

## Original Article

# Genetic connectivity analysis of blue swimming crab (*Portunus* sp.) in fisheries management areas FMA 713 and FMA 714 using a DNA barcoding approach: Implications for blue swimming crab resource management in Indonesia

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**Abstract:** Effective management of blue swimming crab (BSC) resources requires a comprehensive understanding of their morphological and genetic characteristics. This study aimed to determine genetic distances, phylogenetic relationships, diversity, population structure, and connectivity of BSC populations in Fisheries Management Areas (FMA) 713 and 714, and to confirm their species identity. A total of 24 BSC samples (12 from each FMA; 6 males and 6 females) were collected from Poleang waters (FMA 713) and Lasongko Bay (FMA 714). The results identified two Portunidae species: *Portunus armatus* and *Portunus pelagicus*, with *P. armatus* being dominant (83.33% in FMA 713; 91.67% in FMA 714). Phylogenetic analysis showed that *P. armatus* had closer genetic relationships among individuals than *P. pelagicus*. Both species exhibited high haplotype diversity with no significant difference ( $P = 0.4571$ ), and very low genetic differentiation between regions ( $F_{ST} = -0.06164$ ), indicating strong genetic connectivity. These findings suggest that BSC stocks in both FMAs are predominantly *P. armatus*. Consequently, resource management and conservation strategies should focus on *P. armatus*, since most past assessments referred to *P. pelagicus*, potentially misrepresenting population structure and stock dynamics.

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## Introduction

Fisheries Management Areas (FMAs) in Indonesia were established under the Regulation of the Minister of Marine Affairs and Fisheries of the Republic of Indonesia number 18/PERMEN-KP/2014 to optimize the management of fisheries resources. One of its implementations is the management of fisheries resources in FMA 713 and FMA 714. Geographically, these two FMAs are connected to the waters of Southeast Sulawesi, where the waters of Poleang fall under FMA 713, while the waters of Lasongko Bay are part of FMA 714. Both areas are central to the fishing of blue swimming crab (BSC) (*Portunus* sp.).

The BSC is one of Indonesia's most important fisheries commodities due to its premium economic value in both domestic and international markets, especially in the USA (Luhur et al., 2020). This situation has led to intensified exploitation of BSC

resources (La Sara et al., 2016a, b, 2017). Such intensive exploitation in the waters of Southeast Sulawesi began in the early 2000s, with the establishment of small-scale processing plants near BSC fishing grounds (La Sara et al., 2016b, 2017). BSC fishing occurs year-round, and the catch is sold to small-scale processing plants for meat extraction before being exported by companies associated with the Indonesian Blue Swimming Crab Processors Association. Approximately 50% of Indonesia's BSC production is exported to the USA, with Southeast Sulawesi contributing about 21% of the total (La Sara et al., 2016a, b, 2019; Permatahati et al., 2019, 2020; Luhur et al., 2020).

The increasing domestic demand for fresh BSCs and processed BSC meat for export has further intensified BSC fishing (Ernawati et al., 2014; La Sara et al., 2016a). However, this threatens the BSC

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population, as fishers continue to capture undersized BSCs with carapace widths (CW < 10 cm) and egg-bearing females (La Sara et al., 2016a, b, 2019), practices prohibited under the Regulation of the Minister of Marine Affairs and Fisheries Number 7 of 2024. Such practices contribute to the decline in BSC stock populations (Nitiratsuwan et al., 2013; La Sara et al., 2019).

Understanding the status of BSCs in FMA 713 and FMA 714 is essential for determining whether they constitute a single population and whether their species should be identified as *P. pelagicus*. Advances in science and technology have enabled the analysis of genetic connectivity, defined as gene flow between populations via migration or individual movement, which affects genetic diversity and population structure. Hebert et al. (2003) introduced DNA-based method using mitochondrial markers to identify animal species, in which a single gene sequence suffices to differentiate species. Genetic connectivity and species identification studies for BSCs utilize genetic approaches and molecular techniques (Jung et al., 2019; Hidayani et al., 2020; Suppapan et al., 2023). Genetic markers are tools for analyzing population genetic structure to identify species and elucidate phylogenetic relationships involved in individual dispersal (Selkoe et al., 2016; Lu et al., 2022; Joesidawati et al., 2023; Suppapan et al., 2023). Such analyses have proven highly precise in determining stock units and providing critical information for ecological and conservation studies (Huang and Shih, 2021; Marini et al., 2021; Sun et al., 2021).

Jung et al. (2019) identified *Portunus* through morphological and genetic examinations. Similar studies have been conducted to identify the genus *Portunus* across various regions of Indonesia, including Aceh, Semarang, Barru, and Papua (Hidayani et al., 2020). Joesidawati et al. (2023) noted high genetic diversity among Indonesian *Portunus*. Previous studies in Southeast Sulawesi waters have been foundational for *Portunus* management policies, addressing biological aspects (La Sara et al., 2016a, b, 2017), morphometrics and condition factors

(Permatahati et al., 2019; Astuti et al., 2020a, b), stock estimation and population status (La Sara et al., 2019; Permatahati et al., 2020), population parameters (La Sara et al., 2017; Cardin et al., 2023), and mitochondrial DNA-inferred genetic populations (Madduppa et al., 2021).

Despite these efforts, no studies have analyzed genetic connectivity and species identification of the genus *Portunus* using DNA barcoding from waters with differing characteristics, such as FMA 713 and FMA 714, even though genetic methods for connectivity measurement have become increasingly common since 2005 (Waples and Gaggiotti, 2012; Bryan-Brown et al., 2017; Balbar and Metaxas, 2019). Therefore, it remains unknown whether the *Portunus* populations in these regions exhibit genetic connectivity and whether they should be accurately identified as *P. pelagicus*. This study aimed to analyze genetic distances, phylogenetic relationships, genetic diversity, population structure, and genetic connectivity among *Portunus* populations from waters associated with FMA 713 and FMA 714, and to identify the *Portunus* species in these regions. The findings will be crucial in formulating *Portunus* management regulations for Indonesia's FMAs to ensure stable, productive, and sustainable BSC populations.

## Materials and Methods

**Study area and sampling procedure:** The Poleang waters and Lasongko Bay were selected as the sampling locations for BSCs, which are directly connected to FMA 713 (coordinates: 4°46'59"S 121°34'36"E) and FMA 714 (coordinates: 5°17'50"S 122°29'26"E), respectively. These locations were intentionally selected based on their geographic position and the hydrological conditions of their respective FMAs (Fig. 1). Both areas are significant BSC fishing grounds, heavily used by small-scale fishermen.

Poleang waters located to the west and south are directly connected to the Bone Strait and are influenced by the hydro-oceanographic conditions of

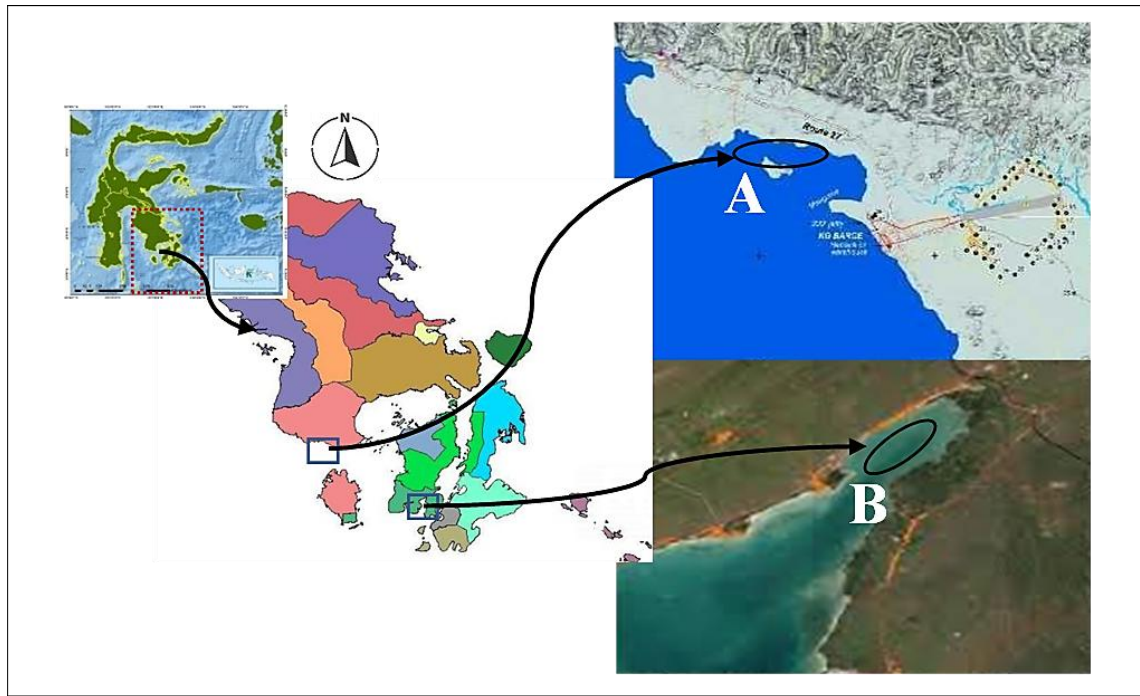


Figure 1. Map of BSC sampling locations in Poleang waters connected to FMA 713 (A) and in Lasongko Bay connected to FMA 714 (B) of Indonesia (black oval circles represent BSC sampling locations).

FMA 713. The region features scattered coral reefs and seagrass in waters 5-7 m deep. The substrate primarily consists of fine sand mixed with mud. To the north and east, it borders the mainland of Bombana Regency, while Lasongko Bay, in the region's south, is dominated by mangroves on the west and has sandy substrates with low mud content. Coral reefs with sandy substrates are found in the central and eastern parts. The southern bay mouth connects directly to the waters of Baubau and Spelman Strait, and is influenced by the hydro-oceanographic conditions of FMA 714. In both locations of FMAs, fishermen use bottom gillnets to catch BSCs (Fig. 2). Sampling of BSCs was conducted during July–September 2024.

BSC samples from each location were obtained monthly from fishermen or BSC collectors. For DNA analysis, 12 individuals were collected from each area, comprising six males and six females. Specimen collection was carefully documented to prevent contamination. Muscle tissue from the swimming legs was extracted and stored in sterile 1.5 mL tubes containing 96% ethanol for long-term preservation (Madduppa et al., 2021). These preserved samples were analyzed at the Central Laboratory of Life Sciences at Borneo Tarakan University in North

Kalimantan, Indonesia, where they were stored at  $-20^{\circ}\text{C}$  for subsequent analysis (Klinbunga et al., 2010).

#### **DNA extraction, amplification, and sequencing:**

Genomic DNA (50-100 mg) from BSC muscle tissue was extracted using the TIANamp Marine Animals DNA Kit (TIANGEN, Beijing, China) (Duan et al., 2022). The extracted DNA was diluted to a total volume of 100  $\mu\text{L}$  per specimen. Amplification of the mitochondrial gene Cytochrome Oxidase subunit I (COI) was performed using Polymerase Chain Reaction (PCR) (Madduppa et al., 2021). For this purpose, universal primers COIa (5'-AGT ATA AGC GTC TGG GTA GTC-3') and COIf (5'-CCT GCA GGA GGA GGA GAT CC-3') (Bhavan et al., 2015) were used. The PCR reaction (35  $\mu\text{L}$  total volume) contained 17.5  $\mu\text{L}$  PCR mix, 2  $\mu\text{L}$  DNA template, 1  $\mu\text{L}$  COIa primer, 1  $\mu\text{L}$  COIf primer, and 13.5  $\mu\text{L}$  nuclease-free water. The reaction was run in an Eppendorf X50s Thermal Cycler with the following steps: initial denaturation at  $95^{\circ}\text{C}$  for 4 minutes, followed by 30 cycles of  $95^{\circ}\text{C}$  for 15 seconds, annealing at  $45^{\circ}\text{C}$  for 15 seconds, elongation at  $72^{\circ}\text{C}$  for 10 seconds, and final extension at  $72^{\circ}\text{C}$  for 2 minutes. PCR products were electrophoresed on 1% agarose gel and stained with FloroSafe DNA Stain (1st

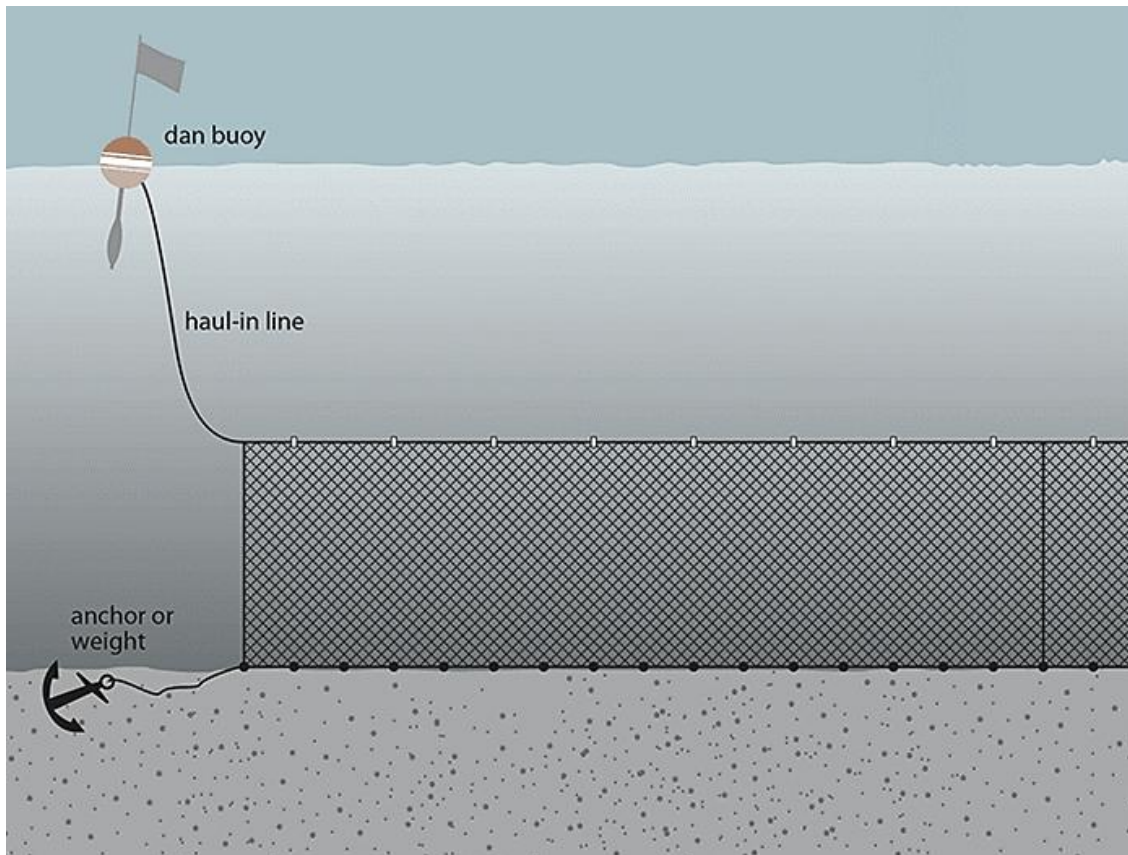


Figure 2. Bottom gillnet used for BSC sampling in Poleang waters (FMA 713) and Lasongko Bay (FMA 714) of Indonesia.

BASE). Furthermore, COI gene sequencing was performed in both forward and reverse orientations using the ABI BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). The mixture contained 5-7  $\mu\text{L}$  of purified PCR product and 0.8  $\mu\text{L}$  of each primer per reaction. The resulting sequencing reaction products were then loaded into the ABI 3500 Genetic Analyzer (Applied Biosystems), and the amplicons were sequenced in both the forward and reverse directions.

#### Data analysis

**Species validation:** The sequences obtained were visualized as chromatograms and edited using MEGA11 (Molecular Evolutionary Genetics Analysis 11.0.13) software (Tamura et al., 2021). The editing process involved reviewing and correcting nucleotide-reading errors to ensure the accuracy of the resulting sequence data. After editing, the sequences were analyzed using BLAST (Basic Local Alignment Search Tool) against the GenBank database via the National Center for Biotechnology Information

(NCBI) (<http://www.ncbi.nlm.nih.gov/>, accessed November 3, 2024) to validate that the nucleotide sequences matched homologous genes from the same species or genus.

**Genetic distance and phylogenetic tree construction:** Genetic distance is a measure used in population genetics to assess genetic differences based on variations in DNA or protein sequences between species, populations, or individuals. A smaller genetic distance indicates a closer genetic relationship, whereas a higher value indicates greater genetic divergence (Nei, 1972). COI gene sequences from *Portunus* species were aligned with sequences from other populations or species (ingroup and outgroup) using the ClustalW method in MEGA11. As the ingroup, COI gene sequences from *P. pelagicus* and *P. armatus* from different populations were used, including *P. pelagicus* from the Philippines (KF604896), *P. pelagicus* from China (KP9763421), *P. armatus* from Japan (MN184695), and *P. armatus* from Australia (EF661885). The COI gene sequence

Table 1. BLAST results on the NCBI site for *Portunus* species obtained from the Poleang waters (FMA 713) and Lasongko Bay (FMA 714) of Indonesia.

Location	Number of Samples	Sample ID	Query Cover	Percentage Identity	BLAST GenBank ID	Species
Poleang waters (FMA 713)	1.	BGF01	100%	91.34%	ON990068.1	<i>P. armatus</i>
	2.	BGF02	99%	94.11%	ON990077.1	<i>P. armatus</i>
	3.	BGF03	97%	96.93%	ON990077.1	<i>P. armatus</i>
	4.	BGF04	100%	93.84%	ON990077.1	<i>P. armatus</i>
	5.	BGF05	100%	97.17%	ON990077.1	<i>P. armatus</i>
	6.	BGF07	99%	93.68%	ON990077.1	<i>P. armatus</i>
	7.	BGM01	99%	91.54%	ON990068.1	<i>P. armatus</i>
	8.	BGM02	98%	92.89%	KT382858.1	<i>P. pelagicus</i>
	9.	BGM03	100%	97.14%	KT382858.1	<i>P. pelagicus</i>
	10.	BGM04	100%	95.43%	ON990077.1	<i>P. armatus</i>
	11.	BGM05	99%	91.23%	ON990068.1	<i>P. armatus</i>
	12.	BGM06	96%	91.34%	ON990077.1	<i>P. armatus</i>
Lasongko Bay (FMA 714)	1.	LGF01	97%	96.93%	ON990077.1	<i>P. armatus</i>
	2.	LGF02	100%	93.42%	ON990077.1	<i>P. armatus</i>
	3.	LGF03	100%	93.44%	ON990077.1	<i>P. armatus</i>
	4.	LGF04	99%	94.62%	ON990077.1	<i>P. armatus</i>
	5.	LGF05	100%	97.40%	ON990077.1	<i>P. armatus</i>
	6.	LGF06	100%	91.01%	ON990068.1	<i>P. armatus</i>
	7.	LGM01	99%	91.82%	ON990068.1	<i>P. armatus</i>
	8.	LGM02	100%	93.33%	KT382858.1	<i>P. pelagicus</i>
	9.	LGM03	98%	97.65%	ON990077.1	<i>P. armatus</i>
	10.	LGM04	100%	92.92%	ON990077.1	<i>P. armatus</i>
	11.	LGM05	100%	93.55%	ON990077.1	<i>P. armatus</i>
	12.	LGM06	99%	91.61%	ON990068.1	<i>P. armatus</i>

of *S. serrata* (KM528133) was used as the outgroup. All sequences were then aligned with the COI gene sequences obtained from the waters of Poleang (FMA 713) and Lasongko Bay (FMA 714). The alignment results were used for genetic distance analysis and phylogenetic tree reconstruction. Genetic distance analysis was performed using the Pairwise Distance method in MEGA11. The results were presented as a genetic distance matrix, which illustrates the degree of difference between species. The phylogenetic tree was reconstructed using a Bootstrapped Neighbor-Joining (NJ) Tree with 1000 bootstrap repetitions to improve the reliability of the analysis. This phylogenetic tree illustrates the evolutionary relationships among COI genes from *Portunus* species from the regions listed above. All analyses were conducted using MEGA11. To visualize evolutionary relationships among species, genetic distance values were used to construct a phylogenetic tree with the Neighbor-Joining method and a p-distance model, with 1000 bootstrap replicates.

**Genetic diversity and population structure:** Genetic diversity was evaluated based on the number

of haplotypes (Hn), haplotype diversity (Hd), and nucleotide diversity ( $\pi$ ) using DNASP v6 (DNA Sequence Polymorphism V6.1.03). Population structure was assessed using Wright's fixation index ( $F_{ST}$  = F-statistic), with a significance threshold ( $\alpha$ ) of 0.05. Pairwise  $F_{ST}$  values were calculated to determine genetic differentiation between populations. Analyses were performed using DNASP v6.

## Results

**Species validation:** A total of 12 *Portunus* sample sequences (6 male and 6 female) from each study location, namely Poleang waters (FMA 713) and Lasongko Bay (FMA 714), were successfully amplified using the COI gene. The BLAST results on the NCBI site indicated that the *Portunus* sample sequences from both study locations were identified as two species in the family Portunidae, namely *P. armatus* and *P. pelagicus* (Table 1).

The BLAST analysis revealed that *P. armatus* from the Poleang waters (FMA 713) and Lasongko Bay (FMA 714) showed similarity to sequence data in the NCBI GenBank database, specifically to IDs

Table 2. Genetic distance of *Portunus* species from the waters of Poleang waters (FMA 713) and Lasongko Bay (FMA 714) of Indonesia, along with sequences from NCBI GenBank.

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	BGF01 <i>P. armatus</i>																												
2	BGF02 <i>P. armatus</i>	0.052																											
3	BGF03 <i>P. armatus</i>	0.096	0.039																										
4	BGF04 <i>P. armatus</i>	0.059	0.013	0.034																									
5	BGF05 <i>P. armatus</i>	0.095	0.043	0.005	0.034																								
6	BGF07 <i>P. armatus</i>	0.062	0.031	0.047	0.028	0.046																							
7	BGM01 <i>P. armatus</i>	0.008	0.006	0.103	0.066	0.102	0.069																						
8	BGM02 <i>P. pedegans</i>	0.032	0.025	0.063	0.029	0.063	0.039	0.039																					
9	BGM03 <i>P. pedegans</i>	0.076	0.056	0.093	0.053	0.092	0.055	0.084	0.053																				
10	BGM04 <i>P. armatus</i>	0.077	0.025	0.015	0.018	0.015	0.037	0.084	0.046	0.074																			
11	BGM05 <i>P. armatus</i>	0.013	0.006	0.104	0.066	0.102	0.069	0.007	0.035	0.084	0.084																		
12	BGM06 <i>P. armatus</i>	0.02	0.044	0.08	0.044	0.079	0.055	0.027	0.025	0.072	0.062	0.023																	
13	LGF01 <i>P. armatus</i>	0.092	0.057	0.01	0.036	0.017	0.045	0.099	0.059	0.089	0.02	0.099	0.076																
14	LGF02 <i>P. armatus</i>	0.043	0.014	0.049	0.015	0.048	0.025	0.049	0.017	0.04	0.032	0.049	0.035	0.047															
15	LGF03 <i>P. armatus</i>	0.054	0.023	0.051	0.018	0.05	0.035	0.058	0.018	0.056	0.033	0.052	0.04	0.047	0.013														
16	LGF04 <i>P. armatus</i>	0.094	0.042	0.007	0.034	0.036	0.046	0.102	0.062	0.092	0.015	0.102	0.079	0.019	0.048	0.05													
17	LGF05 <i>P. armatus</i>	0.057	0.018	0.036	0.008	0.036	0.023	0.064	0.027	0.055	0.027	0.064	0.049	0.034	0.017	0.016	0.035												
18	LGF06 <i>P. armatus</i>	0.018	0.066	0.11	0.072	0.109	0.075	0.012	0.041	0.09	0.091	0.005	0.025	0.106	0.055	0.056	0.108	0.07											
19	LGM01 <i>P. armatus</i>	0.01	0.048	0.092	0.055	0.091	0.058	0.01	0.029	0.072	0.073	0.01	0.017	0.088	0.039	0.046	0.09	0.053	0.015										
20	LGM02 <i>P. pedegans</i>	0.041	0.018	0.05	0.017	0.05	0.03	0.048	0.018	0.044	0.034	0.048	0.034	0.052	0.012	0.024	0.05	0.025	0.053	0.037									
21	LGM03 <i>P. armatus</i>	0.089	0.04	0.008	0.032	0.005	0.041	0.096	0.057	0.086	0.013	0.096	0.073	0.013	0.042	0.044	0.005	0.03	0.102	0.085	0.048								
22	LGM04 <i>P. armatus</i>	0.056	0.048	0.063	0.057	0.063	0.047	0.063	0.052	0.097	0.054	0.059	0.045	0.056	0.056	0.055	0.063	0.052	0.061	0.052	0.057	0.057							
23	LGM05 <i>P. armatus</i>	0.05	0.033	0.051	0.041	0.05	0.037	0.057	0.041	0.082	0.044	0.057	0.039	0.047	0.039	0.042	0.05	0.036	0.059	0.046	0.041	0.044	0.029						
24	LGM06 <i>P. armatus</i>	0.01	0.054	0.096	0.059	0.095	0.062	0.01	0.032	0.078	0.077	0.01	0.02	0.092	0.042	0.048	0.094	0.057	0.015	0.007	0.044	0.088	0.056	0.053					
25	<i>P. armatus</i> Australia EF661885	0.12	0.111	0.143	0.11	0.139	0.119	0.14	0.108	0.086	0.127	0.118	0.123	0.142	0.102	0.108	0.138	0.113	0.125	0.11	0.106	0.14	0.138	0.136	0.12				
26	<i>P. armatus</i> japonica MN184695	1.059	1.089	1.064	1.035	1.075	1.038	1.035	1.056	1.118	1.056	1.034	1.062	1.091	1.034	1.072	1.071	1.028	1.018	1.039	1.048	1.071	1.062	1.044	1.054	1.178			
27	<i>P. pedegans</i> Philippines KF604896	1.056	1.081	1.035	1.018	1.041	1.008	1.032	1.038	1.097	1.024	1.031	1.044	1.06	1.017	1.077	1.037	1.011	1.015	1.037	1.03	1.037	1.048	1.027	1.051	1.176	0.047		
28	<i>P. pedegans</i> China KP976342	1.078	1.11	1.073	1.033	1.078	1.027	1.061	1.06	1.09	1.06	1.06	1.065	1.084	1.037	1.087	1.074	1.031	1.043	1.057	1.066	1.058	1.071	1.047	1.073	1.221	0.063	0.038	
29	<i>Scylla serrata</i> KM628133	1.083	1.059	1.094	1.032	1.116	1.044	1.059	1.03	1.061	1.059	1.058	1.071	1.097	1.031	1.024	1.103	1.032	1.042	1.064	1.051	1.088	1.102	1.07	1.079	1.185	0.212	0.192	0.221

Table 3. Haplotype diversity of the Portunidae family in the Poleang waters (FMA 713) and Lasongko Bay (FMA 714) of Indonesia.

Species	Population	N	Hn	Hd	$\pi$	Chi-square (P-value)
<i>P. armatus</i>	Poleang waters (FMA 713)	10	10	1	0.05004	0.4571
	Lasongko Bay (FMA 714)	11	11	1	0,04766	
	Both population	21	20	0,995	0,04731	
<i>P. pelagicus</i>	Poleang waters (FMA 713)	Analysis could not be performed for populations with fewer than 2 samples. The Poleang waters (FMA 713) had 2 samples, while Lasongko Bay (FMA 714) had only 1 sample.				
	Lasongko Bay (FMA 714)					
	Both populagtion					

N = Number of sequences; Hn = Number of haplotypes; Hd = Haplotype diversity;  $\pi$  = Nucleotide diversity  
Indicator values:

Analysis	Category			Literature
	Low	Moderate	High	
Haplotype diversity (Hd)	0.1 - 0.4	0.5 - 0.7	0.8 - 1.00	Nei (1987)

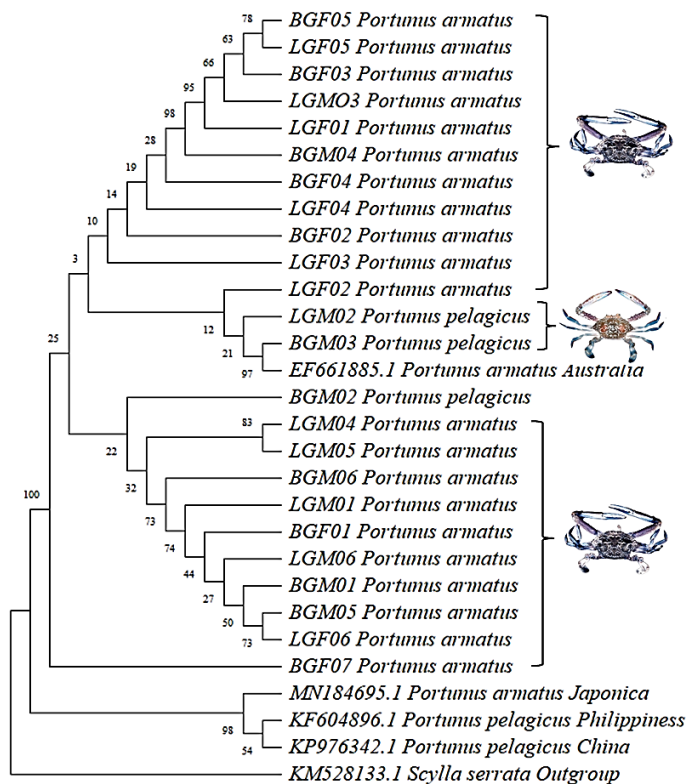


Figure 3. Phylogenetic tree constructed using the Neighbor Joining method from COI gene sequencing results, comprising 24 sequencing data of *Portunus* species from the Poleang waters (FMA 713) and Lasongko Bay (FMA 714) of Indonesia, and 5 from GenBank data with accession numbers.

ON990077 and ON990068. BLAST results for *P. armatus* sequences from the Poleang waters (FMA 713) showed a query coverage of 96-100% and an identity of 91.34-97.17%. Meanwhile, *P. armatus* sequences from Lasongko Bay (FMA 714) showed a query coverage of 97-100% and a percentage identity of 91.01-97.65%. For *P. pelagicus*, sequences from Poleang waters (FMA 713) showed a query cover percentage of 98-100% and a percentage of identity of

92.89-97.14%, while sequences from Lasongko Bay (FMA 714) showed a query cover percentage of 100% and a percentage of identity of 93.33%. These sequences matched the sequence data in the NCBI GenBank database (ID KT382858).

**Genetic distance and phylogenetic tree construction:** The genetic distance values of the current study (Table 2) show the proportion of genetic differences between each pair of populations. The constructed phylogenetic tree showed major groupings between *P. armatus* and *P. pelagicus* specimens. The results indicated that *P. armatus* dominated the phylogenetic tree, with several subgroups showing high bootstrap support. The evolutionary relationships result (Fig. 3) demonstrates that *P. armatus* is more closely related phylogenetically than *P. pelagicus*, as indicated by the bootstrap scores on the tree branches. Higher bootstrap values indicate greater confidence in the validity of the groups formed by those branches.

**Haplotype diversity and population structure:** DNA amplification of the COI gene successfully identified 24 samples from the family Portunidae, with nucleotide lengths ranging from 654 to 682 bp. The haplotype diversity analysis of *P. armatus* from the waters of Poleang (FMA 713) and Lasongko Bay (FMA 714) yielded a haplotype diversity value of 1 at each location. For the overall *Portunus* population across both locations, a value of 0.995 was obtained (Table 3). Based on the haplotype diversity data, only *P. armatus* met the analysis criteria (a minimum of 2 samples), whereas haplotype diversity for *P. pelagicus* could not be analyzed because it had only one sample.

Table 4. Population structure analysis (FST) of *Portunus armatus* species from the Poleang waters (FMA 713) and Lasongko Bay (FMA 714) of Indonesia.

Species	Population	Poleang waters (FMA 713)	Lasongko Bay (FMA 714)	
<i>P. armatus</i>	• Poleang waters (FMA 713)	-	-	
	• Lasongko Bay (FMA 714)	-0.06164	-	
<i>P. pelagicus</i>	• Poleang (FMA 713)	Analysis could not be performed for populations with fewer than 2 samples (Poleang waters: 2 samples, Lasongko Bay: 1 sample).		
	• Lasongko Bay (FMA 714)			
Indicator values:				
Analysis	Category			Literature
	Low	Moderate	High	
Population Structure $F_{ST}$	0.1 - 0.3	0.4 - 0.7	0.8 - 1.00	Excoffier et al. (1992)

Figure 4. Dorsal carapace morphology of *Portunus sanguinolentus* (A) (<https://www.crustaceology.com>) and *P. pelagicus* (B) (<https://m.singapore.biodiversity.online/>).

This data indicates that the haplotype diversity of *P. armatus* from the Poleang waters (FMA 713) and Lasongko Bay (FMA 714) is high, with a  $P$ -value of 0.4571. This high  $P$ -value suggests that haplotype diversity between the two *Portunus* populations is not significantly different. The population structure analysis of *P. armatus* from both waters yielded an  $F_{ST}$  value of -0.06164 (Table 4), indicating very low genetic differentiation between the compared populations.

## Discussions

**Species validation:** The validation of *Portunus* species involves a combination of morphological, genetic, and ecological analyses. This approach not only ensures accurate species identification but also underpins stock management, trade regulation, and biodiversity conservation. Commonly used morphological data, such as body size, carapace shape, frontal margin spines, antero-lateral border, ninth antero-lateral tooth, and carapace coloration patterns, often serve as supplementary data because

these characteristics can change due to environmental or localized genetic factors. To address these limitations, genetic analysis is essential to achieve more accurate species validation. Combining these analyses provides more reliable results in the taxonomy and ecology of *Portunus* species.

Traditionally, the BSC commonly caught by fishermen in the waters of Southeast Sulawesi (associated with FMA 713 and FMA 714) has been identified as *P. pelagicus*. However, observations and sampling have occasionally revealed the presence of other species. In some cases, another species, *P. sanguinolentus*, was identified based on morphology. The most striking morphological difference between these two species is observed on the carapace. *Portunus sanguinolentus* is easily distinguishable from *P. pelagicus* by having three white spots on the dorsal carapace (Fig. 4), which are absent in *P. pelagicus* or *P. armatus*. This underscores the importance of comprehensive validation through both morphological observation and genetic analysis to ensure effective and sustainable fisheries resource

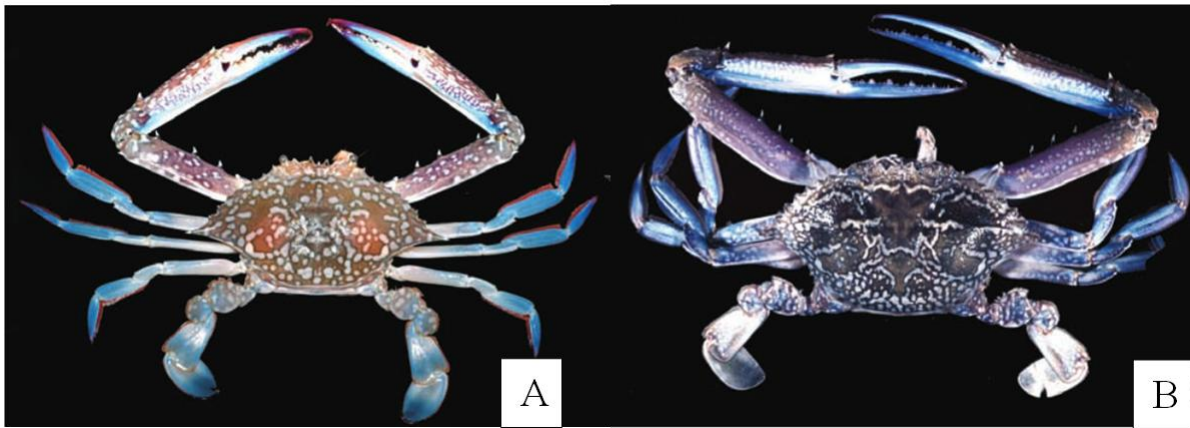


Figure 5. Live colours of males. (A) *Portunus pelagicus* (Linnaeus, 1758), and (B) *P. armatus* (A. Milne-Edwards, 1861) (Lai et al., 2010).

management.

The naming of BSC species is critical for determining management strategies based on species-specific life habits, life cycles, habitat preferences, and population dynamics. This study analyzed tissue samples from 12 BSC specimens at each research site. Morphologically, these samples were previously considered as *P. pelagicus* since distinguishing them from other species based solely on morphology was challenging. Such species with indistinguishable morphological characteristics are referred to as "cryptic species," a term long recognized for causing taxonomic confusion (Struck et al., 2017; Shin and Allmon, 2023). Chenuil et al. (2019) explained that both cryptic species *sensu stricto* and *sensu lato* often reflect genetic differences despite minimal morphological variation. Studies focusing on phenotypic and genetic characteristics (Aini et al., 2020), or on both simultaneously, can reveal disparities (Hollander and Butlin, 2010). In the current study, genetic analysis of BSC samples from Southeast Sulawesi waters linked to FMA 713 and FMA 714 revealed two distinct species: *P. pelagicus* and *P. armatus* (Fig. 5). The populations at both research sites were predominantly *P. armatus*, while *P. pelagicus* was represented by only two samples from the Poleang waters (FMA 713) and one sample from Lasongko Bay (FMA 714). Lai et al. (2010), who collected samples from various locations such as Japan, Indonesia, Australia, Singapore, Thailand, Sri Lanka, India, Madagascar, Israel, and the United Arab Emirates, noted that BSCs comprise a species

complex consisting of four species: *P. pelagicus*, *P. reticulatus*, *P. segnis*, and *P. armatus*. These species exhibit broad, diverse geographical distributions and share similar carapace morphology, but they can be distinguished by DNA analysis. Several studies in tropical waters have shown the geographical distribution of *P. pelagicus* and *P. armatus* (Table 5), with *P. pelagicus* having a wider distribution than *P. armatus*, which is more commonly found in Australian waters.

**Genetic distance and phylogenetic tree construction:** In this study, genetic distances greater than 0.03 indicate distant relatedness between the two species, suggesting they are distinct species or exhibit significant genetic diversity (Hebert et al., 2003). The genetic distance between *P. armatus* and *P. pelagicus* within the same population in Poleang waters (FMA 713) ranged from 0.005 to 0.108. The lowest genetic distance (0.005) was observed between male specimen LGM03 (*P. armatus*) and female specimen LGF04 (*P. armatus*), while the highest (0.108) was between male LGF06 and female LGF04 (*P. armatus*). Similarly, in Lasongko Bay (FMA 714), the genetic distance for *P. armatus* and *P. pelagicus* ranged from 0.005 to 0.104. The lowest distance (0.005) was observed between two female *P. armatus* specimens (BGF05 and BGF03), and the highest (0.104) was observed between male BGM05 and female BGF03 specimens (*P. armatus*). Despite these variations, the genetic distances fall within the category of close genetic relationships.

The results revealed the genetic distance between

Table 5. Geographical distribution of *Portunus pelagicus* and *P. armatus* in tropical regions.

No.	Species	Type locality	Sources
1.	<i>P. pelagicus</i>	Eastern Coast of Lampung (FMA 711), Indonesia	Yulianto et al. (2024)
2.	<i>P. pelagicus</i>	Andaman Sea Coast, Thailand	Suppapan et al. (2023)
3.	<i>P. pelagicus</i>	North Central Java (FMA 712)	Novianingrum et al. (2023)
4.	<i>P. pelagicus</i>	Kezailiao Kaohsiung and Penghu in Taiwan Xiamen and Hong Kong in mainland of China Hanoi in Vietnam Singapore	Lu et al. (2022)
5.	<i>P. pelagicus</i>	Batu Bara (FMA 571), Bangka Belitung (FMA 711), Rembang (FMA 712), Halmahera (FMA 715)	Maduppa et al. (2021)
6.	<i>P. pelagicus</i>	Gulf of Thailand	Supmee et al. (2020)
7.	<i>P. pelagicus</i>	Sorong, Raja Ampat, dan Kaimana (FMA 717), Indonesia	Hidayani et al. (2018)
8.	<i>P. pelagicus</i>	Southeast Sulawesi waters (713), Indonesia	La Sara et al. (2016a, b; 2017)
9.	<i>P. pelagicus</i>	<ul style="list-style-type: none"> <li>• Chanthaburi, Prachup Khiri Khan, and Suratthani, Gulf of Thailand, and Ranong</li> <li>• Krabi of Andaman Sea, Thailand</li> </ul>	Klinbunga et al. (2010)
10.	<i>P. pelagicus</i> var <i>sinensis</i>	China	Shen (1932)
11.	<i>P. armatus</i>	Western Australian coastline	Briggs et al. (2024)
12.	<i>P. armatus</i>	Peel-Harvey Estuary, Cockburn Sound, and Swan-Canning Estuary, Australia	Johnston et al. (2020)
13.	<i>P. armatus</i>	Shark Bay, Eastern Australia	Johnston et al. (2020)
14.	<i>P. armatus</i>	Cape Naturaliste in Western Australia, Northern Territory, Queensland, and the east coast to New South Wales – Victoria	Johnston et al. (2012)

*P. armatus* populations from the waters of Poleang (FMA 713) and Lasongko Bay (FMA 714). The lowest genetic distance between these populations was 0.000, between LGF04 and BGF05, while the highest genetic distance was 0.110, between LGF06 and BGF03. A similar pattern was observed for *P. pelagicus* from the Poleang waters (FMA 713) and Lasongko Bay (FMA 714). The lowest genetic distance between these populations was 0.018, recorded between male *P. pelagicus* specimens BGM02 and LGM02, while the highest was 0.044, recorded between male specimens BGM03 and LGM02. As with genetic distances within the same *Portunus* population, genetic distances between different *Portunus* populations also showed variations. However, these values still fall within the category of close genetic relationships. A genetic distance value  $<0.05$  among populations is generally interpreted as normal variation within a single species, although small differences between geographically distinct populations may exist (Hartl and Clark, 2007).

Genetic distance values between *Portunus* from Poleang waters (FMA 713) and Lasongko Bay (FMA 714), and between *P. armatus* from Australia, ranged from 0.086 to 0.143, indicating some genetic

differences but relatively close evolutionary relationships. This suggests possible shared evolutionary histories or genetic flow among populations. However, the genetic distances between *Portunus* populations from Poleang waters and Lasongko Bay and those from Japan, the Philippines, and China were  $>0.5$ , indicating significant divergence.

The genetic relationships among species showed that *Portunus* from the waters of Poleang (FMA 713) and Lasongko Bay (FMA 714) were intermixed, forming a single cluster with *P. armatus* from Australia. In contrast, *Portunus* populations from Japan (*P. armatus* Japonicus), the Philippines (*P. pelagicus*), and China (*P. pelagicus*) formed distinct clusters separate from those in Poleang waters and Lasongko Bay. This clustering pattern highlights closer genetic relationships between *Portunus* from Poleang waters and Lasongko Bay, and from Australia, than with other populations. The genetic closeness between *P. armatus* from Australia (EF661885), *Portunus* from Poleang (BGM03), and Lasongko Bay (LGM02) suggests a shared common ancestor in Southeast Asian waters. This hypothesis aligns with evolutionary biogeographic research,

indicating that Southeast Asia serves as a global center of marine biodiversity and a source of species dispersal (Hoeksema, 2007; Carpenter et al., 2011). While *Portunus* populations from other regions formed separate clusters, they still showed some genetic connections. The distinct clustering of *P. armatus Japonica*, *P. pelagicus* from the Philippines, and *P. pelagicus* from China reflects significant genetic divergence from the Poleang and Lasongko Bay populations. This divergence may result from geographic isolation, local adaptations, and limited genetic flow among regions (Hartl and Clark, 2007). The phylogenetic tree supports the understanding that specimens with close genetic relationships form solid, consistent clusters. High bootstrap values (100%) within the clusters indicate the robustness and reliability of the phylogenetic branching, affirming that the specimens belong to the same genetic group with high confidence (Kumar et al., 2018).

**Genetic diversity and population structure:** The genetic diversity analysis, which combines DNA sequences from *P. armatus* from the Poleang waters (FMA 713) and Lasongko Bay (FMA 714), indicates high genetic variation. Both *Portunus* populations exhibit high haplotype diversity with no significant differences ( $P=0.457$ ). This shows that *Portunus* species found in the Poleang waters (FMA 713) and Lasongko Bay (FMA 714) form a mixed cluster (interact), including the *P. armatus* sequence from Australia (EF661885). Genetic diversity is a crucial aspect in population genetics studies, particularly for understanding genetic variation and distribution patterns of species within the genus *Portunus*. Studies of haplotype diversity in *P. pelagicus* show distinct haplotype patterns across the Indo-Pacific. The haplotype diversity of *P. pelagicus* populations in the Indian Ocean tends to be more homogeneous than that of populations in the Pacific Ocean (Fazhan et al., 2020). Khamnamtong et al. (2021) explained that genetic populations are differentiated into distinct stocks, even though *P. pelagicus* is biologically considered a species with high dispersal potential. It is suspected that human activities influence genetic

diversity, resulting in specific haplotype distribution patterns in certain water regions.

Theoretically,  $F_{ST}$  values range from 0 (no differentiation between populations) to 1 (populations are highly genetically distinct). Negative  $F_{ST}$  values indicate that genetic variation within populations is lower than expected based on allele frequencies across all populations. This may suggest no genetic differentiation between populations or that the populations have very similar structures. In other words, compared populations may have high gene flow or genetic homogeneity. When there is high gene flow or strong migration between populations, they tend to have nearly identical genetic structures. In this case, a small but negative  $F_{ST}$  value is not problematic; rather, it indicates high genetic homogeneity, making populations difficult to distinguish genetically. Understanding population connectivity through genetic structure has significant implications for conservation, as genetic assessments serve as a criterion for determining appropriate units and spatial scales for conservation and management (Waples and Gaggiotti, 2012). Studies (Akey et al., 2002; Maiorano et al., 2018; Hu et al., 2024) suggest that negative  $F_{ST}$  values are interpreted as 0 in final assessments because biologically, negative values do not indicate meaningful genetic differentiation. Population structure based on COI gene data reveals significant genetic differentiation among populations in the South China Sea, the Bay of Bengal, and Northern Australia, with  $F_{ST}$  values indicating moderate to high genetic isolation (Fazhan et al., 2020). Several studies (Nei and Kumar, 2000; Supmee et al., 2020; Madduppa et al., 2021; Briggs, 2024) explain factors influencing population structure, such as geographical barriers, particularly ocean currents and geographic distance, which limit gene flow between populations. Other factors include local adaptation, in which environmental conditions, such as salinity or water temperature, drive genetic selection.

In conclusion, this research identified differences in BSC between Poleang waters (FMA 713) and Lasongko Bay (FMA 714) using a DNA barcoding approach targeting the COI gene, resulting in two

species: *P. armatus* and *P. pelagicus*. The BSC populations in both regions are dominated by *P. armatus*, while *P. pelagicus* in both areas exhibited a very low frequency. The phylogenetic analysis showed that *P. armatus* from both locations shares a close genetic relationship, with high haplotype diversity (no significant differences). Population structure analysis ( $F_{ST} = -0.06164$ ) in the two water regions indicated very low genetic differentiation between populations, reflecting high gene flow or genetic homogeneity among BSC populations. These findings also suggest that resource management policies for BSCs in FMA 713 and FMA 714 should prioritize *P. armatus* as the primary management target, given its dominance and prior misidentification as *P. pelagicus*.

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