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Genetic differentiation in populations of two snappers, *Lutjanus malabaricus* and *Pristipomoides multidens,* in the Makassar Strait and adjacent waters, Indonesia: Implications for management

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ABSTRACT

The Makassar Strait and adjacent waters, which is crossed by the Wallace line, has variations in bathymetry and unique ocean currents. This condition allows for genetic differences in the Malabar blood snapper (*Lutjanus malabaricus*) and the Goldband snapper (*Pristipomoides multidens*) in the strait. Specimens were collected from some landing bases in Makassar Strait and adjacent waters as part of Indonesia's Fisheries Management Area (FMA) 713 and assessed using d-loop mtDNA. Both *L.malabaricus* and *P.multidens* obtained the same sequencing results of around 400 bp with 67 and 71 of number haplotypes, respectively. The results of the polymorphism of the two species showed high genetic diversity (*L.malabaricus*: $h = 0.9284$, $\pi = 0.0434$; *P.multidens*: $h = 0.9766$, $\pi = 0.0532$). Based on differences analysis to examine the population genetic structure showed different results. *L. malabaricus* was identified as having no population genetic structure. On the other hand, *P. multidens* has significant ($\Phi_{ST} = 0.07010$, $p < 0.001$) structural differences among sub-areas, the western part of the Makassar Strait, the eastern part of the Makassar Strait, and south of the Makassar Strait, Flores Sea. The different stock units need to be considered in the development of fisheries management and surveillance. Management of fish resources requires a flexible and adaptive approach, taking into account the fishery characteristics of each population and the broad ecosystems in which they occur.

1. Introduction

The snappers (Lutjanids) are economically important, supporting livelihoods, exploited in both small and industrial-scale as well as recreational fishing (Gomes et al., 2012; Mzingirwa et al., 2019; Souza et al., 2019; Dimarchopoulou et al., 2021; Ernawati et al., 2021). Its distribution area encompasses the eastern Pacific, Indo-West Pacific, eastern Atlantic, and Western Atlantic. Two snapper species, *Lutjanus malabaricus* (Malabar blood snapper) and *Pristipomoides multidens* (Goldband snapper), are notable tropical fish in Indonesia. The first inhabits relatively shallow water with 12–100 m depths (Allen, 1985), even shallower than 10 m (Salini et al., 2006). This species occurs along the continental shelf associated with inshore and offshore reef areas, shoal grounds, and flat bottom areas with occasional epibenthos (Newman, 2002). In comparison, the second is a deepwater snapper living in association with hard bottom, rocky, and uneven sea floors with a 40–200 m depth range (Allen, 1985; Guo et al., 2016; Ovenden et al., 2004). In Makassar Strait and adjacent waters as a part of Fisheries Management Area (FMA) 713 (Fig. 1), these two species are the main target generally caught together by various fishing gears dominated by bottom longline and drop line (Salini et al., 2006; Ernawati and Budiarti, 2020). According to national fisheries statistics at FMA 713, during the 2018–2022 period, the average total production of snappers (Lutjanidae) was recorded at 30,304 tons per year, while *L. malabaricus* and *P. multidens* contributed around 25 % and 22 %, respectively (DGCF-MMAF, 2024). The Makassar Strait accounts for around 80 % of

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the snapper fishery, and the rest of the catch derives from other waters in FMA 713, namely the Bali Strait, Bone Bay, and the Flores Sea (Regulation of The Minister of Marine Affairs and Fisheries No. 18/2014).

The Makassar Strait and adjacent waters are part of the Coral Triangle, which has the highest marine biodiversity in the world (Veron et al., 2009). Repeated glaciations during the Pleistocene (~2.5 million to 12 thousand years ago) caused extreme changes in regional geography as the Sunda and Sahul shelves repeatedly rose above and fell below sea level (Voris, 2000). This geographic history allows for population differences (Barber et al., 2006; Ackiss et al., 2013). Makassar Strait and adjacent waters are also one of the areas crossed by the Wallace line (a transitional zone with mixed fauna from Asia and Australia). The line in the Indonesian archipelago stretches from the Indian Ocean through the Lombok Strait (between the islands of Bali and Lombok), north through the Makassar Strait which separates the shallow waters east of the island of Kalimantan (part of Sunda Shelf) and the deep waters west of Sulawesi (part of Sahul Shelf), to the Sulawesi Sea (Wallace, 1860; Lourie and Vincent, 2004). There are two connecting deep water basins in this strait, i.e., the North Makassar basin, bounded south by the edge of the paternoster platform with a narrow and deep channel joining the South Makassar basin (Hall et al., 2009). Water mass passes through the Makassar Strait are the Indonesian Through Flow (ITF/*Arlindo*) that connects the Pacific and Indian oceans, carrying around 77 % of water mass (Gordon et al., 2019). After passing the Makassar Strait, some of water masses goes directly out through the Lombok Strait to the Indian Ocean, and some of it enters the Banda Sea via Flores Sea (Fig. 1) (Sprintall et al., 2009; Fritz et al., 2023).

The combination of deep basins and shallow waters within habitable areas can be used as a basis for structuring population differences in groundfish such as snapper. In general, bathymetry affects ocean currents, limiting larval transport or causing poor larval survival in deeper water due to poor nutrition (Knutsen et al., 2009). Water depths and ocean currents play an important role in shaping genetic connectivity between populations in deep waters, either as barriers or promoters of gene flow, leading to genetic structure differences on a spatial and temporal scale (Zeng et al., 2020). Identifying areas of limited connectivity in species distributed in the Makassar Strait and adjacent waters (part of the Coral Triangle) can provide insights into fisheries stock structure for management and the mechanisms driving lineage divergence in this region (Ackiss et al., 2013). In addition, since larval dispersal is a major means of demographic and genetic connectivity among most populations, understanding larval dispersal patterns has been identified as one of the most important components in effectively reserve networks developing (Sale et al., 2005). The pelagic larval duration (PLD) of fish varies both spatially and temporally, extending from several days to months (Bay et al., 2006; Luiz et al., 2013). Lutjanids or snappers, although adult fish undertake spawning migrations and juvenile fish make ontogenetic movements, the primary process linking connectivity between fragmented adult populations is believed to be through the dispersal of pelagic larval stages (Cowen and Sponaugle, 2009; D'Alessandro et al., 2010). Thus, considering the bathymetry, ITF, dynamics of larval dispersal and history of geography, the snapper species inhabiting Makassar Strait and adjacent waters may form different populations. This encourages the importance of population identification to determine stock units as a prerequisite for conducting stock and population dynamics assessments (Cadrin et al., 2013).

Little information was available from the studies on the genetic

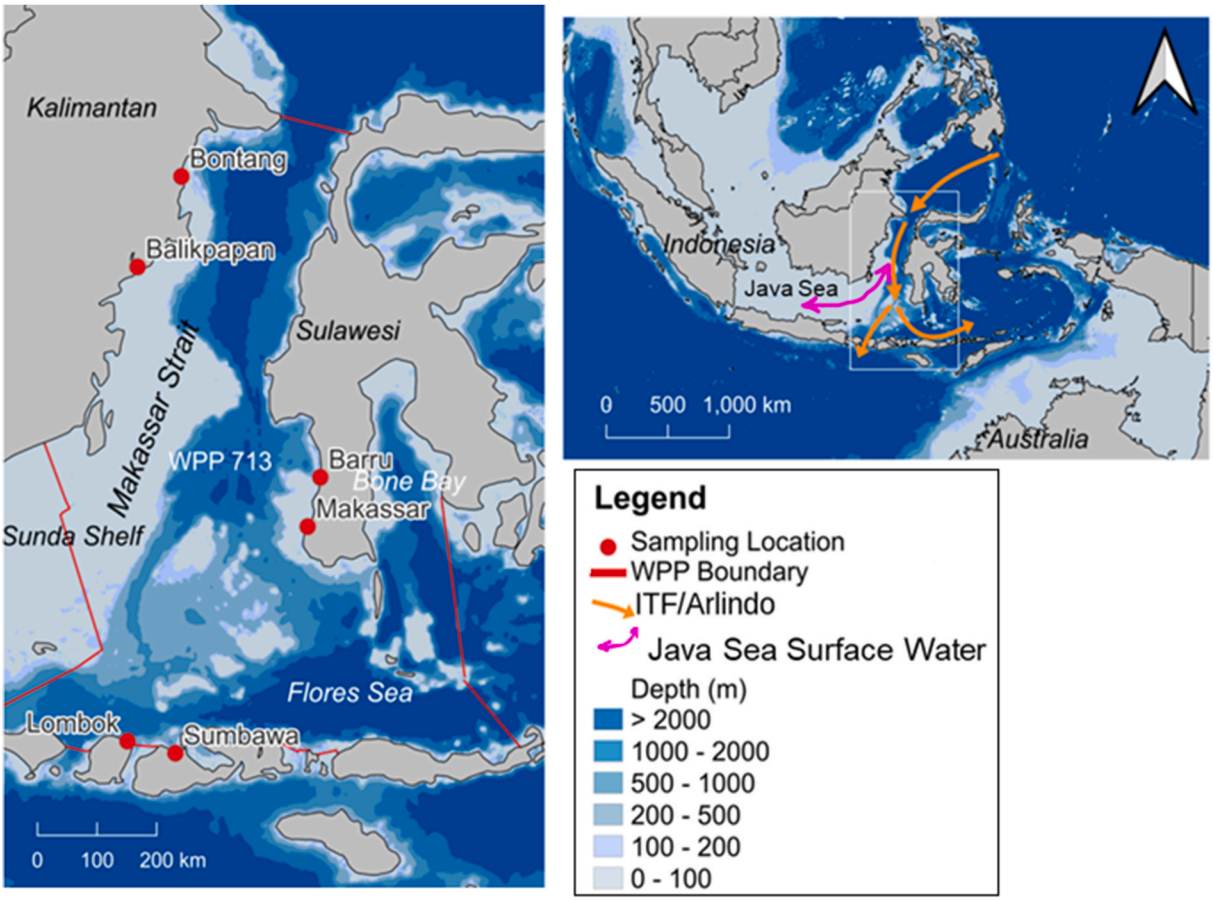

Fig. 1. Map of WPP 713, sampling locations of *L.malabaricus* and *P.multidens*. Bathymetry, Indonesian Through Flow (ITF/Arlindo) and Java Sea Surface Water referred to Gordon (2005).

differentiation of snapper or other groundfish-reef fish populations in Indonesia (Ackiss et al., 2013; Ovenden et al., 2002, 2004; Ovenden and Street, 2003; Salini et al., 2006; Zamroni et al., 2021). The relevant results for *P.multidens* are that its population structure is confined within a small geographic area (Newman et al., 2016; Kennington et al., 2017; Ovenden et al., 2004), whereas *L.malabaricus* has genetic boundaries in eastern Indonesian waters between Sape and Kupang (Salini et al., 2006). Various techniques in genetics marker to determine genetic differences are allozymes, mitochondrial DNA (mtDNA), microsatellites, and SNPs. The mtDNA is a highly useful genetic marker for maternal lineage, with a simple structure and no intermolecular genetic recombination (Hamilton et al., 2017; Wu et al., 2014; Zhang et al., 2019). However, mtDNA has a more biased base composition than nDNA (Rubinoff and Holland, 2005).

This study aims to identify genetic diversity, phylogeography relatedness, and population structure for determining the stock units of two commercial snappers, *L. malabaricus* and *P. multidens*, towards a more optimal and rational stock assessment of these snappers in the Makassar Strait and adjacent waters. The results of this study can provide strong scientific evidence related to snapper stock units. Thus, it allows the development of fisheries management based on stock units compared to fisheries management based on FMA in Indonesia.

2. Materials and methods

2.1. Samples collection

Snapper fish tissue collection was conducted between July 2021 to March 2022, representing the western part (Balikpapan and Bontang), eastern part (Barru and Makassar), and southern part of Makassar Strait (Flores Sea). Sampling sites were similar for both species except in the southern area, taken at different localities (Lombok and Sumbawa, Fig. 1). The southern area of the Makassar Strait is considered to be directly adjacent (no barriers), still connected and influenced by the ITF, as it is known that the main gateway to the Indian Ocean is through the Lombok Strait. We used a grid map (1° x 1°) to help confirm the fishing grounds (FG) of the fishermen whose catches would be sampled, to ensure that fish samples were not mixed between different FG.

The total tissue collected was 170 and 128 specimens for *L. malabaricus* and *P. multidens*, respectively (Table 1). A permit for tissue collection is not required, as the species is commercial and dead when landed at the fishing port. Tissue was taken from the flesh around the dorsal fin of dead fish, stored in a 2 mL microtube containing 96 % ethanol with a label recording identity of the sample.

2.2. DNA analysis

DNA isolation follows the spin column method with DNeasy Blood and Tissue Kit from Qiagen. The fish's tissue in 96 % ethanol was washed with distilled water, of which 25 mg of tissue was transferred into a 1.5 ml microcentrifuge tube. A 180 µl of ATL Buffer and 20 µl of Proteinase K with a concentration of 40 mAU/mg were added, then vortex thoroughly before incubation at 56 °C for 3 h, or until the sample lysate became clear. DNA extraction refers to the instructions from the Qiagen Kit for tissue.

Table 1
The number of samples at each location of *L. malabaricus* and *P. multidens*.

Location	*n* samples of *L. malabaricus*	*n* samples of *P.multidens*
1. Balikpapan (BPN)	35	34
2. Bontang (BTG)	30	31
3. Barru (BRU)	35	16
4. Makassar (MKS)	35	12
5. Lombok (LBK)	–	35
6. Sumbawa (SBW)	35	–

The primers used for d-loop mtDNA amplification were Pro889U20 5′-CCW CTAACT CCCAAA GCTAG-3′ and TDKD1291L21 5′-CCT GAA ATA GGA ACC AAA TGC-3' (Ovenden et al., 2002; Ovenden and Street, 2003; Salini et al., 2006; Chu et al., 2013). Having been amplified using PRO and TDKD primers, the length of the mtDNA sequences for red snapper and goldband snapper was around 400 bp. The PCR protocol firstly was to make a 50 µl PCR mixture consisting of a 25 µl master mix (bioline), 1.5 µl of each primer, 19 µl of ddH2O, and 3 µl of DNA samples. The denaturation procedure referred from (Chu et al., 2013) was initiated by denaturation for PCR at 94 °C for 1.5 min, followed by 35 cycles of denaturation at 94 °C for 5 s, annealing at 50 °C for 0.5 min, and elongation step at 72 °C for 0.5 min, final elongation at 72 °C for 5 min and held at 4 °C.

The PCR products on polyacrylamide gels of similar size to the main design were purified using the agarose-gel cutting method and continued with spin-column DNA extraction from the gel. The purified PCR products were imprinted into sequenced PCRs using the same primer pair with initial efficacy. This work was carried out at the Macrogen's Sequencing Service of Singapore.

2.3. Data analysis

The nucleotide sequencing results were checked and aligned using Clustal W in the MEGA X (Molecular Evolutionary Genetics Analysis) software (Kumar et al., 2018). The nuclear haplotype rearrangement was done using DnaSP 6.12.03 software (Librado and Rozas, 2009). This process consisted of 1000 burn-in iterations and 1000 main iterations. The DnaSP based on Nei 1987 formula made identification and estimation of haplotype frequency and the number of polymorphic sites. The polymorphism level of each marker was calculated based on the haplotype (h) and nucleotide (π) diversity indices, available in the software Arlequin 3.5.2.2 (Excoffier and Lischer, 2010).

A total of 170 *L. malabaricus* sequences and 128 *P. multidens* sequences were used for phylogenetic reconstruction. The phylogenetic tree was constructed using MEGA 10 (Kumar et al., 2018) based on the Neighbor Joining (NJ) method (Saitou2 & Nei, 1987) with 1000 bootstrap replicates. Distances were calculated with Kimura-2 parameter (Kimura, 1980). Kimura-2 parameter is a nucleotide substitution model used to estimate genetic distances and phylogenetic relationships (Madduppa et al., 2021a,b).

Examination of the respective haplotype networks of *L.malabaricus* and *P.multidens* was carried out using the minimum spanning network (MSN) method (Bandelt et al., 1999) using PopART (https://popart.otago.ac.nz). This estimation was a depiction of population connectivity from the genetic distribution of the two snapper species in each population.

In estimating the genetic differences level among the population groups, we applied the two pairwise F_{st} parameters using 1000 permutations with a significance level of 0.05 and an exact test of sample differentiation based on haplotype frequencies using 100,000 steps of Markov chain (Raymond and Rousset, 1995). That analysis was carried out in the Arlequin 3.5.2.2 program package (Excoffier and Lischer, 2010). An unbiased estimate can be obtained using the Markov chain method by using an exact test of sample differentiation, in addition to being determined based on exact probability. The Markov chain is a step towards generating an exact probability distribution under the null hypothesis, which is unbiased by rare alleles with small sample sizes (Raymond and Rousset, 1995).

The hierarchical population genetic structure analysis in two species was also conducted using analysing molecular of variance (AMOVA) if differentiations were occurred between locations. Knowing this makes examining the population's genetic structure permissible based on the frequency and number of mutations between haplotypes (Excoffier and Quattro, 1992). AMOVA was applied to evaluate genetic differences among and within populations based on localities. To investigate the presence of barriers such as bathymetry and sea current influences, we

also used the AMOVA framework to group sampling localities and test for hierarchical population structure. The group was divided into three sub-areas, including: 1) East of Kalimantan Island (EKI) consisting Balikpapan and Bontang was represented the western part of the Makassar Strait which is dominated by shallow waters as part of the Sunda shelf; 2). West of Sulawesi Island (WSI) consisted of Barru and Makassar representing the eastern part of the Makassar Strait which is dominated by deep waters or sea trenches; and 3) the south of the Makassar Strait (SMS) includes Lombok and Sumbawa which are part of the Flores Sea, as the main area where Arlindo water masses pass through.

3. Results

3.1. Genetic diversity

A total of approximately 400 base pairs (bp) fragments of the d-loop mtDNA *L. malabaricus* were amplified from 170 specimens distributed in 67 haplotypes from Balikpapan, Bontang, Barru, Makassar, and Sumbawa, and 102 polymorphic sites (*S*) (Table 2). The haplotypes consisted of 48 which were only found in one location and the remaining 19 were spread in more than one site. Each location's *S* number varied from the lowest in Barru (37) to the highest in Bontang (69). The Malabar blood snapper in Makassar Strait showed a high genetic diversity indicated by *h* (haplotype diversity) and π (nucleotide diversity) of 0.9284 and 0.0434, respectively. The lowest haplotype diversity occurred in the Sumbawa samples (0.8336), and the highest was from Makassar (0.9613). For nucleotide diversity, the lowest was the Balikpapan sample (0.0344) and the highest from Sumbawa (0.0482) (Table 2).

The d-loop mtDNA sequence of *P. multidens* was also approximately 400 bp. From 128 samples, 71 haplotypes were identified from Balikpapan, Bontang, Barru, Makassar, and Lombok, and 136 segregation sites (*S*) (Table 3). The number of *S* varied between locations; the highest was from Bontang samples (69), and the lowest was from Barru (37). Genetic diversity of *P. multidens* in Makassar Strait comprised h= 0.9766 and π= 0.0532, higher than that of *L. malabaricus*. The highest *h* came from Lombok specimens (0.9782) and the lowest from Makassar (0.9546). Meanwhile, the highest π occurred from Bontang (0.086), and the lowest was from Balikpapan (0.0224) (Table 3). The nucleotide composition at the five locations is relatively different between Bontang and other locations.

3.2. Phylogeography relatedness

Construction of the NJ phylogeny tree resulting from d-loop mtDNA haplotypes showed that there was relatively no clustering in the species *L. malabaricus* (Fig. 2A), whereas clustering occurred in *P. multidens* (Fig. 2B). Although L.*malabaricus* seems to exist in two groups, it is not clear because they are mixed with each other in all populations. Meanwhile, for *P. multidens* it is very clear that there is a structuring of three population groups, namely Bontang, Balikpapan-Barru-Lombok, and Makassar.

The 67 haplotypes of *L.malabaricus* and 71 haplotypes of *P.multidens* were used for constructing minimum spanning network to determine population connectivity. All haplotypes of *L.malabaricus* are interconnected between locations, although there are several haplotypes identified in one location but they were connected to other sites (Fig. 3A). Haplotype-3 (Hap_3) dominates among the other haplotypes with a total frequency of 34 times, spread across all locations, followed by haplotype-2 (Hap_2) and haplotype-8 (Hap_8) with a total frequency of 17 and 12 occurrences, respectively. Hap_3 appears to be the ancestral haplotype showing the highest number of connections. In contrast to *P. multidens*, although most of the haplotypes are connected between locations, there are endemic haplotypes in a locality that are not connected to other locations. These haplotypes were found in Bontang and Makassar populations (Fig. 3B). There were six haplotypes (Hap_40, Hap_41, Hap_39, Hap_42, Hap_43 and Hap_44) in Bontang population which were isolated, while in the Makassar population four haplotypes were found that were not connected to other populations (Hap_28, Hap_29, Hap_31 and Hap_32). There are two dominant haplotypes, namely Hap_11 and Hap_19 which appear 11 times. Hap_19 is dispersed throughout the population while Hap_11 is distributed across four populations. Hap_20 seems to be the ancestral haplotype characterized by the largest number of connections.

Table 2
Indexes of genetic diversity of *L.malabaricus* in the Makassar strait populations.

Locations	n	Nh	S	*h*	π
Balikpapan (BPN)	35	24	43	0.9361	0.0344
Bontang (BTG)	30	18	69	0.9402	0.0402
Barru (BRU)	35	21	37	0.9445	0.0478
Makassar (MKS)	35	20	43	0.9613	0.0468
Sumbawa (SBW)	35	16	52	0.8336	0.0482
Total	170	67	102	0.9284	0.0434

Note: Number of individuals (n); Number of haplotypes (Nh); Number of polymorphic sites (S).

Table 3
Indexes of genetic diversity of *P. multidens* in the Makassar strait populations.

Locations	n	Nh	S	*h*	π
Balikpapan (BPN)	34	24	25	0.9644	0.0224
Bontang (BTG)	31	22	72	0.9699	0.0860
Barru (BRU)	16	13	24	0.9667	0.0249
Makassar (MKS)	12	10	40	0.9546	0.0391
Lombok (LBK)	35	25	88	0.9782	0.0419
Total	128	71	136	0.9766	0.0532

Note: Number of individuals (n); Number of haplotypes (Nh); Number of polymorphic sites (S).

3.3. Population genetic structure

The pairwise F_{st} test of *L.malabricus* and *P. multidens* for five localities represents different results (Table 4). It revealed no evidence of any genetic structure of *L. malabaricus* among the samples from all locations. The F_{st} value showed insignificant results ($p > 0.05$) in each location. Meanwhile, the genetic structure analysis for *P. multidens* by the pairwise F_{st} test proved the formation of a population structure between sites. This finding was supported by a high F_{st} value and a highly significant ($p < 0.01$) where the populations of Bontang and Makassar differed from the populations of other locations.

Pairwise F_{st} test was carried out on *L.malabaricus* and *P. multidens* in three sub-areas to take into account the limitation of differences in bathymetry and sea current patterns (Table 5). *L.malabaricus* was not significantly different ($p > 0.05$). In contrast, *P.multidens* was very significant difference in genetic structure ($p < 0.001$) between two subregions in the Makassar Strait, the eastern part of Kalimantan Island (EKI) with the western part of Sulawesi Island (WSI) and the southern part of the Makassar Strait (SMS). This reveals the three sub-areas are

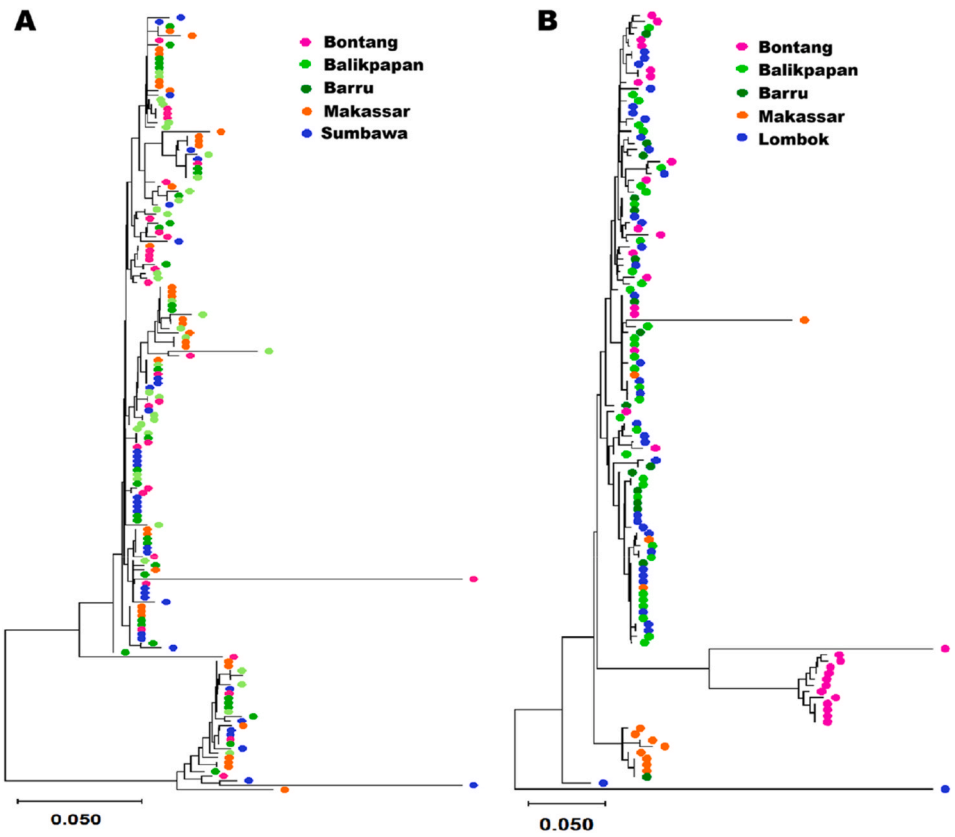

Fig. 2. Phylogenetic trees reconstruction of *L.malabaricus* with 67 haplotypes (A) and *P.multidens* with 71 haplotypes (B) from d-loop mtDNA using Neighbor Joinning (NJ) Kimura-2 parameter with 1000 bootstrap replicates of five populations. Populations are shown in different colors. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

divided into three distinct populations. Differentiation also occurred significantly ($p < 0.05$) between the WSI and SMS populations.

The result of the global exact test of sample differences based on haplotype frequencies of *L. malabaricus* supported the output of F_{st}; namely, there was no significant difference among populations (exact $p = 0.08923 \pm 0.04462$SD) (Table 6). Although the samples from Makassar and Sumbawa were different, they were not strong enough to indicate the occurrence of the *L.malabaricus* structure in the Makassar Strait. Furthermore, the exact test of pairwise differentiation based on haplotype frequencies of *P.multidens* also confirmed the results of the F_{st} analysis by showing highly statistically significant differences (exact $p < 0.01$). However, there was a distinction between the results of the F_{st} test and the exact test where the grouping of the population structure in the pairwise exact differentiation test only occurs between Bontang and four other locations (Table 6). Thus, it could be stated that the population structure of the pairwise F_{st} results was divided into three groups, while two population groups obtained the pairwise exact differentiation test.

Based on the results of the differences analysis, strong evidence was obtained for the existence of diversities in genetic structure in *P.multidens*. AMOVA as a hierarchical model was used to confirm this distinctness through three scenarios. First, the five populations were regrouped into 3 populations (BTG, MKS, BPN-BRU-LBK), based on the results of pairwise F_{st}. Second, all locations were arranged into two groups (BTG, MKS-BPN-BRU-LBK), referring to the produce of pairwise differentiation of exact test. Third, grouping based on consideration of bathymetric boundaries and current pattern systems which are categorized into three sub-areas (EKI, WSI, SMS). The results showed strong genetic division among all scenarios (Table 7). Grouping based on sites were divided into three populations and two population, indicates diversity of genetic structure highly significant (Φ_{ST} 0.27771, $p < 0.001$) and (Φ_{ST} 0.29644, $p < 0.001$), respectively. Furthermore, the third scenario produces very significant variations in genetic structure (Φ_{ST} 0.07010, $p < 0.001$).

4. Discussion

Considering global environmental changes and the effects of overfishing, it is important to know the condition of the target fish population in relation to the sustainability of these resources. In marine fish conservation and management, one important consideration is understanding population structure and genetic diversity (Yao et al., 2024). This study is to explore the genetic diversity and differentiation in the population of two important species of snapper *L. malabaricus* and *P. multidens* with d-loop mtDNA inhabiting the Makassar Strait and adjacent waters, Indonesia. The mtDNA gene is especially useful in population studies due to its fast mutation rate and high nucleotide and haplotype diversity, thereby providing the variation needed to explore parameters such as subdivision, gene flow (Zhang et al., 2006) and highly sensitive in discovering the genetic structure of populations (Zhang et al., 2019).

4.1. Genetic diversity

The d-loop mtDNA analysis of *L. malabaricus* and *P. multidens* reveals high haplotype and nucleotide diversity (Table 2, Table 3). Snapper spawning in different habitats has an important influence on genetic diversity. In general, snappers migrate to deeper waters to spawn (Froehlich et al., 2021), as large and adult fish are found in deep waters, while young and juvenile fish live in shallow waters (Leontiou et al., 2021). This behaviour supports gene exchange among spawning populations and plays a role in maintaining the genetic diversity of the species (Gaggiotti et al., 2009). The combination of high haplotype

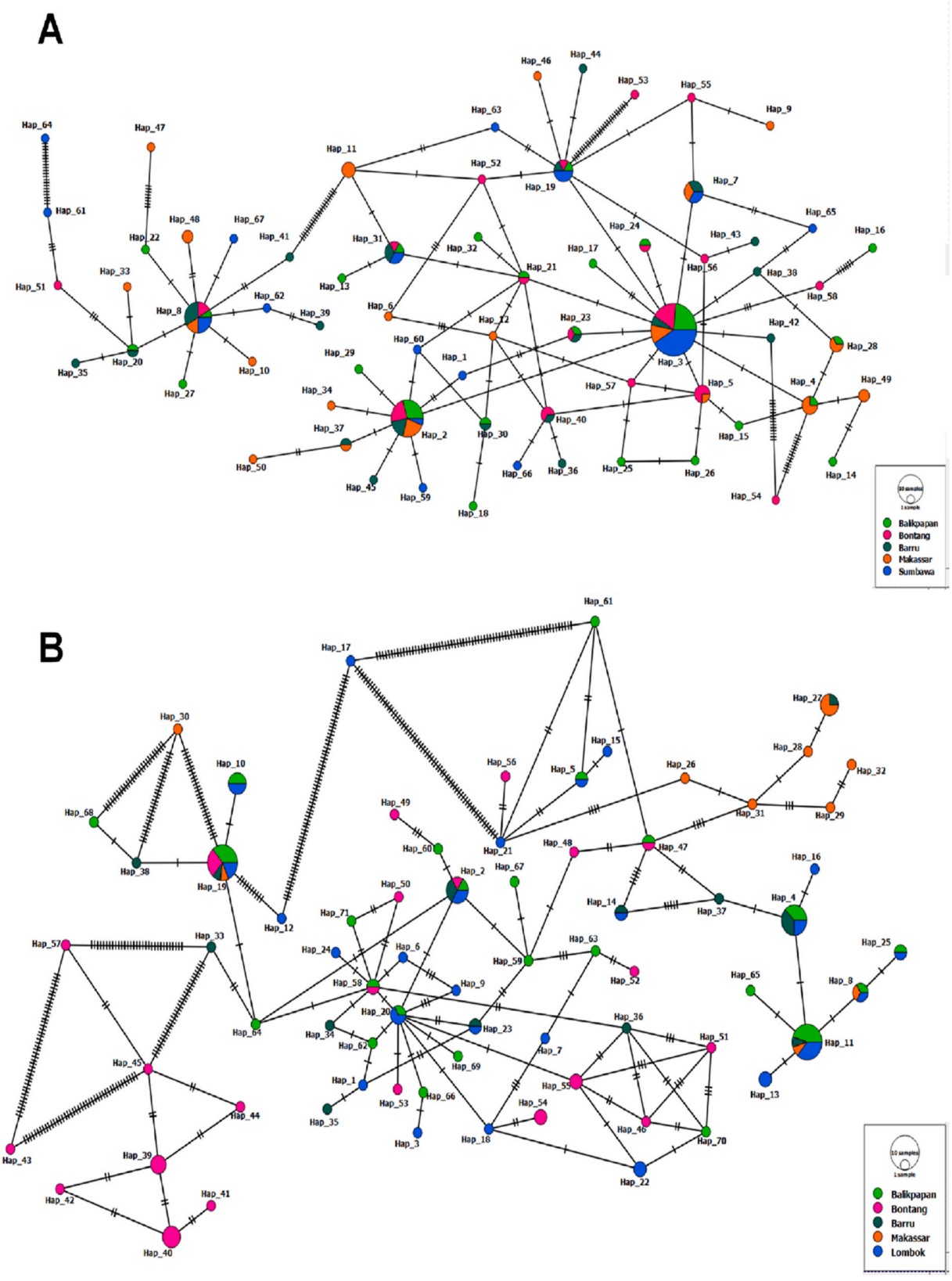

Fig. 3. Minimum Spanning networks of haplotypes in five populations of *L.malabaricus* (A) and *P.multidens* (B) based on d-loop mtDNA. Each circle represents a haplotype and haplotypes number, each line presents mutational step variations, and each color represents. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 4
Pairwise F_{st} values with corresponding *p-values* (in brackets) and significance levels (shown in bold) for the samples of *L.malabricus* and *P. multidens* in all sites.

	Balikpapan	Bontang	Barru	Makassar	Sumbawa
Lutjanus malabaricus					
Balikpapan		–	–	–	–
Bontang	−0.00879 (0.5283)		–	–	–
Barru	0.00912 (0.2559)	0.01748 (0.1787)		–	–
Makassar	0.00117 (0.3086)	0.01839 (0.1484)	−0.01614 (0.7060)		–
Sumbawa	0.00864 (0.2080)	0.01156 (0.1709)	−0.01823 (0.7500)	−0.00363 (0.4023)	
Pristipomoides multidens					
	Balikpapan	Bontang	Barru	Makassar	Lombok
Balikpapan		+	–	+	–
Bontang	0.25215 (**0.0000**)		+	+	+
Barru	−0.02029 (0.7949)	0.19484 (**0.0049**)		+	–
Makassar	0.25383 (**0.0000**)	0.25955 (**0.0010**)	0.18973 (**0.0000**)		+
Lombok	−0.01496 (0.9707)	0.22044 (**0.0000**)	−0.01853 (0.8359)	0.18418 (**0.0000**)	

Table 5
Pairwise F_{st} values with corresponding *p-values* (in brackets) and significance levels (shown in bold) among three sub-areas (EKI: eastern part of Kalimantan Island, WSI: western part of Sulawesi Island, SMS: southern part of Makassar Strait) of *L.malabaricus* and *P.multidens*.

	EKI	WSI	SMS
Lutjanus malabaricus			
EKI		–	–
WSI	0.01831 (0.0898)		–
SMS	0.00510 (0.2529)	−0.01441 (0.7676)	
Pritipomoides multidens			
	EKI	WSI	SMS
EKI		+	+
WSI	0.09113 (**0.0000**)		+
SMS	0.06131 (**0.0000**)	0.03439 (**0.0180**)	

Table 6
Pairwise differentiation exact tests and significance levels for the sample of *L. malabaricus* and *P. multidens* based on five sites.

	Balikpapan	Bontang	Barru	Makassar	Sumbawa
Lutjanus malabaricus					
Balikpapan		–	–	–	–
Bontang	0.89304		–	–	–
Barru	0.92273	0.6292		–	–
Makassar	0.17976	0.08115	0.30847		+
Sumbawa	0.14018	0.06168	0.44388	0.00102	
Global test of differentiation among sample: non-differentiation (exact p = 0.0892 ± 0.0446)					
Pristipomoides multidens					
	Balikpapan	Bontang	Barru	Makassar	Lombok
Balikpapan		+	–	–	–
Bontang	0.0022		+	+	+
Barru	0.5082	0.0237		–	–
Makassar	0.1836	0.0170	0.3009		–
Lombok	0.9404	0.0003	0.7742	0.1889	
Global test of differentiation among sample: non-differentiation (exact p = 0.00000 ± 0.00000)					

Table 7
Analysis of Molecular Variance (AMOVA) for hierarchical analysis of goldband snapper *P.multidens* based on sites and sub-areas under alternative of three scenarios.

Source of Variation	d.f.	Sum of squares	Variance component	Percentage of variation
Sites (BTG vs MKS vs BPN-BRU-LBK)				
Among populations	2	146.285	2.14734 Va	27.77
Within populations	125	698.122	5.58497 Vb	72.23
Fixation index (Φ_{ST})	0.27771 ($p = 0.00000$)			
Sites (BTG vs MKS-BPN-BRU-LBK)				
Among populations	1	119.626	2.42365 Va	29.64
Within populations	126	724.781	5.75223 Vb	70.36
Fixation index (Φ_{ST})	0.29644 ($p = 0.00000$)			
Sub-areas (EKI vsWSI vs SMS)				
Among populations	2	50.657	0.47867 Va	7.01
Within populations	125	793.749	6.35000 Vb	92.99
Fixation index (Φ_{ST})	0.07010 ($p = 0.00098$)			

Note: Va, Vb = Number of variance components.

diversity and nucleotide diversity explains the significant genetic pattern of strong gene flow among populations. The high haplotype and nucleotide diversity indicates the large effective population size, stable population history population (Marini et al., 2021; Sun et al., 2021) that has avoided recent population bottlenecks, and mixed genetic lineages resulting from mating of isolated populations. On the other hand, this genetic variation may be related to the condition of coral reefs, good nutrient flow (the influence of the *ITF* current), and a good reproductive system which happens throughout the year as an advantage for biota living in tropical marines.

Overfishing will cause a decrease in genetic diversity and hinder population recovery (Silva et al., 2018). However, this does not affect the decline in genetic diversity, even though the level of exploitation of snapper fish in the Makassar Strait is extremely high (Ernawati et al., 2024; Ernawati and Budiarti, 2020), reflected by the large number of fishing gear units illustrates that the fishing intensity in FMA 713 (including the Makassar Strait and adjacent waters) is very high (Table 8). This study shows that the genetic diversity of snapper remains high despite overfishing. In fish populations, natural population alterations are rare unless there are very unstable environmental conditions (Hansen et al., 2002). This condition is caused by extensive gene flow and large effective population sizes, as is generally the case in marine species. Furthermore, the timing of overfishing may play a significant role. If fishing pressure is relatively recent, and the population has not declined drastically over a long period of time, the impact on genetic

Table 8
The number of the main fishing gear units targeted Snapper in Fisheries Management Area (FMA) 713 (include in Makassar Strait and adjacent waters).

Fishing Gears	Number of Fishing Gear Units				
	2019	2020	2021	2022	2023
Handline	41,975	59,056	58,750	46,861	50,519
Bottom-longline	6158	7731	5675	4585	5254
Bottom-gillnet	21,734	27,309	22,804	18,923	23,114
Traps	8781	10,245	7301	6980	8666
Others	6193	7145	9131	8563	8918

Noted: The result of reconstruction fishing data based on Statistics of Marine Capture Fisheries by Fisheries Management Area (713) (Source: DGCF-MMAF, 2024).

diversity may not be immediately apparent. The population may still have a large number of diverse haplotypes and genetic markers.

4.2. Phylogeography relatedness

The phylogenetic relationships of *L.malabaricus* were constructed using the NJ analysis approach. It produced no structural differences phylogenetically, pointed out by short branches or close genetic distances. Regarding, the principle of the NJ method is to look for pairs of operational taxonomic units (OTUs) that minimize branch length at each clustering stage using a distance matrix (Saitou and Nei, 1987), indicating no populations separated of *L.malabaricus* in Makassar Strait. While, compiling a haplotype network using the MSN method gave similar results to the NJ phylogenetic tree, there were no separate populations. From the MSN analysis, no isolated *L.malabaricus* haplotypes were detected in certain geographic areas within the species distribution. This is reflected in all the haplotypes being interconnected, indicating the absence of phylogeographic structure. In addition, the haplotypes of individuals from five locations were scattered and mixed-up, referring that the species has experienced population expansion with shared haplotypes among sites (Aini et al., 2021; Gwak and Roy, 2023). The shared haplotypes between locations may be explained by panmixia occurs in the long-term. Previous study of the reef fish species *Naso hexacanthus* showed similar events as a single long-term panmictic population, without differentiation across the Indo-Pacific Barrier (Horne and van Herwerden, 2013). Moreover, the absence or lack of haplotypes isolation of *L.malabaricus* can be explained that during glacial periods (Pleistocene), fluctuations in sea level may have affected shallow-water species (*Lutjanus*). These changes altered habitat and population distribution, potentially leading to repeated population mixing during interglacial periods (sea level rise).

In contrast, the results of the *P.multidens* phylogenetic tree from five locations showed branching with relatively long branch lengths. Although most of the haplotypes from the five locations were scattered and mixed, multiple haplotypes from individuals from the Bontang and Makassar populations formed separate groups. This denoted the differentiation of genetic structure of *P.multidens* based on the phylogenetic tree. On the other hand, MSN analysis also strengthened the results from the phylogenetic tree. Based on MSN, there were six haplotypes which were only possessed by individuals in the Bontang population and were not connected to populations from other areas (Fig. 3B). Four haplotypes were also identified as not connected to populations from other locations and only belonged to populations in Makassar (Fig. 3B). These two facts illustrated the existence of restrictions on population mixing. It can be summarised, based on the phylogeographic structure there were differences in *P. multidens* in the Makassar Strait. There is no connectivity in some locations because *P. multidens* are deep-water inhabitants. Although deep currents can affect the distribution of *Pristipomoides*, they are constrained by the bathymetry of the strait. Furthermore, it can be explained by the biogeographic history of the Southeast Asian region where the Makassar Strait is located between Kalimantan (part of the Sunda shelf) and Sulawesi (part of the Sahul shelf) (Voris, 2000). During the Pleistocene, the area experienced prolonged and repeated sea-level fluctuations, followed by population expansion in the Coral Triangle (including the Makassar Strait and adjacent waters) (Gaither et al., 2011a) which is a part of Central Indo-Pacific province (Fig. 4A) (Kulbicki et al., 2013) or Indo-West Pacific region (Fig. 4B) (Cowman et al., 2017). This biogeographic history has the potential to cause differences in patterns of isolation and connectivity.

4.3. Population genetic structure

This current study showed that *L. malabaricus* performed homogeneity in the Makassar Strait, as there was no evidence of genetic population structure in five locations (Balikpapan, Bontang, Barru, Makassar and Sumbawa). Phylogenetic tree, haplotypes network, F_{st} test, and exact differentiation test did not detect evidence of genetic structures within the *L. malabaricus* population. It is estimated there is a high gene flow of *L. malabaricus* in the Makassar Strait, which is indicated by a very low and insignificant value of F_{st}. High gene flow plays an important role in determining the low level of genetic subdivision (Gopalakrishnan et al., 2018). Furthermore, the very low F_{st} of L. *malabaricus* indicates a high breeding rate and high connectivity. This reflects that individuals are able to migrate between populations so that mating can occur. In other words, Malabar blood snapper has a predominantly panmictic population in the Makassar Strait.

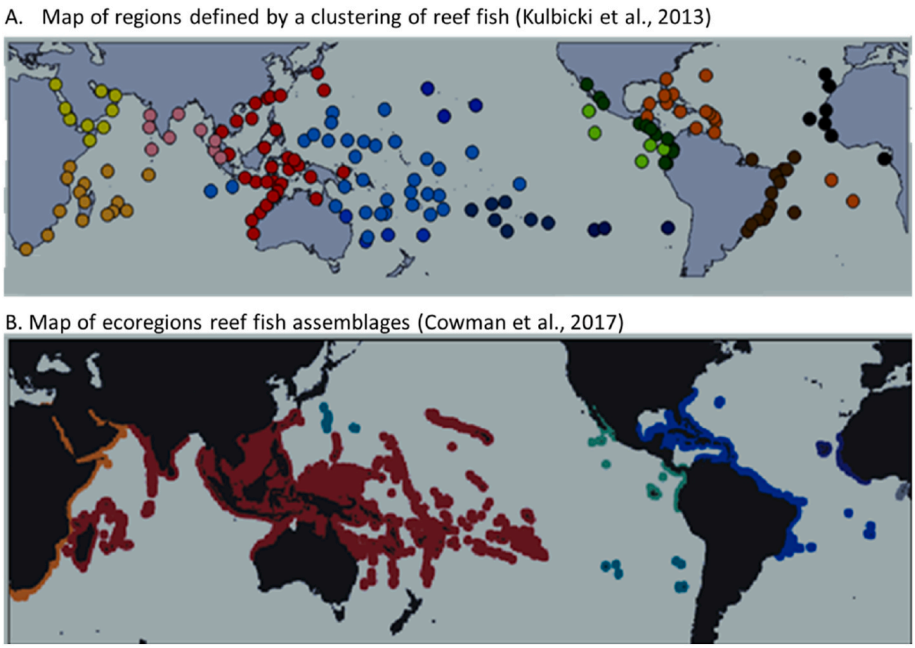

Fig. 4. Biogeographical maps, (A) regions defined by a clustering of reef fish based on the reliable species, red dots point out Central Indo-Pacific Region, (B) reef fish assemblage ecoregions, red dots figure out Indo-West Pacific Region. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Most *Lutjanus* species live in shallow water environments (0–100 m depth), so their connectivity is enhanced by surface currents. Their pelagic larval stages can disperse effectively across complex marine geography. *L.malabaricus* larvae inhabit the sea surface at a depth of between 0 and 20 m (Leis et al., 2009) before reaching the settlement phase. The mean PLD of the genus *Lutjanus* is approximately 25 days (D'Alessandro et al., 2010; Silva et al., 2024). Leis (2010) explained that significant swimming orientation in the within-trajectory was found in *L.malabaricus* larvae. This means that individual larvae do not swim randomly in the ocean. Thus, this has a major impact on the spatial distribution of larvae during the pelagic phase and the determination of the locations where they settle at the end of the pelagic phase.

The PLD dispersal is also greatly influenced by current patterns such as velocity, variation and direction. The characteristics of the surface current pattern of the Makassar Strait and adjacent waters are driven by wind pressure so that they show significant seasonal variations and are influenced by the monsoon season pattern (Susanto and Gordon, 2005; Wijffels et al., 2008). Therefore, the highest current speed in the Makassar Strait occurs in the upper depth range and near the western boundary (Mayer and Damm, 2012). This is clarified by Fig. 5A and B, showing high current speeds in the surface layer (depths of 0 and 25 m). Furthermore, the influence of the monsoon season on the current patterns at depths <50 m gives different variations in current characteristics. During the first monsoon break in April, the water mass is originated from the Sunda Shelf flow with low salinity (<30.0 PSU) and warm temperature (>30.0 °C). In the east monsoon period (June), the water mass with relatively high salinity (>33.0 PSU) from the Makassar ITF enters the Java Sea (Sunda Shelf) past two strong streams to the west, while the strong current flowing to the west from the Flores Sea and the Makassar upwelling area slues to the southwest and enters the Lombok Strait. During the southeast monsoon season (August), some of the strong currents from the Makassar ITF flow into the Java Sea, bringing water masses with high salinity (>34.0 PSU), then some of the Makassar ITF current and the monsoon current from Flores flow to the southwest and enter the Lombok Strait towards the Indian Ocean (Apriansyah et al., 2024). Therefore, with these current characteristics, it is very possible for *L. malabaricus* larvae which is inhabit in surface sea to spread more widely and more quickly.

Marine fish species typically show high levels of gene flow and low population structure due to the absence of clear physical barriers to genetic interchange, huge effective population sizes, and their high dispersal ability (Beheregaray and Sunnucks, 2001). However, the results for *P. multidens* did not match the general characteristics of this marine fish population. *P. multidens* showed signs of genetic structuring based on strong significantly results of various differentiation analysis, confirmed by the phylogeographic constructions, F_{st} and exact differentiation tests. AMOVA as hierarchical analysis confirmed the results of the difference analysis with three scenarios based on the locality grouping framework, and sub-area grouping based on bathymetric boundaries and current patterns. In all three scenarios, very significant genetic differences were obtained. Based on pairwise F_{st}, the population in three sub-areas (EKI, WSI and SMS) differed significantly (Table 5).

P. multidens is a deep-water snapper, where bathymetric barriers, different oceanographic conditions and current patterns may limit gene flow. In glacial periods, during low sea level would have affected deep-water species (*Pristipomoides*) differently, potentially leading to different patterns of population isolation and reconnection. Deep-water snapper may have different larval behaviors and settlement patterns, reducing

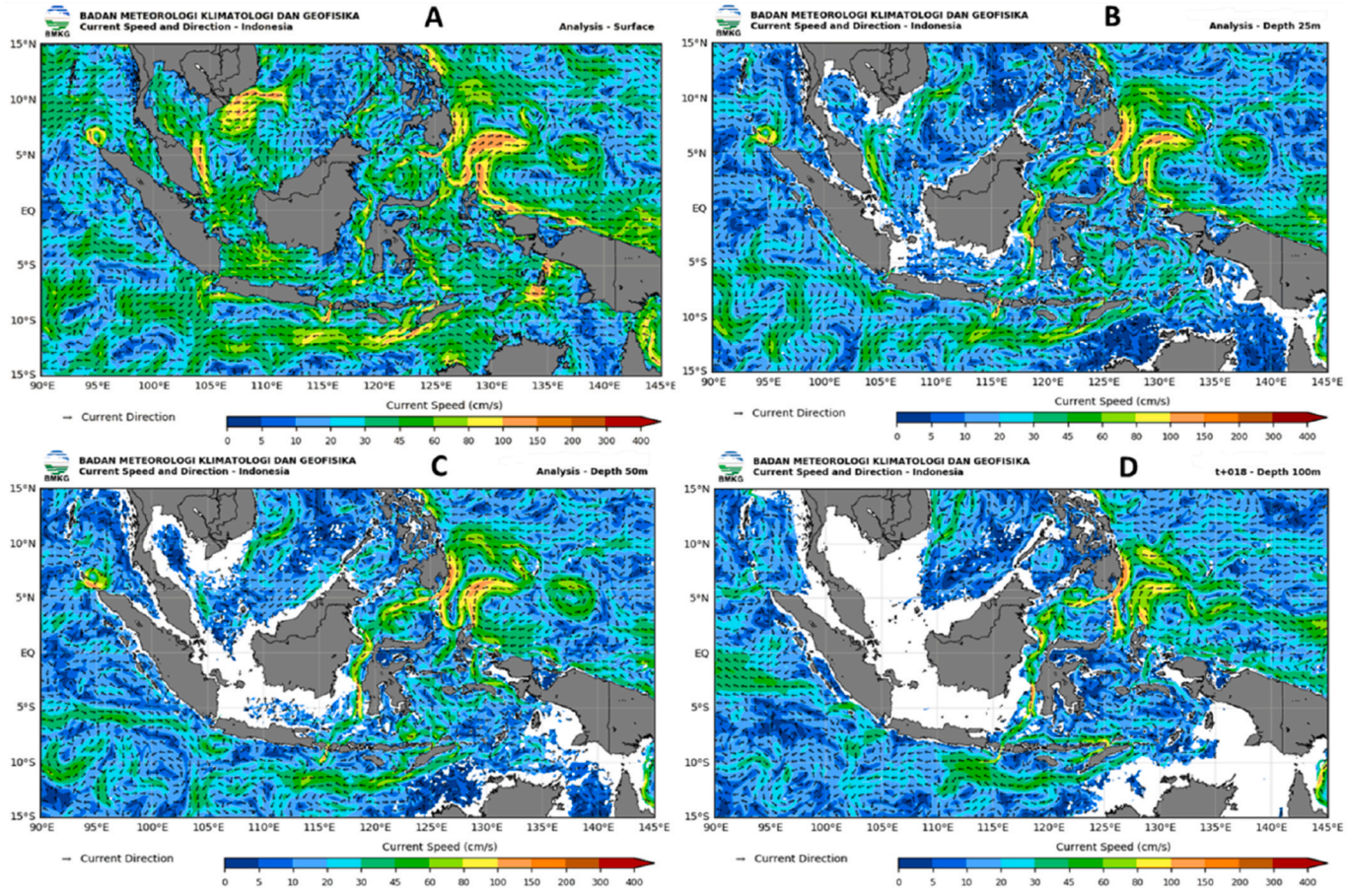

Fig. 5. Current speed and direction at depth surface/0m (A), 25m (B), 50m (C) and 100m (D) of Makassar Strait where the white area illustrates the seabed (source: *Badan Meteorologi Klimatologi dan Geofisika* accessed from the website https://peta-maritim.bmkg.go.id/ofs-static, June 12, 2025).

connectivity between populations across the complex bathymetry of the Makassar Strait and adjacent waters. Though the PLD of *Pristipomoides* is relatively longer than *Lutjanus*, this does not guarantee a wider distribution of larvae. Larval dispersal can be influenced by the spawning pattern and early development of the species (Bohonak, 1999). No information available of PLD for *P. multidens*, is assumed around 40 days (Ovenden et al., 2004), while the PLD for another species of the same genera, *P. filamentosus* is suggested to be 60–180 days (Gaither et al., 2011b). During the larval phase, the depth of *Pristipomoides* is in the range of 10–100 m (D'Alessandro et al., 2010), before reaching the settlement phase. It is known that deep-snappers such as *Pristipomoides* larvae undertake vertical migration patterns and avoid surface seas during the day (Leis, 1987), and larvae of these snapper species spread deeper in the water column and deepen as their ontogeny (D'Alessandro et al., 2010). The vertical distribution behavior (swimming and orientation) of fish larvae can greatly influence dispersal during the pelagic larval stage (Leis, 2006). Due to this, the distribution of *Pristipomoides* larvae is relatively limited which has implications for the differentiation of genetic structures.

On the other hand, the current pattern of the Makassar Strait in the western part which borders the island of Kalimantan (EKI) is very different from that in the eastern part which barriers the Sulawesi Island (WSI). The WSI is dominated by very deep bathymetry which creates a barrier to other areas. Meanwhile, the EKI area is generally dominated by shallow bottom waters (part of the Sunda Shelf) (Fig. 1), and this area is influenced by surface waters from the Java Sea (Gordon, 2005). Furthermore, the current pattern of the Makassar Strait in EKI (Sunda shelf) at depths below 50 m is "obstructed" by the seabed (Fig. 5C and D), thus becoming an obstacle in the distribution of *Pristipomoides* larvae. While the SMS is the area south of the Makassar Strait, part of the Flores Sea also has its own current characteristics locally, which boundaries by Dewakang Sill with depth 680 m (Fig. 1) (Gordon, 2005). All the characteristics of the Makassar Strait and adjacent waters become barriers and form isolated habitats between subareas, thus limiting the movement of *P. multidens* which results in population differences. This finding supported by Salini et al. (2006), who stated that the deep water is a barrier to population mixing during adult, juvenile and larval stages. Previous studies investigated *P.multidens* in central-eastern Indonesia (Bali, Tanjung Luar, Kupang, and Tanimbar -Tual) (Fig. 1), which resulted in population genetic separation in all sites, Bali with Tanjung Luar (Lombok), Tanjung Luar with Sumbawa (Sape) and Tual with Tanimbar, though the distance between the islands is less than 500 km (Ovenden et al., 2002, 2004).

4.4. Management implications

This study reveals no genetic structuring of the population of *L. malabaricus*. *P. multidens* in the Makassar Strait and adjacent waters based on sub-areas has been identified as having two distinct populations in the Makassar Strait (West and East) and one population in the Flores Sea area south of the Makassar Strait (North of Lombok Island). These findings should be taken into consideration in fisheries management at FMA 713. The different populations should be managed as units requiring separate monitoring and management (Waples, 1998). Nevertheless, it is not easy to implement fish resource management based on different population units according to genetics. This is considering the condition of fisheries in Indonesian archipelagic waters, which are characterized by multi-species and multiple fishing gears. For example, the *P.multidens* deep snapper fishery could not be separated from other snapper fisheries where interactions occur in fishing activities. Furthermore, it is necessary to carry out a stock assessment for each population to obtain stock conditions and biological parameters from each population. By the condition that the biological parameters and stock status are the same for different stocks, fishery management can be carried out using the same form of measurement and monitoring. On the other hand, genetically the population is the same in this study, exemplified by *L. malabaricus*, and may have different management options. These could apply, if in several areas there are indications of stock status and different biological parameters in a broad ecosystem. Thus, management activities would be more effective with different measurement and monitoring mechanisms.

Finally, managing fish resources requires a flexible and adaptive approach that examines each population's fishery characteristics and the broad ecosystems in which they exist. In addition, apart from the limitation of d-loop mtDNA techniques as a tool to identify marine fish population structure, this is the first study to examine the population structure of snapper in the Makassar Strait. Therefore, it is necessary to conduct further research using other genetic markers to increase certainty in determining the population structure of snappers. Studies related to the population genetic connectivity of snappers or other demersal-reef fish also need to be carried out regarding the condition of Indonesia, which is an archipelagic-waters with various bathymetry and oceanography characteristics. These allow the occurrence of stock differences which are certainly a consideration in fisheries management.

CRediT authorship contribution statement

Tri Ernawati: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Mennofatria Boer:** Writing – review & editing, Supervision. **Mohammad Mukhlis Kamal:** Writing – review & editing, Supervision. **Nurlisa Alias Butet:** Writing – review & editing, Supervision. **Fayakun Satria:** Writing – review & editing, Supervision. **Peter J. Mous:** Writing – review & editing, Supervision.

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Declaration of competing interest

The authors declare that they have no known competing financial interest or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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