of the population(s) under study, such as genetic diversity within the population, the genetic relationship among populations, historical demography, and phylogeography, is important to answer ecological questions related to conservation genetics. These valuable data serve as the input for a sustainable bioresource management program. Genetic variability reflects the health and viability of a population. In particular, a population with high genetic diversity is regarded as having a substantial effective population size and thus a lower risk of population or species extinction. In contrast, a population with a low level of genetic diversity is associated with reduced values for fitness traits, such as high juvenile mortality, depressed population growth (Leberg 1990), reduced immunity (Ferguson and Drahushchak 1990; King and Lively 2012), and, ultimately, a higher extinction risk (Frankham 2005; Hellmair and Kinziger 2014; Vitorino et al. 2017). Therefore, if genetic aspects are ignored, extinction risk will be underestimated,

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and inappropriate rehabilitation strategies may be applied (Frankham 2005).

Saurida undosquamis (Richardson, 1848) (Aulopiformes: Synodontidae) commonly known as brushtooth lizardfish, checkered lizardfish, or large-scale grinner/saury is a bottom-living marine fish occurring natively in the eastern Indian Ocean, Malay Peninsula, southern Philippines, northern Java, Arafura Sea, Louisiade Archipelago, and northern half and southwestern Australia (Inoue and Nakabo 2006). It has dark spots on the upper margin of the caudal fin, the large body scales, and the posterior tip of the pectoral fin exceeding the pelvic fin origin. These external characteristics lead to misidentification with four other morphologically close species, i.e., *S. longimanus*, *S. macrolepis*, *S. umeyoshii*, and *S. lessepsianus* (Inoue and Nakabo 2006; Russell et al. 2015). For instance, *S. undosquamis* was reported as an introduced species in Mediterranean and Red Sea (Mahmoud et al. 2014). Yet, the re-examination of the morphological characteristics and molecular analysis confirmed that the previous records of *S. undosquamis* from Red Sea or Mediterranean Sea were misidentifications of *S. lessepsianus* (Tikochinski et al. 2016). *Saurida undosquamis* is an important demersal fishery resources in countries such as China, Japan, Korea, Taiwan (Yoneda et al. 2002; Zhao et al. 2014), India (Metar et al. 2011; Chhandaprajnadarsini et al. 2019), and Turkey (Keskin and Atar 2013) due to its high nutritive value and utilization as food fish in fresh and dried forms (Mach and Nortvedt 2009). In Malaysia, *S. undosquamis* is regarded as a non-target species and harvested largely as bycatch by the bottom fishing trawls. As such to date, it has not attracted much research interest. However, being a component of the bycatch, the potential risk to its decline exists, and therefore, active measures are needed to ensure its conservation.

Previous works on *S. undosquamis* were limited to its biology, population dynamics, life-history traits, and some early genetic studies. These have involved studies in the Indian waters (Rajkumar et al. 2003; Metar et al. 2011; Kadharsha et al. 2013, 2014; Kalhoro et al. 2014; Nansimole et al. 2014; Mali et al. 2017; Chhandaprajnadarsini et al. 2019), northern part of South China Sea (SCS) (Shu and Qiu 2004; Chen et al. 2012; Wang et al. 2012a), East China Sea (ECS) (Yoneda et al. 2002), Taiwan (Du et al. 2011; Hu et al. 2015), the Philippines (Ingles and Pauly 1984), Australia (Thresher et al. 1986), Thailand (Boonwanich 1991), and around Mediterranean Sea (Amin et al. 2007; El-Halfawy et al. 2007; Gökçe et al. 2007; Çiçek and Avşar 2011; Manaşırlı et al. 2011). Population dynamics and stock assessment studies indicate that populations of *S. undosquamis* at the northeastern Mediterranean coast of Turkey (Manaşırlı et al. 2011) were underexploited, while those in Thailand (Boonwanich 1991), Egyptian Mediterranean coast (Mahmoud et al. 2014), and Taiwan (Du et al. 2011) experienced severe overexploitation. Molecular studies of *S. undosquamis* include characterization of its complete mitochondrial genome from the SCS (Zhao et al. 2014), DNA barcoding from Korea (Kim et al. 2012) and Turkey (Keskin and Atar 2013), the genetic pathway of colonization from the Red Sea to Mediterranean Sea based on the restriction fragment length polymorphism analysis (Yağlıoğlu and Turan 2012) (revised as a misidentification of *S. lessepsianus* by Tikochinski et al. 2016), the genetic divergence of *Saurida* species from southern Japan based on alloenzymes (Yamaoka et al. 1989), and the population genetics of samples from the coast of China inferred from the mitochondrial D-loop and cytochrome b sequences (Li et al. 2019, 2020). *Saurida undosquamis* populations from the coast of China were characterized by a high haplotype diversity and relatively low nucleotide diversity. These populations were proposed to be managed as a single-stock based on the genetic homogeneity (Li et al. 2019, 2020).

The current study focused on elucidating the population genetics of *S. undosquamis* from the east coast Peninsular Malaysia (ECPM), Malaysia, inferred from the mitochondrial DNA (mtDNA) 16S rRNA sequences. The phylogenetic relationships of *S. undosquamis* from a broader geographical range were also investigated. For the latter, we sequenced subsamples of S. *undosquamis* from the ECPM using the mtDNA cytochrome c oxidase subunit 1 (COI) gene and conducted a comparative analysis with sequences from the GenBank database. This study provides the first report on the genetic diversity and structure of *S. undosquamis* from the ECPM and insights on its phylogenetic relationships among populations inhabiting various sea basins; both are important baseline data for a fishery resource management.

Materials and methods

Sampling and sample preservation

Random samples of *S. undosquamis* were collected from 10 localities within the exclusive economic zone (EEZ) along the east coast Peninsular Malaysia (ECPM), Malaysia (Fig. 1, Table 1). Samples were obtained through a 1-h trawling activity at each sampling station, using the research vessel. Following the topography of this area, the sampling stations were categorized into shallow (20–50 m) vs. deep water (50–100 m) and nearer to shore (12–30 nautical miles (NMi)) vs. further from shore (30–200 NMi) (Table 1). Specimens were identified following the description of Inoue and Nakabo (2006). A small portion of the caudal fin of each individual was cut and preserved in 1.5-mL tubes containing 95% ethanol and stored at room temperature until further use. Five tissue specimens and genomic DNA extracts of *S. undosquamis* were

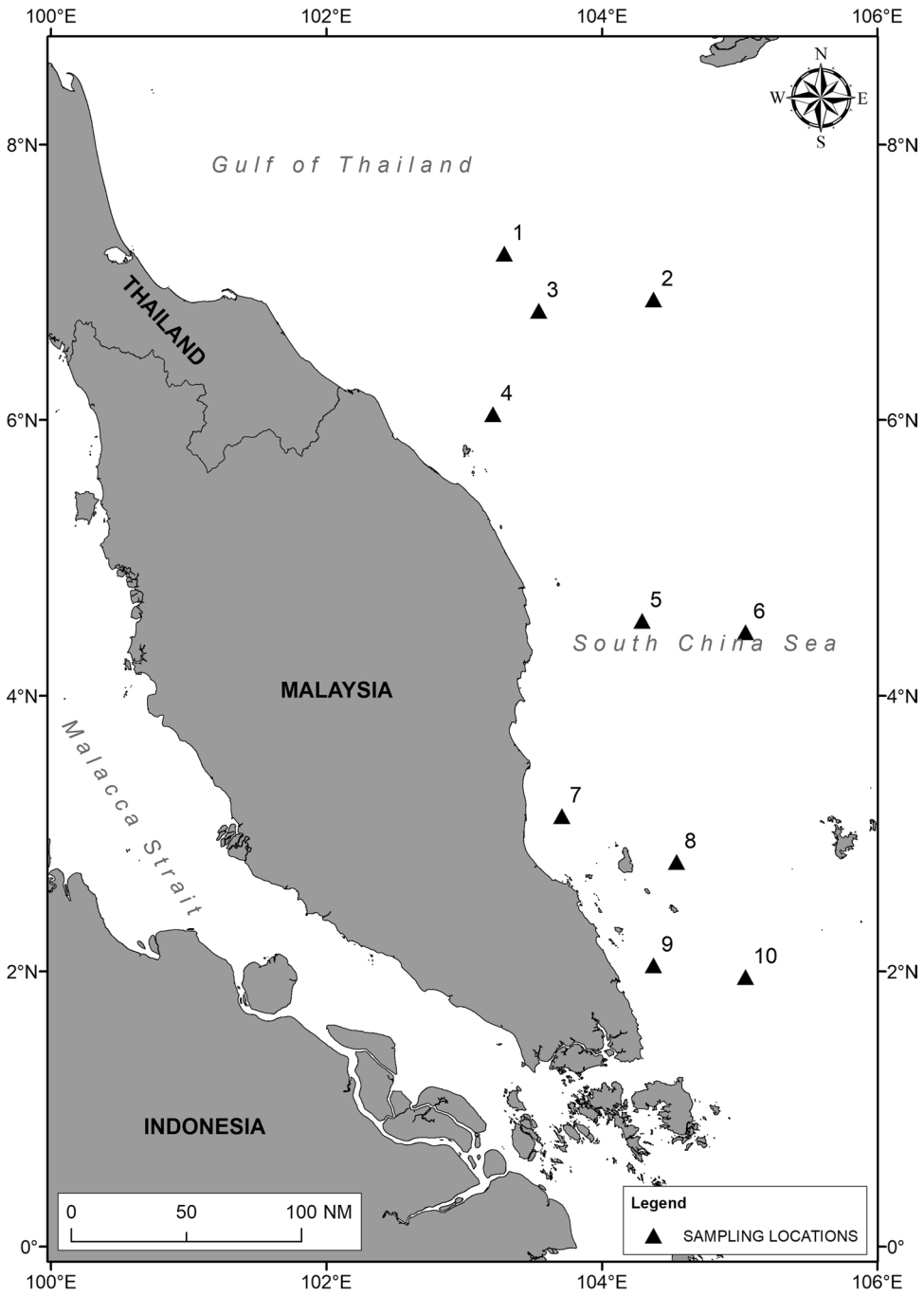


Fig. 1 Ten sampling stations of *Saurida undosquamis* within the exclusive economic zone (EEZ) of the east coast Peninsular Malaysia (ECPM), Malaysia (map was generated in ArcGIS 10.8)

deposited at the South China Sea Repository and Reference Centre (RRC), Institute of Oceanography and Environment (INOS), Universiti Malaysia Terengganu (UMT), Malaysia, under voucher number UMTF9380 to 9384 and UMTGen2323 to 2327, respectively.

DNA extraction and PCR amplification

Total genomic DNA was isolated from the fin tissues by a standard salting-out protocol (Aljanabi and Martinez 1997). The partial mitochondrial 16S rRNA gene was then

Table 1 Sampling locations, sample size (*N*), genetic diversity, neutrality tests, and mismatch distribution parameters of *Saurida undosquamis* based on the mtDNA 16S rRNA

ST	Coordinates		Distance (NMi)	Depth (m)	*N*	Genetic diversity			Neutrality test		Mismatch distribution					
	Lat (N)	Lon (E)				H(S)	*h*	π	Tajima's D	Fu's Fs	*r*	*SSD*	θ_0	θ_1	τ	*T*
1	7° 12.5′	103° 17.5′	30–200	50–100	6	3(2)	0.733	0.0017	−0.93	−0.30	0.22	0.03	0.000	99999.000	1.19	52,841
2	6° 52.5′	104° 22.5′	30–200	50–100	21	3(2)	0.552	0.0016	1.38	1.09	0.25	0.05	0.000	1.800	2.17	96,358
3	6° 47.5′	103° 32.5′	30–200	50–100	8	3(2)	0.679	0.0020	1.17	0.30	0.22	0.05	0.004	6.240	1.78	79,040
4	6° 2.5′	103° 12.5′	12–30	20–50	14	4(4)	0.659	0.0023	−0.53	0.17	0.36	0.10	0.000	3.246	2.06	91,474
5	4° 32.5′	104° 17.5′	30–200	50–100	3	2(1)	0.667	0.0012	0.00	0.20	0.56	0.09	0.000	99999.000	1.05	46,625
6	4° 27.5′	105° 2.5′	30–200	50–100	17	4(3)	0.735	0.0020	0.05	0.06	0.09	0.01	0.002	99999.000	1.29	57,282
7	3° 7.5′	103° 42.5′	12–30	20–50	9	5(3)	0.833	0.0024	0.20	−1.78*	0.14	0.02	0.000	99999.000	1.54	68,383
8	2° 47.5′	104° 32.5′	12–30	50–100	11	4(3)	0.709	0.0023	0.20	−0.23	0.12	0.03	0.000	5.718	1.83	81,261
9	2° 2.5′	104° 22.5′	12–30	20–50	11	4(4)	0.709	0.0026	−0.38	0.06	0.15	0.04	0.005	4.778	2.40	106,571
10	1° 57.5′	105° 2.5′	30–200	50–100	12	5(3)	0.758	0.0022	0.15	−1.39	0.10	0.01	0.000	99999.000	1.44	63,943
		Mean			11.2	3.7(2.7)	0.704	0.0020	0.13	−0.17	0.22	0.04	0.001	50001.678	1.68	74,600
		Overall			112	11(9)	0.682	0.0012	−1.35	−4.90	-	-	-	-	-	-

ST sampling station, *Lat (N)* latitude (north), *Lon (E)* longitude (east), *Distance (NMi)* distance from shore in nautical miles, *Depth (m)* water depth in meter, *N* sample size, *H(S)* number of haplotype (segregating sites), *h* haplotype/gene diversity, π nucleotide diversity, *r* Harpending's raggedness index, *SSD* sum squared deviation between the observed and expected mismatch distribution under a sudden demographic expansion model, θ_0 population before expansion, θ_1 population after expansion, τ *(tau)* relative time since population expansion, *T* time since population expansion

*Significant at $p < 0.05$

amplified using the primer pairs 16S (forward): 5′-CGCCTG TTTATCAAAAACAT-3′ and 16S (reverse): 5′-CCGGTC TGAACTCAGATCACGT-3′ (Palumbi et al. 1991). Samples were PCR amplified in a final volume of 25.0 µL consisting of 12.5 µL of MyTaq DNA Polymerase (Bioline, Meridian Bioscience Inc., UK), 0.5 µM of each primer, 9.5 µL of sterile ultrapure nano water (ddH_2O), and 2.0 µL of the genomic DNA (50 ng/µL). The PCR thermal regime consisted of an initial denaturation at 94 °C for 60 s followed by 35 cycles of 94 °C denaturation for 60 s, 54.7 °C annealing temperature for 60 s, and 72 °C extension period for 120 s, followed by 72 °C final extension for 60 s before termination at 10 °C. For the broad-scale phylogenetic study, randomly selected subsamples of *S. undosquamis* (sample size, $N = 44$) were PCR amplified at mtDNA cytochrome c oxidase subunit 1 (COI) gene using primer pairs FishF1: 5′-TCAACCAAC CACAAAGACATTGGCAC-3′ and FishR1: 5′-TAGACT TCTGGGTGGCCAAAGAATCA-3′ (Ward et al. 2005). The PCR setup condition for COI gene was similar with 16S rRNA, and the thermal regime consisted of an initial denaturation at 94 °C for 5 min followed by 35 cycles of 94 °C denaturation for 30 s, 50 °C annealing temperature for 30 c, and 70 °C extension period for 60 s, followed by 72 °C final extension for 8 min before termination at 10 °C. The PCR products were visualized on a 1.7% agarose gel stained with SYBR Safe, and the clear and single bands of each product were sent to Apical Scientific Sdn. Bhd. (Selangor, Malaysia) for DNA sequencing by using forward primer only.

Sequence alignment and diversity analyses

DNA sequences were aligned and edited using ClustalW implemented in MEGA 6.0 (Tamura et al. 2013). Species identity was verified through the Basic Local Alignment Search Tool (BLAST). The final mtDNA 16S rRNA sequence alignment was truncated to 563 base pair (bp) and was analyzed for the nucleotide segregating sites (S), the number of haplotypes (H), haplotype diversity (h), and nucleotide diversities (π) in Arlequin 3.5.2.2 (Excoffier and Lischer 2010). All haplotypes were deposited in GenBank under accession number MT328738–328748. To determine whether sample size correlates with the diversity indices, Pearson's correlation test was conducted separately for h and π (both h and π were normally distributed). The correlation coefficient (r) for h (-0.415) and π (0.207) was respectively statistically non-significant ($p > 0.05$), indicating that the sample sizes used in this study do not affect the diversity indices. Next, to investigate whether the diversity indices were influenced by the ecological factors such as distance from shore (12–30 vs. 30–200 nautical miles (NMi)) and depth of sea water (20–50 vs. 50–100 m), Student's t-tests were performed in the SPSS software.

Historical demography

Selective neutrality tests that evaluate deviation from neutral expectation which may arise from historical population range expansion or mutation-drift disequilibrium were examined through Tajima's D (Tajima 1989) and Fu's Fs (Fu 1997) statistics using Arlequin 3.5.2.2. To detect whether populations were demographically stable or expanding or decreasing over time, the demographic parameters θ_0 (population before expansion), θ_1 (population after expansion), and tau, τ (relative time since population expansion), were calculated using Arlequin 3.5.2.2. The tau (τ) value is used to estimate the actual time (T) since population expansion using the formula $T = \tau/2\mu$ where μ is the mutation rate per site per generation. In the present study, the mutation rate of 2.0×10^{-8} mutations per site and year (animal mtDNA) was applied (Brown et al. 1979). Furthermore, Harpending's (1994) raggedness index (r) and the sum of squared deviation (SSD) were measured in Arlequin 3.5.2.2, where r has been shown to be a powerful measurement in quantifying population growth with limited sample sizes (Ramos-Onsins and Rozas 2006). In addition, the mismatch distribution was calculated in DnaSP 6.0 (Rozas et al. 2017), to provide an insight into the past population demography.

Genetic structure and phylogenetic relationships

A hierarchical analysis of molecular variance (AMOVA) was conducted to identify the relative contribution of genetic variation at various levels (among and within regions and within sampling locations) using Arlequin 3.5.2.2. The population pairwise comparison Θ_{ST} that calculates relative genetic differentiation between sampling locations was performed based on Kimura 2-parameter (K2P) distance method (Kimura 1980) in Arlequin 3.5.2.2. Statistically significant pairwise comparisons were tested with 10,000 permutations and then adjusted by performing the false discovery rate procedure (FDR) at $\alpha = 0.05$, which controls the family-wise error rate (FWER), a conservative type I error rate that originates from multiplicity (Benjamini and Hochberg 1995). Genetic differentiation among sampling locations was also assessed employing haplotype-based statistics, HST (Nei 1973), and sequence-based statistics, KST*, and significant levels were estimated using permutation tests with 1,000 replicates (Hudson et al. 1992) in DnaSP 5.10. Estimates of gene flow (Nm) based on both haplotype-based and sequence-based statistics were derived from the same program. Genetic distance estimates between sampled populations were calculated using a K2P distance method in MEGA 6.0.

The maximum likelihood (ML) gene tree was constructed by using the K2P model in MEGA 6.0, incorporating 1,000 bootstrap replications (Felsenstein 1985).

Available GenBank sequences of *S. undosquamis* from India (KR231751 to 231753) and SCS (KJ511779) (Zhao et al. 2014) were also included in the phylogenetic study. The Wanieso lizardfish (*S. wanieso*) (AB297972) was included as the outgroup taxon. The relationship among haplotypes was viewed in minimum spanning network (MSN) by applying the median-joining calculation in Network 5.0.1.1 (Bandelt et al. 1999).

To elucidate the phylogenetic relationships of *S. undosquamis* from a broad-scale geographical region, a total of 99 COI GenBank sequences originating from various regions, including Australia, India, West Asia, Japan, Vietnam, and SCS, were aligned with haplotypes from the ECPM (this study). It should be noted that only limited 16S rRNA GenBank sequences were available; thus, COI marker was used instead. These sequences were trimmed to a final length of 519 bp, and only unique sequences were analyzed using the ML gene tree and genetic distance in MEGA 6.0. Our initial analysis revealed several deep divergences in the ML gene tree (Online Resource 1), and they were in agreement with high pairwise genetic distance values (9.44–35.36%) (Table 2). According to the barcoding study on marine fishes by Asgharian et al. (2011), Mat Jaafar et al. (2012), and Wang et al. (2012b), the typical mean genetic divergence for within species and within genus were 0.18 to 0.37% and 10.53 to 17.26%, respectively. Based on a study of carangids in the Indo-Malay Archipelago, Mat Jaafar et al. (2012) recorded a maximum genetic divergence of 4.82% for within species, while the minimum and maximum genetic divergence of within genus were 6.19% and 20.23% (Asgharian et al. 2011), respectively. These suggest incorrect species identity reported in the public database. After careful re-examination (by using the *S. lessepsianus* COI sequence as reference (Tikochinski et al. 2016), BLAST and analyses of genetic divergence within and between species), we believe that these anomalous COI sequences represent *S. lessepsianus*, *Saurida* sp., and *Platycephalus* sp. (Table 2), thus were excluded from the final analyses. Final data set of the COI sequences comprised of *S. undosquamis* from the ECPM (14 haplotypes) (Hap01-12, 14–15; MT511723-511734, 511736–511737), Japan – East China Sea (ECS) (AP002920), SCS (KJ51179), India (FJ347931-347932, KF876019) and Turkey (KC501275, 501282, 501292). These sequences were analyzed using the ML gene tree, genetic distance and MSN.

Table 2 Mitochondrial DNA COI sequences of *Saurida undosquamis* from various geographical regions retrieved from the GenBank database and pairwise genetic distance analysis with *S. undosquamis* from the east coast Peninsular Malaysia (ECPM)

GenBank accession number	Locality	Genetic distance with *S. undosquamis* (%)
MT511723–511734, 511736–511737	ECPM (this study)	-
AP002920	Japan	0.48
KJ511779	South China Sea	0.68
KC501275, 501282, 501292	Turkey	0.89
FJ347931–347932, KF876019*	India	2.32
Species misidentification of *Saurida lessepsianus*		
MT076889	United Arab Emirates	9.71
KR861552, 861554	Lebanon	9.44
KM538520–538521, 538530	Israel	9.44
KU499724	Saudi Arabia	9.71
KY675901	Red Sea	9.71
KR105872–105873*, 105875*, 105877*	India	9.90
HQ956097*, 956206*, 956217*, 956237*, 956095*, 956099*	Australia	9.78
Species misidentification of *Saurida* sp.		
JF494428, 494432	South Africa	17.09
HQ956235–952636*, 956095*	Australia	18.76
MK777115	Vietnam	20.04
KU943087	Taiwan	20.04
KP266852*	South China Sea	20.04
Misidentification of *Platycephalus* sp.		
HM180836	Korea	35.36

*Unpublished article

Results

Genetic diversity and historical demography

The final alignment of 112 16S rRNA sequences revealed nine segregating sites including one indel, resulting in a total of 11 putative haplotypes and an average of 3.7 haplotypes per location (Table 1). The overall genetic diversity was moderate ($h = 0.682$, $\pi = 0.0012$), with an average of $h = 0.704$ (ranged from moderate to high (0.552 to 0.833) and $\pi = 0.0020$ (low values, ranged from 0.0012 to 0.0026) per sampling location. Haplotypes Hap03 and 04 were the most widespread and dominant, each found in 90% of the sampling stations. Student's *t*-tests showed that h was not differentiated by the distance from shore and sea water depth ($p > 0.05$). However, the π was significantly higher at 12–30 nautical miles (NMi) from shore as compared to 30–50 NMi and at 20–50 m sea water depth compared to 50–100 m.

Neutrality tests of Tajima's D (− 1.35) and Fu's Fs (− 4.90) for the overall data set revealed non-significant negative value. The observed mismatch distribution based on the 16S rRNA sequences was unimodal (Fig. 2). The goodness of fit tests (*r* and *SSD*) for all sampling locations and the overall data set were not significant ($p > 0.05$) (Table 1). In addition, the test for population expansion showed large differences before ($\theta_0 = 0.001$) and after ($\theta = 50{,}001.678$) population expansion, and the estimated time of population expansion was 74,600 years ago (tau = 1.68), while the hypothetical time since expansion at the individual sampling locations ranged from 106,571 to 46,625 years ago (Table 1).

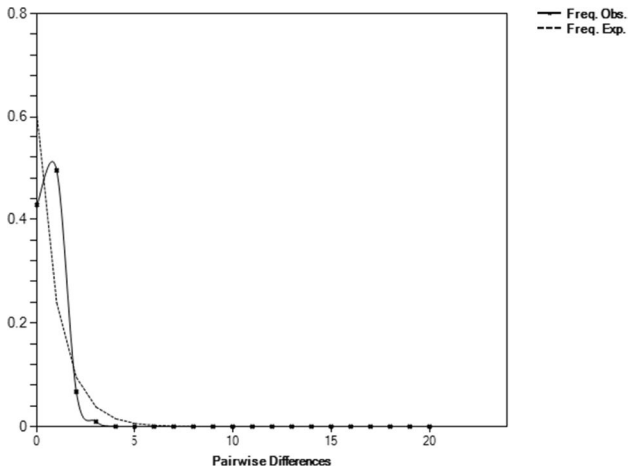


Fig. 2 Mismatch distribution (pairwise number of differences) of *Saurida undosquamis* from the east coast Peninsular Malaysia inferred from the mitochondrial DNA 16S rRNA, constructed in DnaSP software

Genetic structure and phylogenetic relationships

AMOVA depicted that the overall genetic variance of *S. undosquamis* in the ECPM was contributed mostly by the genetic differences within sampling location (99.22%) and a negligible amount of genetic variance contributed by between sampling locations (0.78%). This paralleled the low and non-significant values for all pairwise comparison Θ_{ST} (ranging from − 0.292 to 0.460) (Table 3), HST (− 0.0089), KST* (− 0.0072), and low pairwise genetic distances (0.08 to 0.15%) (Table 3). As expected, the gene flow estimates based on the haplotype-based and sequence-based statistics were relatively high (5.87 and 18.40, respectively).

A single 16S rRNA haplotype further north in the SCS (GenBank sequence KJ511779) was identical to Hap04 from the ECPM. However, the ECPM populations were significantly differentiated from those of India, as evident in AMOVA, pairwise comparison Θ_{ST} (Table 3), genetic distance (Table 3), ML tree (Fig. 3a), and MSN analyses (Fig. 4). Specifically, in AMOVA, when the ECPM haplotypes were grouped separately from those of India, among groups variation contributed 93.47% of the total genetic variation, followed by variation within populations (6.46%) and variation among sampling locations within groups (0.07%). Accordingly, all pairwise comparisons Θ_{ST} involving haplotypes from India and ECPM were relatively high (0.927–0.964) and significant ($p < 0.05$) except for the pairwise comparison with ST5 (Table 3). This also aligned with the higher pairwise genetic distances involving samples from India (1.71 to 1.81%) (Table 3). However, it should be noted that these values still lie within the expected intra-specific distances (Ward et al. 2005).

Similarly, the ML gene tree clusters the ECPM and SCS haplotypes into the same clade, separated from the Indian haplotypes. Each clade is well supported (Fig. 3a) although within clade relationships are not as well resolved indicating relative homogeneity. Overall, single-site mutation differentiates neighboring haplotypes in the ECPM, while eight nucleotide substitutions were observed between the two haplotypes linking the two clades, namely Hap08 (ECPM) and KR231751 (India) (Fig. 4a).

Broad-scale phylogenetic relationships inferred from the COI gene marker

The ML gene tree clusters *S. undosquamis* from the ECPM, Japan (ECS), SCS, and Turkey into the same clade (herein referred as clade I) with 81% bootstrap support, with Indian Ocean forming a sister group (clade II) (Fig. 3b). This is concordance with the genetic distances of 0.20 to 0.90% within clade I, while it ranges from 1.40 to 2.30% between the two clades. MSN analysis depicts two to three mutation sites between the neighboring haplotypes within clade I. The MSN highlights some level of

Table 3 Pairwise comparison Θ_{ST} (below diagonal) and genetic distance (above diagonal) among sampling stations (ST) in the east coast Peninsular Malaysia (ST1-10) and India

ST	1	2	3	4	5	6	7	8	9	10	India
1		0.0014	0.0014	0.0012	0.0015	0.0010	0.0013	0.0013	0.0015	0.0012	0.0171
2	0.439		0.0009	0.0012	0.0008	0.0011	0.0011	0.0011	0.0013	0.0011	0.0180
3	0.439	-0.094		0.0012	0.0008	0.0011	0.0011	0.0011	0.0013	0.0011	0.0180
4	0.117	0.066	0.020		0.0013	0.0012	0.0013	0.0013	0.0014	0.0013	0.0175
5	0.460	-0.229	-0.292	-0.068		0.0011	0.0011	0.0011	0.0013	0.0011	0.0181
6	0.150	0.077	0.040	-0.047	-0.030		0.0012	0.0012	0.0013	0.0011	0.0176
7	0.202	-0.005	-0.053	-0.079	-0.164	-0.051		0.0013	0.0014	0.0012	0.0175
8	0.218	-0.008	-0.053	-0.046	-0.160	-0.043	-0.079		0.0014	0.0012	0.0179
9	0.181	0.000	-0.050	-0.056	-0.165	-0.034	-0.100	-0.065		0.0014	0.0177
10	0.188	0.019	-0.025	-0.052	-0.121	-0.051	-0.075	-0.068	-0.059		0.0178
India	0.964*	0.953*	0.954*	0.932*	0.956	0.945*	0.937*	0.940*	0.927*	0.941*	

*Significant at $p < 0.05$ after FDR correction

structuring, albeit minimal within clade I of the ML tree, between haplotypes from Turkey and the ECPM-SCS-ECS populations. This is in agreement with the moderate support for clade I in the ML tree and the range in genetic distances.

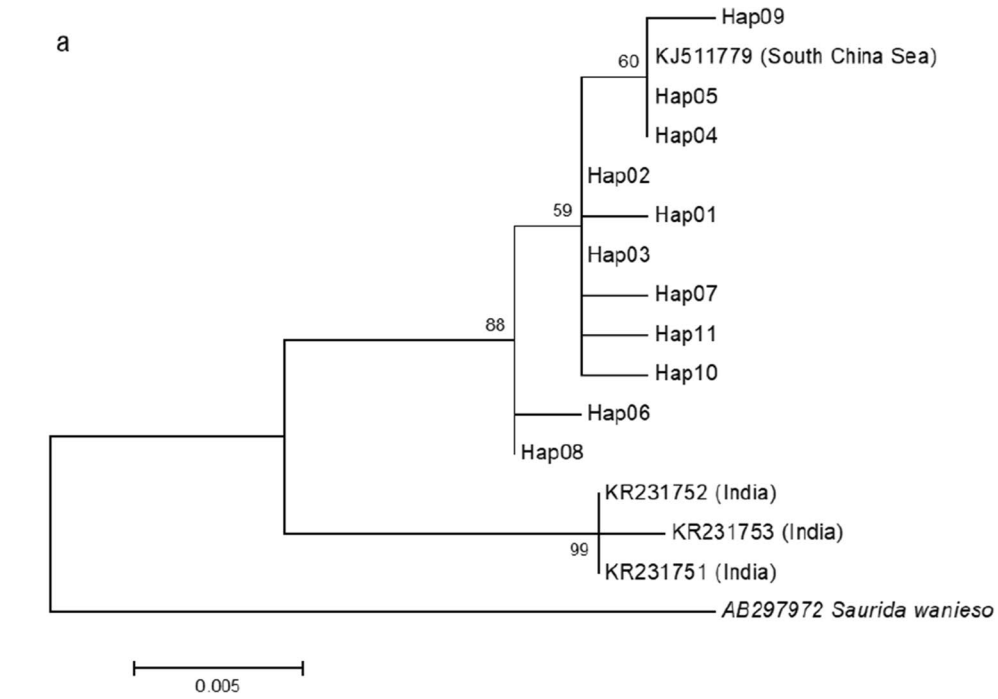
Discussion

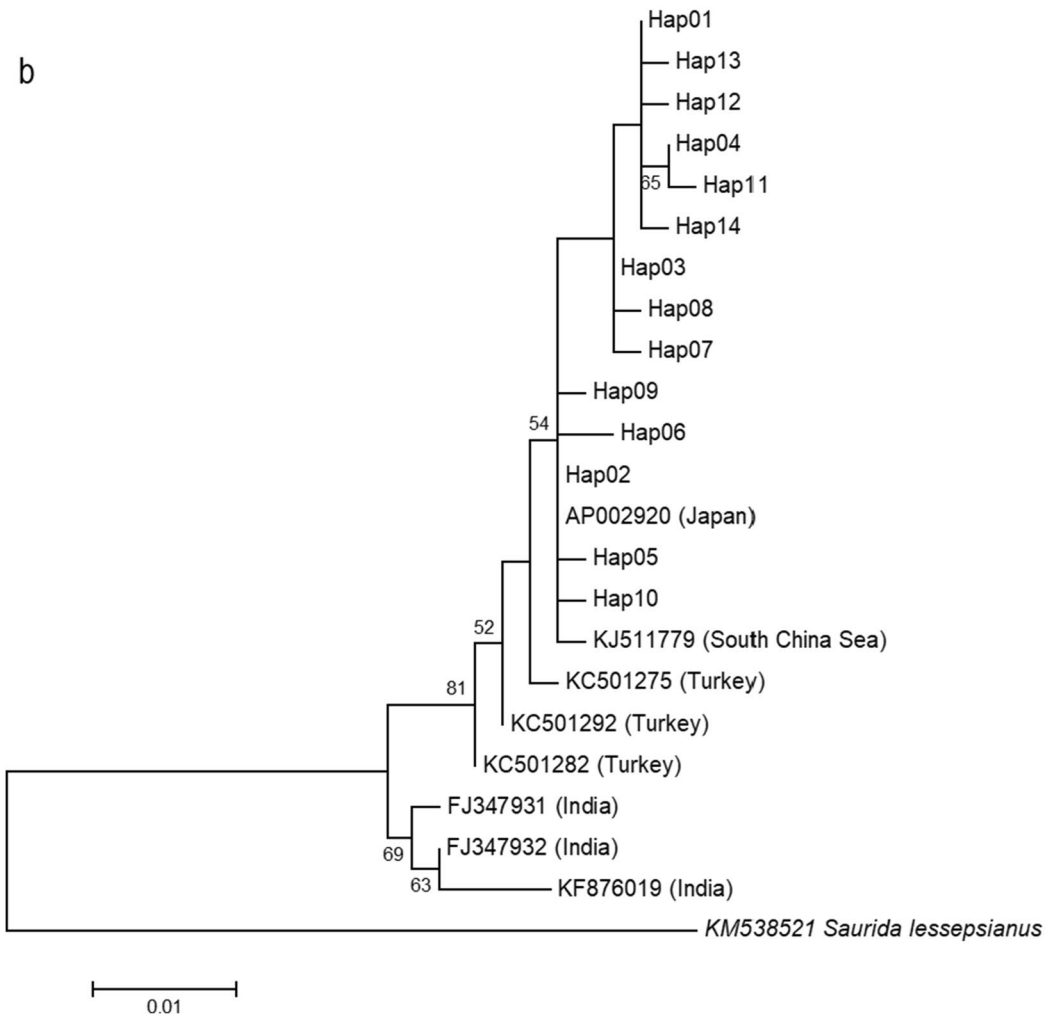
An overall moderate level of haplotype diversity and low nucleotide diversity was estimated in *S. undosquamis* from the ECPM, suggesting that the populations may have undergone a severe, rapid population reduction, followed by a rapid expansion from a low effective population size (Liu et al. 2019). The neutrality tests and the historical demography analyses collectively suggest that the populations had experienced a recent population expansion, possibly during the Late Pleistocene epoch (74,600 years ago). This time span afforded an adequate time for the increase in haplotypes through mutation but inadequate time for accumulation of large sequence differences (Lowe et al. 2004) which translated to a moderate level of haplotype diversity but a low nucleotide diversity. Another plausible explanation for the low level of genetic variation (only 11 different haplotypes from 112 samples) could be the consequence of the use of the relatively conserved gene marker; thus, a more rapidly mutated genetic marker should be applied in the future to support this hypothesis.

Genetic polymorphism of *S. undosquamis* from the ECPM (h: 0.552–0.883, π: 0.0012–0.0026) was relatively lower than those from the coast of China (h: 0.925–0.993, π: 0.0031–0.0039) (Li et al. 2019), suggesting for a smaller maternal effective population size of *S. undosquamis* at the ECPM than at the coast of China. Studies on other marine species within the ECPM have indicated a high level of haplotype diversity and low nucleotide diversity as reported in the pelagic Japanese threadfin bream (*Nemipterus japonicus*) (Lim et al. 2016), Indian mackerel (*Rastrelliger kanagurta*) (Akib et al. 2015), crescent perch (*Terapon jarbua*) (Chanthran et al. 2020), and longtail tuna (*Thunnus tonggol*) (Kasim et al. 2020). Moderate haplotype diversity and low nucleotide diversity was reported in the amphibious fish, the Pearse's mudskipper (*Periophthalmus novemradiatus*) (Tan et al. 2020). A significantly higher nucleotide polymorphism was observed in near shore and shallower water populations, possibly due to an environmental healthier habitat for survival and/or less fishing pressure at these areas. Thus, protecting these sites is vital in maintaining the genetically variable *S. undosquamis* populations.

No distinct genetic cluster of *S. undosquamis* within the ECPM was observed, as shown in the AMOVA, population pairwise comparison analyses, and the gene flow estimates. High gene flow of marine populations within this region (which lies in the southern part of the SCS), as well as within the broader SCS waters, was also reported in several species, such as the Japanese threadfin bream (*Nemipterus japonicus*) (Lim et al. 2016), Indian mackerel (*Rastrelliger kanagurta*) (Akib et al. 2015), crescent perch (*Terapon jarbua*) (Chanthran et al. 2020), and longtail tuna (*Thunnus tonggol*) (Kasim et al. 2020). Panmixia is associated with the dispersal ability of a species during one or more phases of its life history, ocean currents, and the absence of a physical barrier to migration. Our results imply that the populations of *S. undosquamis* from the ECPM could be treated as a single-stock management unit. Our study also provides evidence of a shared genetic pool or a common ancestor between ECPM and other sites investigated in the SCS. Nevertheless, more samples from the SCS need to be included in future studies to strengthen this hypothesis. A significant

Fig. 3 Scaled maximum likelihood gene tree of *Saurida undosquamis* based on the mitochondrial DNA **a** 16S rRNA and **b** COI gene, constructed in MEGA 6.0 software. Bootstrap support value less than 50% is not shown


a
Hap09
KJ511779 (South China Sea)
Hap05
Hap04
Hap02
Hap01
Hap03
Hap07
Hap11
Hap10
Hap06
Hap08
KR231752 (India)
KR231753 (India)
KR231751 (India)
AB297972 Saurida wanieso
60
59
88
99
0.005


b
Hap01
Hap13
Hap12
Hap04
Hap11
Hap14
Hap03
Hap08
Hap07
Hap09
Hap06
Hap02
AP002920 (Japan)
Hap05
Hap10
KJ511779 (South China Sea)
KC501275 (Turkey)
KC501292 (Turkey)
KC501282 (Turkey)
FJ347931 (India)
FJ347932 (India)
KF876019 (India)
KM538521 Saurida lessepsianus
65
54
52
81
69
63
0.01

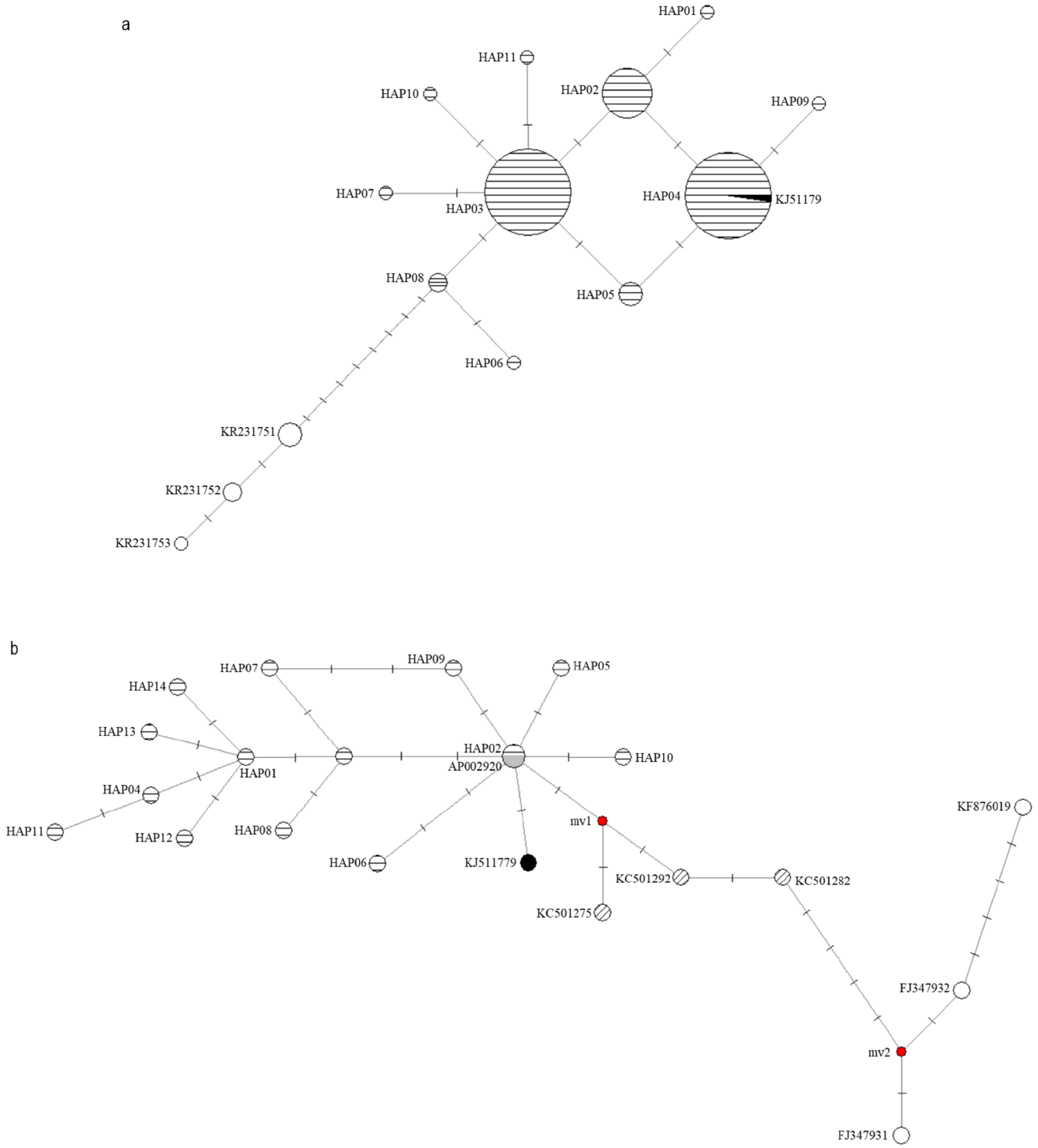


Fig. 4 Haplotype network diagram of *Saurida undosquamis* inferred from the mitochondrial DNA **a** 16S rRNA and **b** COI gene, constructed in Network 10.2.0.0. The size of the node is proportioned to the number of individuals. Haplotype from the east coast Peninsular Malaysia is represented by horizontal lines, South China Sea (KJ511779) solid black, Japan (East China sea) (AP002920) solid gray, India (KR231751-231753, FJ347931-347932, KF876019), solid white, and Turkey (KC501275, 501282, 501292) backward diagonal. The dash between haplotypes indicates one nucleotide site mutation. mv, median vector

genetic structure, however, was observed between the Indian Ocean and the ECPM and other SCS populations, indicating an effective regional isolation that is consistent with the effect of lowered sea level during the Pleistocene (Otwoma and Kochzius 2016), which limited gene flow and enabled complete lineage sorting of *S. undosquamis* inhabiting these regions, as evidence from the ML gene tree (Fig. 3a) and population pairwise Θ_{ST} (Table 2).

In support of the above findings, the COI gene marker also grouped the ECPM populations with other SCS populations as well as the ECS population of Japan, suggesting an admixed genetic pool or a common ancestor of *S. undosquamis*. This is expected as SCS and ECS are adjacent waters within the West Pacific Ocean. The higher than typical genetic divergence (2.32%) between the ECPM and the Indian Ocean suggests presence of an effective regional genetic break between the two seas as was also observed in the reef grouper (*Epinephelus merra*) (Muths et al. 2014), Indian mackerel (*Rastrelliger kanagurta*) (Akib et al. 2015), and longtail tuna (*Thunnus tonggol*) (Kasim et al. 2020). Future studies should involve a narrower scale sampling of sites lying between ECPM and those of the Indian Ocean to identify the precise genetic boundary. In contrast, maternal haplotype sharing between these regions was reported in the crescent perch (*Terapon jarbua*), likely associated to the range expansion after glacial retreat (Liu et al. 2015).

Saurida undosquamis from the ECPM, SCS, and ECS were closely related with individuals from the Mediterranean coast of Turkey (Keskin and Atar 2013), as evident from all relevant analyses despite being more distant than the Indian Ocean populations. It is worth noting that *S. undosquamis* was reported as an introduced species in Turkey (GBIF 2019). Nevertheless, with the current limited data, we are unable to elucidate the genetic origin of *S. undosquamis* from the Mediterranean coast of Turkey. More samples from the study sites and the surrounding seas will be, therefore, necessary to be included in future analysis to fully comprehend the phylogenetic relationships. Tikochinski et al. (2016) had previously confirmed that the earlier records of *S. undosquamis* and *S. macrolepis* in the Red Sea and the Mediterranean are misidentifications of *S. lessepsianus*. Our results, however, support the co-existence of *S. undosquamis* in the Mediterranean Sea of Turkey, evidenced by (1) the low intraspecific genetic distance (0.89%) (Table 2) between our samples and the COI sequences (KC501275, KC501282, KC501292) from Keskin and Atar (2013), (2) clustering of these sequences into the same clade in the ML gene tree (Fig. 3b), and (3) a high pairwise genetic distance between the *S. undosquamis* COI sequences from Keskin and Atar (2013) and *S. lessepsianus* from Tikochinski et al. (2016) that ranges from 8.11 to 9.45%, suggesting a genetic divergence at an interspecific level.

In conclusion, our study showed that *S. undosquamis* from the ECPM was characterized by a moderate level of haplotype diversity and low nucleotide diversity. Coupled with past population expansion, current populations have remained moderately abundant. A higher nucleotide polymorphism was detected in populations nearer to shore and shallower waters, suggesting healthy environment and/or less fishing pressure. Thus, protecting these areas is the way forward to ensure sustainable fishery resource. Genetic homogeneity was observed in *S. undosquamis* from the ECPM, suggesting for a single-stock management strategy. *Saurida undosquamis* from the ECPM, SCS, and Japan (ECS) are closely related with those from the Mediterranean Sea of Turkey. The high genetic divergence between the ECPM and Indian Ocean suggests occurrence of a genetic break lying between these areas, with limited gene flow beyond this boundary. Regional sampling of specimens from the surrounding sea basins needs to be included in future analysis to better comprehend the genetic relationships of *S. undosquamis*.

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Declarations

Conflict of interest The authors declare no competing interests.

Ethics approval No approval of research ethics committees was required to accomplish the goals of this study because no animal testing was performed during the study. The target species is not a threatened species and is listed as least concern in the IUCN Red List status.

Sampling and field studies Samples were obtained during the expedition of the demersal resource survey conducted by the SEAFDEC and Malaysia Department of Fisheries. The study is compliant with CBD and Nagoya protocols.

Data availability Unique DNA sequences (haplotypes) were deposited in GenBank under accession number MT328738–328748 (16S rRNA) and MT511723–511737 (COI). All data generated or analyzed during this study are included in this published article and its supplementary information file.

Author contribution MPT and TNAMJ designed the study and collected and sorted the samples. RS, NFMN, and NISMY conducted laboratory works and data analyses. MPT and RS wrote the first draft of the manuscript. SAMN, YYS, MD, SM, NFMN, NISMY, and TNAMJ reviewed and edited the manuscript. All authors read and approved the manuscript.

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