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Genetic diversity and connectivity of white shrimp (*Penaeus merguiensis*) in the North Coast of Central Java, Indonesia

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Abstract. *Karosekali JJ, Wijayanti DP, Haryanti D, Olivia Y. 2026. Genetic diversity and connectivity of white shrimp* (Penaeus merguiensis) *in the North Coast of Central Java, Indonesia. Biodiversitas 27 (3): d270336. https://doi.org/10.13057/biodiv/d270336*. White shrimp (*Penaeus merguiensis*) is one of the major capture fisheries commodities in Central Java and has been classified as fully exploited under the Minister of Marine Affairs and Fisheries Decree No. 19/2022. Therefore, this study aims to investigate genetic diversity and population structure to provide a reference for capture fisheries management. A total of 48 specimens were collected from Tegal and Rembang, while 70 sequences from Demak waters were obtained from GenBank. DNA was extracted using Chelex, amplified by PCR, and sequenced with the Sanger method targeting the mtDNA Cytochrome C Oxidase subunit I (COI) gene. Results showed high haplotype diversity, low nucleotide diversity, and high-significant population structure. Harpending's Raggedness Index and neutrality tests indicated an expanding population with negative results. However, the Demak population showed a deviation with significant raggedness due to a steep mismatch and low nucleotide diversity. The haplotype network showed population-specific clustering patterns radiating from a central ancestral haplotype, suggesting restricted gene flow among locations. These patterns are consistent with the combined effects of monsoon-driven currents, differences in fishing grounds, and overfishing, although these factors were not directly tested in this study. These findings highlight the need for population-specific management strategies and strict monitoring of fishing efforts to ensure the sustainability of *P. merguiensis* in Central Java, Indonesia.

Keywords: Fisheries Management Area-712, haplotype, MtDNA COI, population structure, shrimp fishery

INTRODUCTION

Indonesia is recognized as the second-largest producer of both wild-capture and aquaculture fisheries, contributing approximately 7% of the global capture fisheries output (FAO 2020). Shrimp is one of the most important export commodities in Indonesia, ranking fourth in export value after tuna (*Thunnus albacares*), mackerel (*Euthynnus affinis*), and skipjack (*Katsuwonus pelamis*). According to the Ministry of Marine Affairs and Fisheries (MMAF), a notable increase in shrimp production was recorded, rising from 231.6 thousand tons in 2018 to 268.5 thousand tons in 2023. All Fisheries Management Areas (FMAs) are fully-exploited, with four experiencing overexploitation (MMAF 2023). FMA-712 records the highest production and is classified as fully-exploited, with an allowable catch of 58,674 tons and an estimated annual potential of 83,820 tons (MMAF 2022). FMA-712 covers the Java Sea, bordered by the Sunda Strait and Karimata Strait to the west and the Makassar Strait to the east.

Shrimp capture fisheries exploit two major life stages: juveniles and adults. Juvenile shrimp are mainly harvested by artisanal fisheries in estuarine habitats, while adult shrimp are targeted by industrial fleets operating in offshore waters (Suman et al. 2017; Agung et al. 2022). In Central Java, shrimp fisheries are dominated by small-scale vessels (<10 GT) operating in nearshore areas using diverse gears, including purse seines, trawls, trammel nets, trap nets, push trawls, and the locally modified "V"-shaped trap net (Wangkong) (Agung et al. 2022; Griselda et al. 2024). The coastal economy of Central Java heavily depends on capture fisheries, with white shrimp constituting the dominant commodity alongside mullet, mackerel, brown shrimp, and crabs (Adlina et al. 2019). Despite this economic importance, most small-scale fisheries remain unregulated, and data collection relies largely on traditional logbook systems with limited accuracy (Wijayanti et al. 2025). Consequently, the official classification of shrimp fishery commodities in Indonesia remains limited to "Penaeid shrimp" due to insufficient data on shrimp population biology.

White shrimp (*Penaeus merguiensis* (De Man, 1888)), also known as Jerbung or banana shrimp, belongs to the family Penaeidae and is widely distributed across the tropical waters of the Indo-West Pacific. As benthic organisms, they exhibit broad adaptability to various bottom types but predominantly inhabit muddy and sandy-loam substrates (Vance and Rothlisberg 2020). During their life cycle, *P. merguiensis* utilize mangrove estuaries as nursery grounds before migrating to offshore waters for growth, gonadal maturation, and spawning (Vance and Rothlisberg 2020). Ecologically, *P. merguiensis* are r-strategists characterized by rapid reproduction, high fecundity, early maturation, and short lifespan. Functioning as detritivore-carnivores, *P.*

merguiensis play a keystone role in tropical marine ecosystems by linking lower and higher trophic levels (Sheaves et al. 2012). The northern coast of Central Java, Indonesia provides favorable environmental conditions for this species due to nutrient-rich estuaries and extensive mangrove coverage (Agung et al. 2022).

Although *P. merguiensis* sustains socio-economic stability in Central Java, information on its genetic status and population connectivity remains insufficient. To date, mtDNA-COI in *P. merguiensis* research has been limited to species identification (Solichin et al. 2020) and has rarely been applied at the population level. Overfishing and environmental disturbances may negatively impact genetic diversity, which is essential for long-term adaptability and productivity. The absence of baseline genetic data limits the ability to identify distinct stock units, evaluate connectivity among fishing grounds, and develop science-based fisheries management strategies aligned with ecosystem sustainability principles.

Genetic studies have become a crucial approach for linking conservation and commercial fisheries management (Dudgeon et al. 2012; Wijayanti et al. 2025). The mitochondrial Cytochrome Oxidase subunit-I (COI) gene is widely used in penaeid shrimp studies due to its high resolution in detecting cryptic species, maternal inheritance, and lack of recombination (Alam et al. 2015). COI gene sequences have been extensively utilized in studies of population genetics, phylogenetics, and fishery management within penaeid shrimp (Mwakosya et al. 2018; Huy et al. 2024). In this study, we analyzed genetic diversity and population connectivity using the mtDNA-COI gene to evaluate the genetic status of wild white shrimp populations in northern Central Java. This work represents the first COI-based assessment of population structure in the region, providing essential scientific support for sustainable fisheries management.

MATERIALS AND METHODS

Sample collection

This study was conducted from December 2023 to April 2024 in Tegal and Rembang Regencies, Central Java, Indonesia, encompassing the northern part of the Java Sea. In total, 48 random-sized individuals of white shrimp were collected. Key morphological characteristics used are a markedly elevated, triangular rostrum at the base bearing 7-8 dorsal teeth and 5-6 ventral teeth; the carapace and abdomen are smooth (glabrous) without transverse bands; and the telson lacks lateral spines (Vance and Rothlisberg 2020). Twenty-four samples were collected from each location to represent the local population within the respective area (Figure 1). Specimens from Tegal were collected on 10 December 2023 from trawl fishers operating vessels <10 GT, with landings recorded at a local trading facility (Depot Adelia). Samples from Rembang were obtained on 17 December 2023 from artisanal trammel net fishers using vessels <5 GT, with landings handled by a local fish collective trader. Entire shrimp specimens were preserved in 15 mL tubes containing 96% ethanol, assigned individual identification numbers, and stored in a cool box for further laboratory analysis. Images of white shrimp samples from Tegal and Rembang are shown in Figure 2.

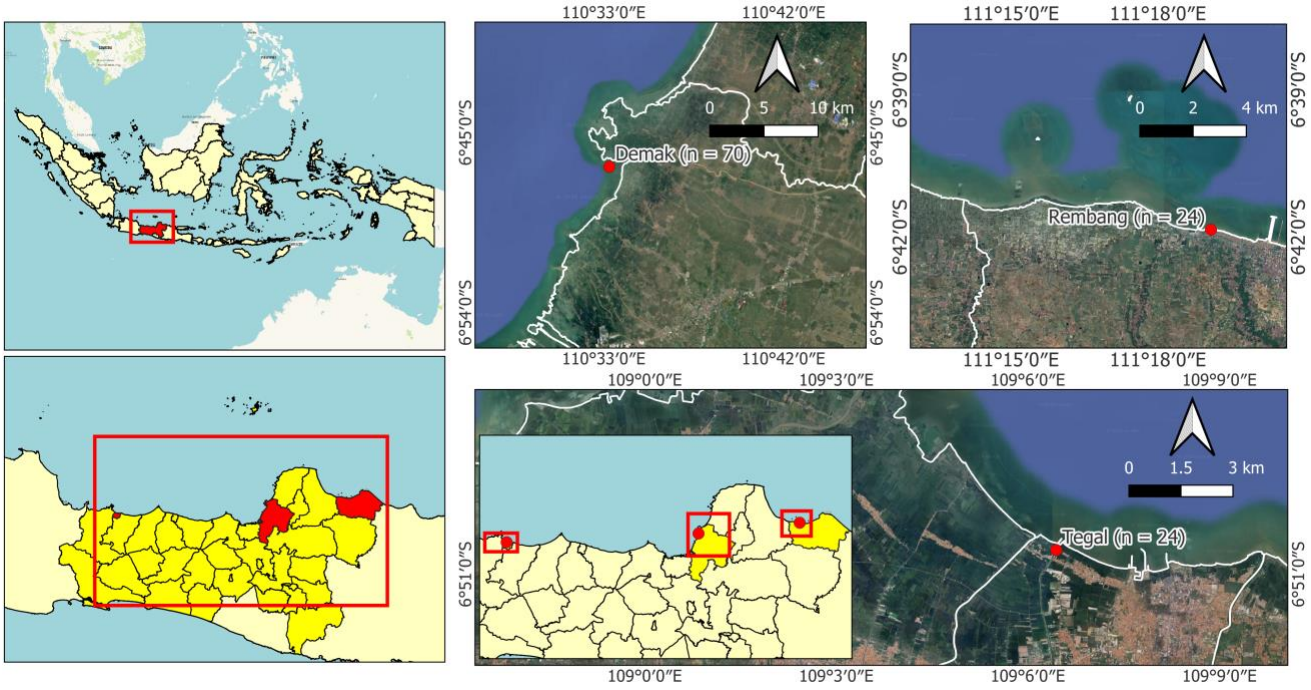

Figure 1. Sampling sites in Rembang (6°41’50.64”S, 111°19’4.98”E), Tegal (6°50’37.03”S, 109°6’26.71”E), including Demak, Central Java, Indonesia

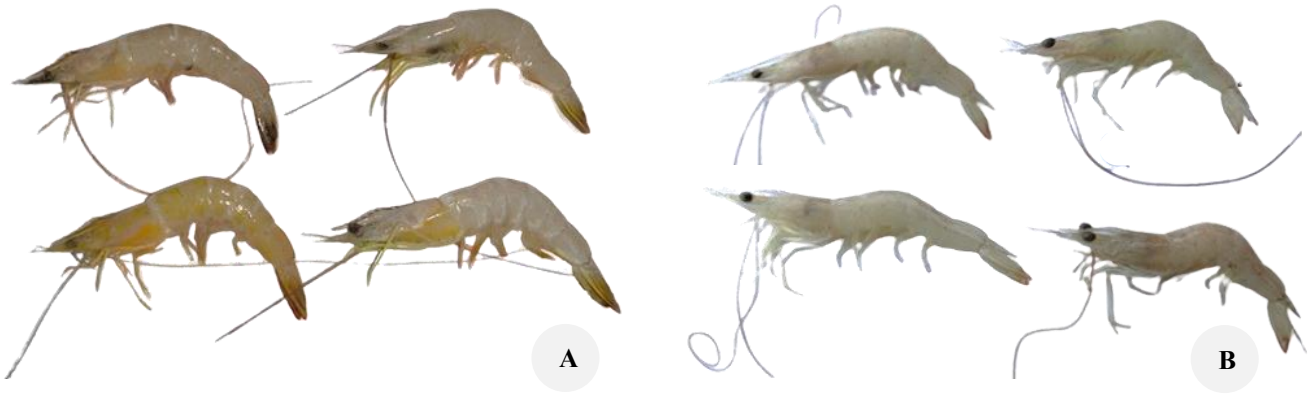

Figure 2. A. White shrimp from Tegal, and B. White shrimp from Rembang, Central Java, Indonesia

Molecular analysis

Genomic DNA was extracted using a 10% Chelex solution following Walsh et al. (1991). Approximately 1 mg of shrimp tissue from the sixth abdominal segment was placed in 10% Chelex solution, vortexed, briefly centrifuged, and incubated at 95°C for 45 min. Supernatant was collected and DNA quality was assessed using a Nanodrop (260/280 and 260/230 spectra). PCR (Polymerase Chain Reaction) amplification targeted mitochondrial DNA Cytochrome Oxidase I (COI) gene using primer pair of forward primer (JgLCO1490): 5'-TITCIACIAAYCAYAARGAYATTGG-3' and reverse primer (JgHCO2198): 5'-TAIACYTCIGGRTGICCRAARAAYCA-3' (Geller et al. 2013). The PCR reaction was carried out in a 25 µL mixture containing 1.25 µL of DNA template; 12.5 µL of My Taq™ HSRed Mix PCR kit (BIOLINE: 25 µM $MgCl_2$, 5 U/µL Taq Polymerase, 10× Taq buffer, and 10 µM dNTPs); 1 µL of each primer and 9.25 µL of distilled water; with a negative control included to verify reliability and rule out contamination. DNA amplification was carried out in a thermal cycler instrument, following PCR cycle: 95°C initial denaturation for 4 min; followed by 40 cycles of denaturation at 95°C for 30 s, primer annealing at 50°C for 30 s, and extension at 72°C for 1 min; and a final extension step at 72°C for 10 min (Insafitri et al. 2023). All PCR products were analyzed using electrophoresis in 1% agarose gel (FMC Bioproduct, Rockland, ME, USA) in 1× TAE buffer; carried out for 40 min (100V; 40 mA). The gel was then visualized under a UV Transilluminator after being stained with Florosafe (FloroSafe DNA Stain: 1st BASE). PCR products were checked on a 1% agarose gel in 1× TAE buffer and visualized under UV. All successful amplicons were sequenced using Sanger Dideoxy Sequencing (BigDye Terminator v3.1) at PT Genetika Science Indonesia.

Genetic diversity and haplotype connectivity analysis

A total of 6 samples were excluded from data analysis. Four samples failed in the amplification process, as Nanodrop results indicated an insufficient amount of DNA (<30 ng/µL). The remaining two samples exhibited poor-quality sequencing chromatograms with overlapping peaks, rendering them unsuitable for further analysis. The remaining 42 sequences were trimmed, edited, and aligned using MEGA11 (Molecular Evolutionary Genetic Analysis software) (Kumar et al. 2018). Species verification was performed through comparison with DNA sequences available in the National Center for Biotechnology Information (NCBI) database using the Basic Local Alignment Search Tool (BLAST) (http://blast.ncbi.nlm.nih.gov/), by evaluating the identity and query cover values. Two non-target *P. merguiensis* individuals were identified and excluded from the population analysis. An additional 70 *P. merguiensis* sequences from Demak, Indonesia, with GenBank accession numbers ON259553-ON259570, ON263286-ON263303, and ON263409, were incorporated for co-analysis. The sequences originated from four fishing grounds in Demak and were collected in October 2022 (Karosekali et al. 2026). All analyses used 110 aligned high-quality *P. merguiensis* sequences, with a maximum length of 683 bp.

Genetic diversity parameters, including Haplotype diversity (Hd), Nucleotide diversity (π), and the number of Segregating sites (S), were calculated using DnaSP v6.0 software (Rozas et al. 2017). All analyses excluded missing sequence data/gaps in the software with 1000 replications. Output files from DnaSP were exported in (.nexus, .hap, and .arp) formats for further analysis. Mismatch distribution analysis was employed to infer historical population expansion hypotheses based on τ (tau), θ_0 (theta zero), θ_1 (theta one), and the Sum of Squared Deviations (SSD). Harpending's Raggedness Index (r) and its associated p-value were calculated to evaluate the smoothness of the distribution. Both analyses used the distance pairwise difference method (no Gamma correction) with 1000 bootstrap replications (Excoffier et al. 2007). Neutrality tests, including Tajima's D and Fu's Fs, were conducted to detect signs of demographic expansion, with 1000 bootstrap replications in Arlequin v3.1 (Excoffier et al. 2007). Genetic differentiation estimate calculated in DnaSP v6.0 software (Rozas et al. 2017). Pairwise mismatch distribution analysis was performed in Arlequin v3.1, and both observed and simulated results were visualized using Microsoft Excel. Pairwise mismatch distribution plots were generated to examine the demographic equilibrium of the shrimp populations, indicating unimodal or multimodal patterns. Genetic variation and population structure were evaluated through AMOVA (Analysis of Molecular Variance), based

on pairwise Fixation Index (FST) values. AMOVA settings used the distance pairwise difference method with 1000 permutations in Arlequin v3.1 (Excoffier et al. 2007). Population connectivity was visualized through haplotype network analysis using PopART v1.7 (Population Analysis with Reticulate Trees) software (Leigh and Bryant 2015). Median-Joining Network reconstruction was implemented based on haplotype data and the (.nexus) file outputs generated by DnaSPv6 (Bandelt et al. 1999).

RESULTS AND DISCUSSION

Species identification and genetic diversity

A total of 42 samples were successfully amplified and sequenced, with sequence lengths ranging from 661 to 683 bp. From these, 40 samples were identified as *Penaeus merguiensis*, while two were identified as *Penaeus penicillatus* (Alcock, 1905), with identity values ranging from 97.79% to 100% and query coverage from 99% to 100% (Table S1). However, six samples were excluded from further analysis. Four samples (T10, R12, R13, and R24) failed to amplify, likely due to low DNA concentrations (<30 ng/μL) as indicated by Nanodrop measurements. The remaining two samples (T2 and R17) showed poor-quality sequencing chromatograms with overlapping peaks, rendering them unsuitable for analysis. In short, here is a sample flow diagram: 48 individuals collected → 4 failed PCR → 44 sequenced → 2 with low-quality chromatograms excluded → 42 high-quality sequences, of which 40 *P. merguiensis* and 2 *P. penicillatus*; *P. penicillatus* were excluded from population analyses. Moreover, all newly generated sequences from Tegal and Rembang (including *P. penicillatus*) have been deposited in GenBank under accession numbers PV450764-PV450783 and PV475585-PV475606.

Genetic diversity and population connectivity analysis were generated using a total of 110 *P. merguiensis* sequences, including 40 deposited sequences and co-analyzed with 70 *P. merguiensis* sequences from Demak, Central Java, Indonesia, with a total 683 bp alignment. The average nucleotide base composition was A: 26.7%, T(U): 33.6%, C: 21.1% and G: 18.6%. Haplotype diversity (gene diversity) was relatively high across all locations (Hd = 0.8704), indicating substantial genetic variability within populations. The highest values were observed in Tegal (Hd = 0.9762) and Rembang (Hd = 0.924), while Demak exhibited comparatively lower diversity (Hd = 0.6936). In contrast, nucleotide diversity remained low across all sites (π = 0.00149-0.00779; mean = 0.00499), suggesting limited sequence divergence among haplotypes (Table 1).

Population expansion

The estimated population size before expansion (θ_0) was relatively close to zero for all populations, while the population size after expansion (θ_1) showed non-identifiability under the chosen model (9999), except in the Tegal population (Table 1). The Sum of Squared Deviations (SSD) showed low and non-significant differences between the observed mismatch distributions and the expected values under the sudden expansion model, supporting the goodness-of-fit. Harpending's Raggedness Index (r) values were low and non-significant, except in the Demak population. The neutrality test results, including both Tajima's D and Fu's Fs, showed negative values across all populations (Table 1).

The mismatch distribution compares observed data with simulated demographic models using pairwise nucleotide differences and haplotype frequencies (Figure 3). The Demak population showed a steep unimodal pattern, indicating recent expansion or recovery from a bottleneck. Conversely, Tegal and Rembang exhibited smoother unimodal distributions consistent with past sudden expansion. A significant SSD p-value indicates a good fit between observed and expected values under the expansion model. However, the significant Raggedness Index (r) in the Demak population confirms the steep unimodal pattern, reflecting very low nucleotide variation.

Table 1. Genetic diversity and population analysis result

Analysis results		Location			
		Demak	**Tegal**	**Rembang**	**All locations**
Sequences	Ns	70	21	19	110
Haplotypes	H	17	17	13	44
Haplotype diversity	Hd	0.6936±0.055	0.9762±0.023	0.924±0.048	0.8704±0.028
Nucleotide diversity	Π	0.00149±0.0002	0.00779±0.00086	0.00401±0.00069	0.00499±0.00047
Segregating sites	S	16	25	13	40
Mismatch distribution analysis	Tau (Ƭ)	1.09570	5.96680	1.43945	2.83398
	Theta 0 (θ_0)	0.00176	0.00527	1.51172	0.50625
	Theta 1 (θ_1)	99999	31.54297	99999	66676.51
	SSD	0.00829	0.00852	0.00901	0.00861
	SSD p-value	0.13	0.34	0.44	0.303
Harpending's raggedness index	Index (r)	0.10845	0.03163	0.04538	0.06182
	p-value	0.010	0.340	0.570	0.30667
Neutrality test	Tajima's D	-2.03977	-0.89513	-0.97121	-1.302
	p-value	0.001	0.192	0.176	0.123
	Fu's Fs	-15.6259	-9.0296	-7.8184	-10.8246
	p-value	0.00	0.00	0.001	0.00033

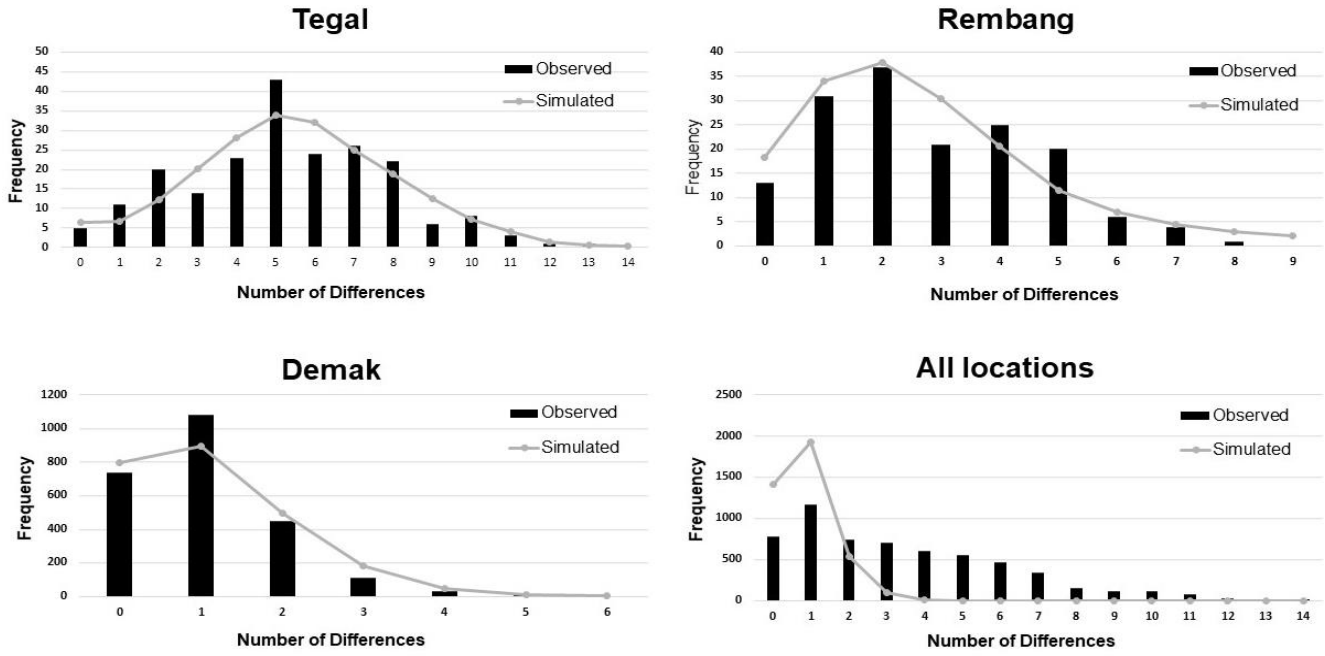

Figure 3. The observed pairwise differences and expected mismatch distribution under the recent expansion for the mtDNA COI haplotypes of *Penaeus merguiensis* on the North Coast of Central Java, Indonesia

Table 2. Genetic differentiation estimate of *Penaeus merguiensis* in Tegal, Demak and Rembang, Central Java, Indonesia

Locations	Demak	Tegal
Demak	-	-
Tegal	0.4885	-
Rembang	0.5327	0.1783

Population structure

The results of the genetic differentiation estimate analysis ranged from 0.1783 to 0.5327 between the three populations studied. Fixation Index (Fst) values revealed high genetic differences between Demak-Tegal and Demak-Rembang and were moderate in Rembang-Tegal (Table 2). The Analysis of Molecular Variance (AMOVA) test indicated that the genetic variance within and among populations was 46.42 and 53.58, respectively (Table 3). The FST result of 0.5358 was classified as high and indicated significant (<0.001) genetic differences between populations (p-value<0.05). These high FST values suggest limited gene flow among the three populations, which may be influenced by geographic distance, habitat differences, or oceanographic features. However, these potential barriers were not directly tested in this study.

Population connectivity

The DnaSP analysis identified a total of 44 unique haplotypes based on all variable positions in the COI gene across the three populations. A total of 3 shared haplotypes were found between the Tegal and Rembang populations. Among these haplotypes, 33 were singletons. The haplotype network revealed one central haplotype (Hap_9), suggesting its role as the maternal ancestor candidate from which several recorded mutational steps originated (Figure 4). Moreover, the haplotype connectivity exhibited a tendency for clustering within each population and forming a star-like network pattern. In Figure 4, Demak haplotypes are predominantly clustered on the right side, with a high frequency haplotype (Hap_29). In contrast, Tegal haplotypes cluster on the left, together with several Rembang haplotypes on the same branch, all connected to the central haplotype (H_9).

Discussion

Genetic diversity

Species identification results revealed the presence of two species, *P. merguiensis* and *P. penicillatus*. These two species are closely related organisms inhabiting tropical waters (Lavery et al. 2004). Furthermore, this species was also found in Demak waters, with indistinguishable morphological similarities and a genetic distance of 5.07% (Karosekali et al. 2026). In this study, nucleotide composition showed a higher proportion of A-T base pairs than G-C. Mitochondrial DNA in marine invertebrates commonly exhibits A-T compositional bias, which is often associated with high haplotype diversity but low nucleotide diversity (Ptacek et al. 2001). Because A-T base pairs are linked by only two hydrogen bonds, they confer lower thermal stability and a relatively less constrained DNA structure. Consequently, haplotype diversity may be high, while nucleotide diversity remains low to moderate due to mutations occurring predominantly among A and T bases (Ptacek et al. 2001). In contrast, genomes with higher G-C content generally display greater structural stability, increased gene density, and elevated mutation and recombination rates.

Table 3. Analysis Molecular Variance (AMOVA) result of *Penaeus merguiensis*

Source of variation		d.f	Sum of squares	Variance components	Percentage of variation
Among populations		2	72.973	1.21833 Va	53.58
Within populations		107	112.927	1.05539 Vb	46.42
Total		109	185.900	2.27372	100
Fixation index	FST		0.5358		
Significance tests	P-value		<0.001		

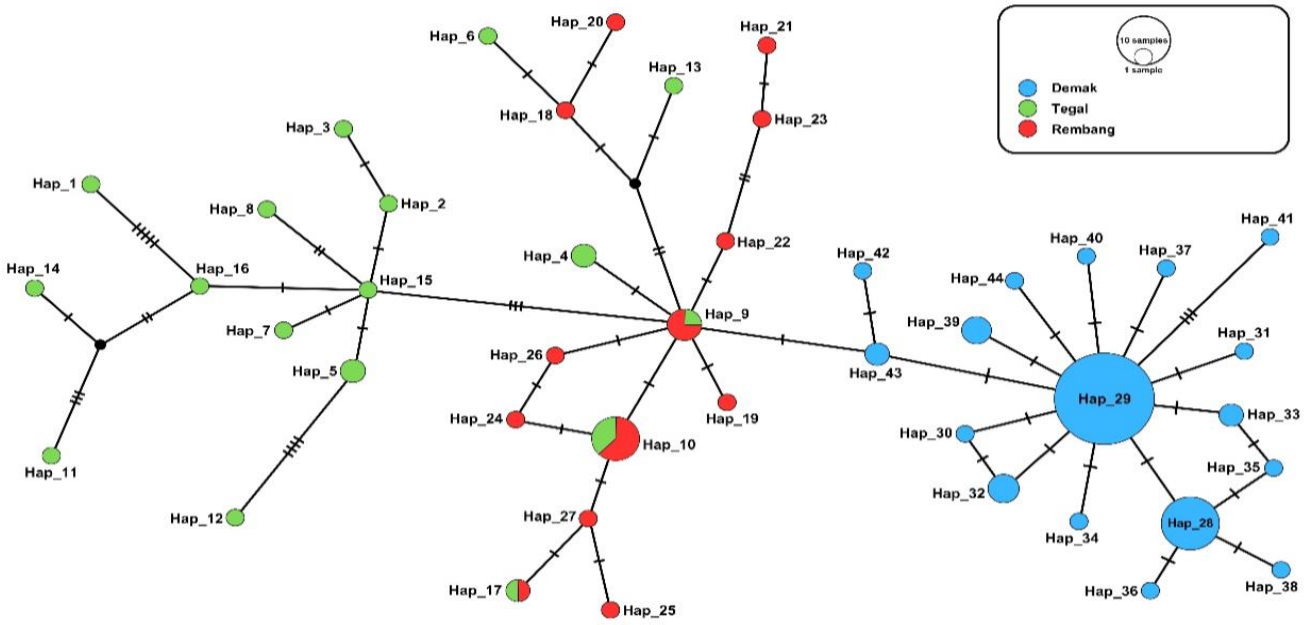

Figure 4. Population connectivity of *Penaeus merguiensis* in the North Coast of Central Java, Indonesia using Median Joining Network-PopART method

This study revealed a high Haplotype diversity (Hd = 0.8704) but low nucleotide diversity (π = 0.00499) in *P. merguiensis* populations along the northern coast of Central Java. High Haplotype diversity (Hd) coupled with low nucleotide diversity (π) is commonly associated with rapid population expansion following a period of low effective population size, which promotes the retention of new mutations (Grant and Bowen 1998).

The Demak population (n = 70) exhibited moderate haplotype diversity (Hd = 0.6936), which may reflect localized genetic effects rather than direct demographic stress. Shrimp harvested in estuarine environments are generally smaller in size and predominantly at the juvenile stage compared to those captured in offshore waters (Griselda et al. 2024). To date, the population growth pattern of *P. merguiensis* in Demak has been classified as isometric, with a relatively balanced sex ratio, indicating no apparent biological stress associated with intensive artisanal fishing activities (Griselda et al. 2024). Nevertheless, genetic diversity indices in the Demak population were comparatively lower than those observed in Tegal and Rembang, which may indicate early signals of reduced gene diversity or localized genetic effects. This diversity value may also be influenced by the relatively enclosed fishing grounds in estuarine habitats, which serve as nursery grounds. Additionally, Demak waters have a complex geographic profile with both erosion and accretion and are dominated by slow tidal waves, which may be associated with genetic isolation (Wirasatriya et al. 2017; Erfiko et al. 2023).

To date, genetic studies of *P. merguiensis* in Indonesia remain scarce and underreported, with available references focused mainly on species identification (Solichin et al. 2020; Muhammadar et al. 2021), phylogenetic delineation (Karosekali et al. 2026), and allozyme-based genetic variation (Sulistiyono et al. 2005). Compared with other Penaeidae with the COI marker, the haplotype diversity (Hd = 0.8704) of *P. merguiensis* was similar to *M. ensis* (Hd = 0.884) in Vietnam (Huy et al. 2024). Our result is relatively high compared to Penaeid shrimp in China (Han et al. 2015), Brazil (Teodoro et al. 2015), Tanzania (Mwakosya et al. 2018), Malaysia (Halim et al. 2021), Egypt (Mohammed-Geba and Yousif 2022), and Thailand (Prasertlux et al. 2024). Differences in genetic diversity between populations are influenced by complex interactions, such as high exploitation and ineffective fisheries management, habitat destruction due to human activities,

geographic isolation, hydro-oceanographic factors, disease, and competition and predation (Cao and Li 2016; Mwakosya et al. 2018; Halim et al. 2021).

Genetic diversity constitutes a fundamental component of living organisms, supporting their capacity to grow, develop, and reproduce. Populations exhibiting high heterozygosity tend to display elevated genetic variation in key phenotypic traits, which enhances their ability to adapt to environmental fluctuations, climatic shifts, and pathogenic threats (Wong et al. 2021). Genetic diversity is influenced by factors such as random mating, migration, mutation, large population size, and natural selection. High Haplotype diversity (Hd) suggests a long evolutionary history or substantial gene flow from other populations (Teodoro et al. 2020). Conversely, lower Hd values may indicate historical bottlenecks or small isolated populations. High Haplotype diversity (Hd) in Tegal and Rembang indicates relatively good long-term conditions despite ongoing exploitation. Ecologically, high Hd and low π patterns are common in marine species with large population sizes and extensive larval dispersal and are often associated with recent demographic expansions. These conditions indicate a higher reproductive success and retain functional genetic variation important for resilience to environmental change (Wijayanti et al. 2025). Moreover, our findings highlight the importance of protecting nursery grounds and incorporating genetic information into stock-based fisheries management to ensure long-term sustainability.

Population expansion and population structure

Neutrality tests (Tajima's D and Fu's Fs) and mismatch distribution analyses were performed to infer the demographic history of *P. merguiensis* populations. Overall, the results indicated signals of demographic expansion across all sites, supported by significantly negative Fu's Fs values. In contrast, Tajima's D values for Tegal and Rembang were negative but not statistically significant, likely reflecting the lower sensitivity of Tajima's D compared with Fu's Fs in detecting recent expansion (Fu 1997). High gene flow in open marine environments may also maintain allele frequencies near neutral equilibrium, reducing detectable deviations under Tajima's D. To date, there is no standard reference for the minimum number of mitochondrial DNA samples to represent a population. Moreover, non-significant Tajima's D values in Tegal and Rembang likely reflect lower statistical power due to smaller sample sizes, whereas the significant Fu's Fs across all sites provide a more robust indication of population expansion across the north coast of Central Java.

Low values of θ_0 in Demak and Tegal populations suggest a recent expansion event, likely preceded by a small ancestral population or an extreme bottleneck. A bottleneck effect occurs when population size is drastically reduced for at least one generation (Beaumont et al. 2010). The θ_1 value in Demak and Rembang (99999) showed non-identifiability under the chosen model and approached a boundary value. Higher Tau (τ) values in Tegal indicate a relatively longer estimated expansion time compared to Demak and Rembang. This evidence of population expansion may also be attributed to *P. merguiensis* being an r-strategist species, characterized by rapid growth, short lifespan, and high fecundity (Singh 2019).

Harpending's raggedness index was applied to assess the smoothness of the mismatch distribution. The Demak population exhibited a steep unimodal pattern (Figure 3), whereas Tegal and Rembang showed smoother unimodal distributions. Unimodal patterns generally indicate past sudden expansion, while a steeper distribution may reflect more recent expansion or recovery from a bottleneck (Rogers and Harpending 1992). A low, non-significant SSD value (Table 1) suggests a good fit between observed and expected distributions under the expansion model. However, the significant raggedness value in the Demak population indicates deviation from the model, likely associated with low nucleotide variation during expansion. This suggests that although Demak shows an overall expansion signal, its mutation frequency distribution is more irregular than that of Tegal and Rembang.

Genetic differentiation estimate result showed a high between the Demak population and the other two populations, whereas moderate differentiation was detected between Tegal and Rembang (Table 2). The AMOVA results (Table 3) indicated that the highest proportion of variation occurred among populations (53.58%). An AMOVA FST value of 0.5358 was classified as high, indicating strong-significant genetic differences among populations ($p<0.05$). The analysis also demonstrated substantial heterogeneity among geographically separated populations. This pattern is consistent with Isolation by Distance (IBD) (Goudarzi et al. 2019). However, formal IBD testing based on geographic distance was not performed and would be valuable in future studies. The observed structure may be influenced by the ~250 km distance between Tegal and Rembang, as well as differences in fishing grounds: open waters in Tegal and Rembang versus estuarine habitats in Demak. In addition, differences in fishing grounds (open water in Tegal and Rembang, while closed estuarine in Demak) are likely structuring the population. Together, these factors suggest the presence of spatial and environmental barriers that restrict gene flow among the three populations.

Evidence of recent population expansion in *P. merguiensis*, with strong genetic structuring among the Demak, Tegal, and Rembang populations, has important implications for fisheries management in Central Java. Although demographic expansion may confer short-term resilience, the high level of genetic differentiation and restricted gene flow indicate that these populations operate as partially independent stock units. Under such conditions, sustained overfishing, particularly the intensive removal of juveniles in estuarine fisheries, has the potential to disrupt local recruitment processes and reduce effective population size. These risks are further intensified by widespread estuarine habitat degradation in Central Java, including mangrove loss and coastal modification (Sagala et al. 2024), underscoring the need for spatially explicit and habitat-based management strategies to prevent localized stock depletion and long-term genetic erosion.

Population connectivity

Haplotype analysis revealed 44 unique haplotypes, including three shared between Tegal and Rembang, and 33 singletons. No haplotypes were shared between Demak and either Tegal or Rembang, whereas sharing occurred between Tegal and Rembang. One key haplotype (Hap_9) occupied the central position in the network (Figure 4), hypothetically being ancestral for several observed haplotypes and theoretical median nodes. The central haplotype is inferred as a putative ancestral one, not necessarily the oldest in absolute time (Bandelt et al. 1999). In this study, the haplotype network showed a tendency for clustering within each population and formed a star-like pattern. Expansion appears to occur within partially separated populations, given high-significant FST and a lack of shared haplotypes with Demak. Star-like patterns typically indicate recent expansion, especially when combined with many singletons. The numerous branches with few mutational steps (hash marks) connected to Hap_9 and Hap_29 suggest ongoing population expansion. In Tegal and Rembang, the presence of numerous singleton haplotypes with interconnected branches reflects populations with a long evolutionary history and high gene flow, resulting in the absence of a dominant haplotype (Rogers and Harpending 1992).

Penaeus merguiensis is a benthic organism, and its population connectivity is influenced by the dispersal of planktonic larvae through surface currents and tides (Riyana et al. 2015; Cao and Li 2016). The Java Sea exhibits seasonal current patterns driven by the monsoon system, which significantly affects surface current direction and intensity throughout the year. The northwest monsoon (November-March) transports water masses from the Karimata and Sunda Straits eastward, while the southeast monsoon (May-September) reverses the flow westward, carrying higher-salinity and cooler water from the Flores Sea into the Java Sea (Wyrtki 1961; Najid et al. 2012). A study by Apriansyah et al. (2023) reported that seasonal current reversals and the surface component of the Makassar Strait Throughflow play a crucial role in pelagic species distribution and fisheries productivity. Ocean circulation plays an important role in shaping genetic differentiation and directional dispersal, resulting in complex spatial patterns of genetic variation in intertidal species. This interpretation is supported by Sartimbul et al. (2023), who demonstrated that large-scale oceanographic processes, including the Indonesian Throughflow (ARLINDO) and seasonal current systems, strongly influence genetic connectivity in *Sardinella lemuru*. Furthermore, the Java Sea has an average depth of approximately 40 m with a relatively gently sloping bathymetric profile (Najid et al. 2012), allowing *P. merguiensis* larval dispersal to correlate positively with monsoon-driven current directions. However, limited information is available on larval behavior and vertical positioning in the water column, as well as their relationship to depth.

Haplotype connectivity is useful for evaluating evolutionary relationships and genetic structure to understand population history, migration patterns, and conservation implications. The combined influence of current systems and topography on population connectivity and structure has been reported for the Hokkai shrimp (*Pandalus latirostris*) in Hokkaido, Japan (Azuma and Chiba 2017). Their findings revealed a fragmented connectivity pattern with a star-like network, similar to our results. Comparable connectivity patterns were also observed in the endemic New Zealand lobster (*Metanephrops challengeri*) (Verry et al. 2020) and the Chinese grass shrimp (*Palaemonetes sinensis*) in China (Zhao et al. 2021). A more complex network pattern with numerous singleton haplotypes was reported for the pink shrimp (*Farfantepenaeus paulensis*) in Brazilian waters (Teodoro et al. 2020), similar to the populations of *P. merguiensis* in Tegal and Rembang. This complex connectivity structures typically indicate demographic expansion driven by ocean currents facilitating larval dispersal. In contrast, a star-like network pattern with non-significant population structure was found in *Fenneropenaeus indicus* from Tanzania, *F. paulensis* from southern Brazil, and *Penaeus semisulcatus* from the Gulf of Suez, Egypt (Mwakosya et al. 2018; Mohammed-Geba and Yousif 2022). Overall, star-like networks can result from expansion regardless of whether populations are structured, and a significant FST indicates limited gene flow among populations despite evidence of expansion.

This study relies on a single mitochondrial marker (COI), which is effective for species identification and detecting broad-scale population structure but has inherent limitations in resolving fine-scale genetic patterns. As a maternally inherited and non-recombining marker, COI reflects only the female lineage and may underestimate contemporary gene flow or recent admixture among populations. Consequently, the observed genetic structure and connectivity patterns should be interpreted as reflecting historical and demographic signals rather than complete genome-wide variation. Nuclear markers have a faster mutation rate and reflect genetic contributions from both parents, making them capable of detecting contemporary events such as new gene flow barriers or subtle population structure not captured by COI. Furthermore, the integration of long-term temporal sampling will allow real-time monitoring of allele frequency changes and confirm overfishing-driven genetic erosion. Integrating nuclear markers and temporal sampling would provide higher-resolution insights into population connectivity.

High shrimp utilization must be balanced with proper management to maintain the sustainability of natural stocks. The establishment of a Shrimp Fisheries Management Plan (FMP) in FMA-712 is necessary to provide direction and guidance for fishermen, industry, and other stakeholders in utilizing shrimp resources. FMP policy has been implemented in the swimming crab, tuna-mackerel-skipjack, and snapper-grouper management plans. The white shrimp species itself lacks regional or national management regulations, yet it remains part of the Penaeid shrimp group. Therefore, our results can provide baseline evidence for recognizing stock units. Based on the significant population structure and the fragmented haplotype network pattern, we recommend that shrimp fisheries management in Central Java treat the Demak, Tegal, and Rembang populations as separate stock units. Each location should be subject to distinct management

measures, including regulations on fishing effort, minimum catch size, and seasonal closures. Managing these populations separately would help preserve local genetic adaptations to site-specific environmental conditions. The management plan should be integrated with science-based evidence, incorporating population dynamics parameters, Maximum Sustainable Yield (MSY), Catch Per Unit Effort (CPUE), and fishing gear selectivity. In particular, shrimp fisheries management in Demak should adopt a more precautionary framework, emphasizing the protection of nursery grounds, restrictions on juvenile harvest, and mangrove restoration efforts.

In conclusion, based on the COI gene, *P. merguiensis* on the northern coast of Central Java, Indonesia, exhibited a high overall genetic diversity, but moderate in the Demak population. Demographic and connectivity analyses reveal an expanding population with three distinct genetic clusters and evidence of genetic isolation in the Demak population. These findings support the classification of Demak, Tegal, and Rembang as independent management units to safeguard spawning stocks and recruitment within estuarine habitats. This study provides the first COI-based genetic baseline for Central Java, offering essential data to inform a spatially explicit Fisheries Management Plan (FMP) for sustainable resource use in FMA-712. Future research integrating nuclear DNA markers and long-term temporal sampling is necessary to resolve fine-scale connectivity and monitor contemporary genetic shifts over multiple generations.

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REFERENCES

Adlina KS, Mudzakir AK, Wijayanto D. 2019. Analisis komoditas unggulan perikanan tangkap di Kabupaten Demak. J Fish Resour Util Manag Technol 8 (2): 16-25. [Indonesian]

Agung AR, Taufiq-SPJ N, Azizah R. 2022. Spesies udang yang ditemukan di perairan Desa Menco, Wedung, Demak. J Mar Res 11 (4): 706-714. https://doi.org/10.14710/jmr.v11i4.34914. [Indonesian]

Alam MMM, Westfall KM, Pálsson S. 2015. Mitochondrial DNA variation reveals cryptic species in *Fenneropenaeus indicus*. Bull Mar Sci 91 (1): 15-31. https://doi.org/10.5343/bms.2014.1036.

Apriansyah, Atmadipoera AS, Nugroho D, Jaya I, Akhir MF. 2023. Simulated seasonal oceanographic changes and their implication for the small pelagic fisheries in the Java Sea, Indonesia. Mar Environ Res 188: 106012. https://doi.org/10.1016/j.marenvres.2023.106012.

Azuma N, Chiba S. 2017. Genetic population structure of the Hokkai shrimp *Pandalus latirostris* Rathbun, 1902 (Decapoda: Caridea: Pandalidae) from *Zostera* seagrass beds in Hokkaido, Japan. J Crustac Biol 38 (2): 147-155. https://doi.org/10.1093/jcbiol/rux116.

Bandelt HJ, Forster P, Röhl A. 1999. Median-joining networks for inferring intraspecific phylogenies. Mol Biol Evol 16 (1): 37-48. https://doi.org/10.1093/oxfordjournals.molbev.a026036.

Beaumont A, Boudry P, Hoare K. 2010. Genetics of population size in conservation and aquaculture. In: Biotechnology and Genetics in Fisheries and Aquaculture, Second Edition. Wiley-Blackwell, Hoboken, New Jersey. https://doi.org/10.1002/9781444318791.ch4.

Cao YY, Li ZB. 2016. Genetic diversity and population structure of *Fenneropenaeus penicillatus* determined by mitochondrial DNA analyses. Genet Mol Res 15 (3): gmr.15038503. https://doi.org/10.4238/gmr.15038503.

Dudgeon CL, Blower DC, Broderick D, Giles JL, Holmes BJ, Kashiwagi T, Krück NC, Morgan JAT, Tillett BJ, Ovenden JR. 2012. A review of the application of molecular genetics for fisheries management and conservation of sharks and rays. J Fish Biol 80 (5): 1789-1843. https://doi.org/10.1111/j.1095-8649.2012.03265.x.

Erfiko MF, Widada S, Atmodjo W. 2023. Pemetaan pola sebaran sedimen dasar di perairan Wedung, Demak. Indones J Oceanogr 5 (2): 132-140. https://doi.org/10.14710/ijoce.v5i2.16660. [Indonesian]

Excoffier L, Laval G, Schneider S. 2007. Arlequin (version 3.0): An integrated software package for population genetics data analysis. Evol Bioinform Online 1: 47-50.

FAO [Food and Agriculture Organization]. 2020. The State of World Fisheries and Aquaculture 2020: Sustainability in Action. FAO, Rome. https://doi.org/10.4060/ca9229en.

Fu Y-X. 1997. Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. Genetics 147 (2): 915-925. https://doi.org/10.1093/genetics/147.2.915.

Geller J, Meyer C, Parker M, Hawk H. 2013. Redesign of PCR primers for mitochondrial cytochrome c oxidase subunit I for marine invertebrates and application in all-taxa biotic surveys. Mol Ecol Resour 13 (5): 851-861. https://doi.org/10.1111/1755-0998.12138.

Goudarzi F, Hemami M-R, Rancilhac L, Malekian M, Fakheran S, Elmer KR, Steinfartz S. 2019. Geographic separation and genetic differentiation of populations are not coupled with niche differentiation in threatened Kaiser’s spotted newt (*Neurergus kaiseri*). Sci Rep 9: 6239. https://doi.org/10.1038/s41598-019-41886-8.

Grant WAS, Bowen BW. 1998. Shallow population histories in deep evolutionary lineages of marine fishes: Insights from sardines and anchovies and lessons for conservation. J Hered 89 (5): 415-426. https://doi.org/10.1093/jhered/89.5.415.

Griselda APK, Saputra SW, Purnomo PW. 2024. Perbandingan produktivitas alat tangkap sodo (push net) dan wangkong (trap net) terhadap hasil tangkapan udang putih (*Penaeus merguiensis*) di perairan Wedung, Kabupaten Demak. Jurnal Pasir Laut 8 (2): 99-106. https://doi.org/10.14710/jpl.2024.65734. [Indonesian]

Halim SAAA, Othman AS, Akib NAM, Jamaludin N-A, Esa Y, Nor SAM. 2021. Mitochondrial markers identify a genetic boundary of the green tiger prawn (*Penaeus semisulcatus*) in the Indo-Pacific Ocean. Zool Stud 60: 8. https://doi.org/10.6620/zs.2021.60-08.

Han Z, Zhu W, Zheng W, Li P, Shui B. 2015. Significant genetic differentiation between the Yellow Sea and East China Sea populations of cocktail shrimp *Trachypenaeus curvirostris* revealed by the mitochondrial DNA COI gene. Biochem Syst Ecol 59: 78-84. https://doi.org/10.1016/j.bse.2014.12.028.

Huy NX, Ty N, Giang TV, Phuong TV. 2024. A first look at genetic diversity of *Metapenaeus ensis* populations in Tam Giang-Cau Hai Lagoon, Vietnam. Isr J Aquac-Bamidgeh 76 (2): 158-167. https://doi.org/10.46989/001c.117579.

Insafitri, Nursalim N, Kholilah N, Kurniasih EM, Cahyani NKD, Nugraha WA, Ambariyanto A. 2023. DNA barcode of seven species coral from Sepulu, Madura Island, Indonesia. Biodiversitas 24 (1): 317-323. https://doi.org/10.13057/biodiv/d240138.

Karosekali JJ, Kholilah N, Syam AAH, Subagiyo S, Wijayanti DP, Bachtiar M. 2026. Utilization of COI marker for species identification and population delineation of white shrimp in the Demak Waters, Indonesia. Ilmu Kelautan: Indones J Mar Sci 31 (1): 37-48. https://doi.org/10.14710/ik.ijms.31.1.37-48.

Kumar S, Stecher G, Li M, Knyaz C, Tamura K. 2018. MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. Mol Biol Evol 35 (6): 1547-1549. https://doi.org/10.1093/molbev/msy096.

Lavery S, Chan TY, Tam YK, Chu KH. 2004. Phylogenetic relationships and evolutionary history of the shrimp genus *Penaeus s.l.* derived from mitochondrial DNA. Mol Phylogenet Evol 31 (1): 39-49. https://doi.org/10.1016/j.ympev.2003.07.015.

Leigh JW, Bryant D. 2015. POPART: Full-feature software for haplotype network construction. Methods Ecol Evol 6 (9): 1110-1116. https://doi.org/10.1111/2041-210x.12410.

Ministry of Marine Affairs and Fisheries (MMAF). 2022. Estimation of Potential, Total Allowable Catch, and Level of Utilization of Fish Resources in WPPNRI. MMAF, Jakarta. [Indonesian]

Ministry of Marine Affairs and Fisheries (MMAF). 2023. Fisheries production. MMAF, Jakarta. [Indonesian]

Mohammed-Geba K, Yousif A. 2022. COI gene sequencing reveals genetic population structuring and a separate lineage of the green tiger prawn *Penaeus semisulcatus* in the Gulf of Suez and the Bitter Lakes, Egypt. Aquat Living Resour 35: 4. https://doi.org/10.1051/alr/2022004.

Muhammadar AA, Putra DF, Widari W. 2021. Diversity and ecological index of penaeid shrimp collected from mangrove area of Kuala Langsa, Aceh, Indonesia. IOP Conf Ser: Earth Environ Sci 869: 012028. https://doi.org/10.1088/1755-1315/869/1/012028.

Mwakosya CA, Mgaya YD, Jiddawi NS. 2018. Genetic connectivity of *Fenneropenaeus indicus* (H. Milne Edwards 1837) among three prawn fishing grounds of Tanzanian coastal waters. Reg Stud Mar Sci 24: 107-112. https://doi.org/10.1016/j.rsma.2018.08.001.

Najid A, Paiwono JI, Bengen DG, Nurhakim S, Atmadipoera AS. 2012. Pola musiman dan antar tahunan salinitas permukaan laut di perairan utara Jawa-Madura. Maspari J 4 (2): 168-177. [Indonesian]

Prasertlux S, Khamnamtong B, Wisuntorn E, Soonsan P, Janpoom S, Tang S, Rongmung P, Ratdee O, Ninwichian P, Sakamoto T, Sae-Lim P, Klinbunga S. 2024. Genetic diversity and population differentiation of wild and domesticated banana shrimp *Fenneropenaeus merguiensis*: Applications for development of its breeding program. Reg Stud Mar Sci 69: 103309. https://doi.org/10.1016/j.rsma.2023.103309.

Ptacek MB, Sarver SK, Childress MJ, Herrnkind WF. 2001. Molecular phylogeny of the spiny lobster genus *Panulirus* (Decapoda: Palinuridae). Mar Freshw Res 52 (8): 1037-1047. https://doi.org/10.1071/mf01070.

Riyana H, Hutabarat S, Widyorini N. 2015. Kelimpahan larva udang penaeid pada saat pasang di saluran tambak Desa Gempolsewu, Kab. Kendal. Diponegoro J Manag Aquat Resour 4 (3): 49-57. https://doi.org/10.14710/marj.v4i3.9209. [Indonesian]

Rogers AR, Harpending H. 1992. Population growth makes waves in the distribution of pairwise genetic differences. Mol Biol Evol 9 (3): 552-569. https://doi.org/10.1093/oxfordjournals.molbev.a040727.

Rozas J, Ferrer-Mata A, Sánchez-DelBarrio JC, Guirao-Rico S, Librado P, Ramos-Onsins SE, Sánchez-Gracia A. 2017. DnaSP 6: DNA sequence polymorphism analysis of large data sets. Mol Biol Evol 34 (12): 3299-3302. https://doi.org/10.1093/molbev/msx248.

Sagala PM, Bhomia RK, Murdiyarso D. 2024. Assessment of coastal vulnerability to support mangrove restoration in the northern coast of Java, Indonesia. Reg Stud Mar Sci 70: 103383. https://doi.org/10.1016/j.rsma.2024.103383.

Sartimbul A, Winata VA, Kasitowati RD, Iranawati F, Rohadi E, Yona D, Anjeli UG, Pranowo WS, Lauro FM. 2023. Seasonal Indonesian Throughflow (ITF) across southern Java determines genetic connectivity of *Sardinella lemuru* (Bleeker, 1835). Deep Sea Res II Top Stud Oceanogr 209: 105295. https://doi.org/10.1016/j.dsr2.2023.105295.

Sheaves M, Johnston R, Connolly RM, Baker R. 2012. Importance of estuarine mangroves to juvenile banana prawns. Estuar Coast Shelf Sci 114: 208-219. https://doi.org/10.1016/j.ecss.2012.09.018.

Singh A. 2019. r-Reproductive Strategy. In: Vonk J, Shackelford T (eds). Encyclopedia of Animal Cognition and Behavior. Springer, Cham. https://doi.org/10.1007/978-3-319-47829-6_450-1.

Solichin A, Saputra SW, Taufani WT, Ayuningrum D. 2020. Studi molekular udang *Pennaeus* (*Fenneropenaeus*) *merguiensis* di perairan Pantai Utara Jawa. Saintek Perikanan: Indones J Fish Sci Technol 16 (4): 294-299. https://doi.org/10.14710/ijfst.16.4.294-299. [Indonesian]

Sulistiyono E, Sutarno S, Moria SB. 2005. Genetic variation of penaeids shrimp (*Penaeus merguiensis* de Man) based on enzyme electrophoresis data. Asian J Trop Biotechnol 2 (1): 1-8. https://doi.org/10.13057/biotek/c020101.

Suman A, Hasanah A, Ernawati T, Pane ARP. 2017. The population dynamics of banana prawn (*Penaeus merguiensis* De Man) in Tanah Laut waters, South Kalimantan. Indones Fish Res J 23 (1): 17-22. https://doi.org/10.15578/ifrj.23.1.2017.17-22.

Teodoro SSA, da Silva Cortinhas MC, Proietti MC, Costa RC, Dumont LFC. 2020. High genetic connectivity among pink shrimp *Farfantepenaeus paulensis* (Pérez-Farfante, 1967) groups along the south-southeastern coast of Brazil. Estuar Coast Shelf Sci 232: 106488. https://doi.org/10.1016/j.ecss.2019.106488.

Teodoro SSA, Terossi M, Costa RC, Mantelatto FL. 2015. Genetic homogeneity in the commercial pink shrimp *Farfantepenaeus paulensis* revealed by COI barcoding gene. Estuar Coast Shelf Sci 166 (Part A): 124-130. https://doi.org/10.1016/j.ecss.2015.07.009.

Vance DJ, Rothlisberg PC. 2020. The biology and ecology of the banana prawns: *Penaeus merguiensis* de Man and *P. indicus* H. Milne Edwards. Adv Mar Biol 86 (1): 1-139. https://doi.org/10.1016/bs.amb.2020.04.001.

Verry AJF, Walton K, Tuck ID, Ritchie PA. 2020. Genetic structure and recent population expansion in the commercially harvested deep-sea decapod, *Metanephrops challengeri* (Crustacea: Decapoda). N Z J Mar Freshw Res 54 (2): 251-270. https://doi.org/10.1080/00288330.2019.1707696.

Walsh PS, Metzger DA, Higuchi R. 1991. Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. Biotechniques 10 (4): 506-513.

Wijayanti DP, Indrayanti E, Haryanti D, Wijayanti MK, Elmir ZG, Fachri FR, Bhagooli R, Nozawa Y. 2025. Molecular and risk-based approaches to the status of goldbanded jobfish *Pristipomoides multidens* (Day, 1871) in Kupang, Indonesia. Biodiversitas 26 (2): 928-940. https://doi.org/10.13057/biodiv/d260242.

Wirasatriya A, Rochaddi B, Faizah AN, Zainuri M, Muslim, Setiyono H, Hariadi, Marwoto J. 2017. Study of longshore current at the mouth of Tuntang River, Morodemak Village, Demak Regency, Indonesia and its possible effect on coastal morphology. Intl J Civil Eng Technol 8 (11): 1-9.

Wong LL, Chun LC, Deris ZM, Zainudin AA, Ikhwanuddin M, Iehata S, Rahman MM, Asaduzzaman M. 2021. Genetic diversity and population structure of wild and domesticated black tiger shrimp (*Penaeus monodon*) broodstocks in the Indo-Pacific regions using consolidated mtDNA and microsatellite markers. Gene Rep 23: 101047. https://doi.org/10.1016/j.genrep.2021.101047.

Wyrtki K. 1961. Physical Oceanography of the Southeast Asian Waters. Naga Report Scientific Results of Marine Investigations of the South China Sea and the Gulf of Thailand. The University of California Scripps Institution of Oceanography La Jolla, California.

Zhao YY, Zhu XC, Li YD, Han ZB, Xu WB, Dong J, Wei H, Li XD. 2019. Mitochondrial genome of Chinese grass shrimp *Palaemonetes sinensis* and comparison with other Palaemoninae species. Sci Rep 9: 17301. https://doi.org/10.1038/s41598-019-53539-x.

Table S1. Homology result of white shrimp from Tegal and Rembang, Central Java, Indonesia

ID	BLAST identification	Base pair (bp)	Ident. (%)	Query cover (%)	Accession code	Deposited code
R1	*Penaeus merguiensis*	683	99.56	100	ON259561.1	PV450764
R2	*Penaeus merguiensis*	683	99.71	100	ON259561.1	PV450765
R3	*Penaeus merguiensis*	683	99.85	100	ON259561.1	PV450766
R4	*Penaeus merguiensis*	683	99.85	100	ON332483.1	PV450767
R5	*Penaeus merguiensis*	683	99.71	100	ON259561.1	PV450768
R6	*Penaeus merguiensis*	683	99.71	100	ON259561.1	PV450769
R7	*Penaeus merguiensis*	683	99.71	100	ON259561.1	PV450770
R8	*Penaeus merguiensis*	661	99.85	100	ON259547.1	PV450782
R9	*Penaeus merguiensis*	661	99.85	99	MT876653.1	PV450783
R10	*Penaeus merguiensis*	661	100	99	MT876653.1	PV450778
R11	*Penaeus merguiensis*	661	99.40	100	ON259561.1	PV450779
R14	*Penaeus merguiensis*	661	99.85	100	ON259561.1	PV450780
R15	*Penaeus merguiensis*	661	99.85	100	ON259561.1	PV450781
R16	*Penaeus merguiensis*	683	99.71	100	ON259561.1	PV450771
R18	*Penaeus merguiensis*	683	99.71	100	ON259561.1	PV450772
R19	*Penaeus penicillatus*	683	97.79	100	ON259562.1	PV450773
R20	*Penaeus merguiensis*	683	99.27	100	ON259561.1	PV450774
R21	*Penaeus merguiensis*	683	99.71	100	ON259561.1	PV450775
R22	*Penaeus merguiensis*	683	99.41	100	ON259561.1	PV450776
R23	*Penaeus merguiensis*	683	99.71	100	ON259547.1	PV450777
T1	*Penaeus merguiensis*	673	99.11	100	ON259537.1	PV475585
T3	*Penaeus merguiensis*	673	99.55	100	ON259537.1	PV475586
T4	*Penaeus merguiensis*	673	99.40	100	ON259537.1	PV475587
T5	*Penaeus merguiensis*	683	99.85	100	ON259561.1	PV475594
T6	*Penaeus merguiensis*	683	99.71	100	ON259561.1	PV475595
T7	*Penaeus merguiensis*	683	98.54	100	ON259561.1	PV475596
T8	*Penaeus merguiensis*	683	98.68	100	ON259561.1	PV475597
T9	*Penaeus merguiensis*	683	99.41	100	ON263561.1	PV475598
T11	*Penaeus merguiensis*	673	99.85	100	ON332480.1	PV475588
T12	*Penaeus merguiensis*	673	99.55	100	ON259537.1	PV475589
T13	*Penaeus merguiensis*	673	99.85	100	ON332480.1	PV475590
T14	*Penaeus merguiensis*	661	99.24	100	ON259561.1	PV475593
T15	*Penaeus merguiensis*	683	98.83	100	ON259561.1	PV475599
T16	*Penaeus merguiensis*	683	99.27	100	ON259561.1	PV475600
T17	*Penaeus merguiensis*	673	99.55	100	ON332480.1	PV475591
T18	*Penaeus merguiensis*	683	99.41	100	ON259561.1	PV475601
T19	*Penaeus merguiensis*	683	99.71	100	ON259561.1	PV475602
T20	*Penaeus merguiensis*	683	99.27	100	ON259561.1	PV475603
T21	*Penaeus merguiensis*	683	99.41	100	ON259561.1	PV475604
T22	*Penaeus merguiensis*	673	99.55	100	ON259537.1	PV475592
T23	*Penaeus merguiensis*	683	99.71	100	ON259561.1	PV475605
T24	*Penaeus penicillatus*	683	97.79	100	ON259562.1	PV475606

Note: R: Samples collected from Rembang waters, T: Samples collected from Tegal waters