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Research Article

Exploring the Genetic Landscape of *Octopus cyanea*: Connectivity and Population Structure in Northern Waters of Sumatra

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ABSTRACT

Octopus cyanea is an ecologically and economically important cephalopod with wide larval dispersal influenced by ocean currents. However, geographic isolation among island clusters in northern Sumatra may restrict gene flow and shape population structure. This study investigated the genetic diversity and connectivity of *O. cyanea* from five populations (Aceh Island, Weh Island, Banyak Island, Simeulue Island, and Nias Island) using mitochondrial cytochrome c oxidase subunit I (COI) sequences. A total of 21 individuals were successfully amplified, yielding 651 bp fragments. Sequence analysis revealed 11 haplotypes across populations, with haplotype diversity (Hd) ranging from 0.285 in Banyak Island to 0.800 in Aceh Island, and nucleotide diversity (π) between 0.001 and 0.009. Pairwise genetic distances varied from 0.000 to 0.004, with the highest divergence observed between Simeulue Island and Nias Island (0.004), while Aceh Island and Weh Island showed no differentiation. AMOVA indicated that most genetic variation occurred within populations (68.74%), with an overall Fst of 0.315, suggesting low to moderate genetic structuring. The haplotype network demonstrated shared haplotypes among four populations, whereas Simeulue Island harbored unique haplotypes, indicating partial genetic isolation. These results highlight substantial genetic connectivity among *O. cyanea* populations in northern Sumatra, facilitated by larval dispersal via ocean currents, but also emphasize localized divergence in Simeulue Island. The findings provide critical baseline data for developing ecosystem-based fisheries management, supporting shared stock strategies while accounting for population-specific conservation needs.

1. Introduction

Octopus cyanea has two larval developmental stages. The first stage is referred to as the larval phase, during which eggs are protected by the female octopus along all her arms and incubated for 21 days (Lenz *et al*. 2015), characterized by passive dispersal behavior (Gutnick *et al.* 2021). The next phase is known as the paralarval stage, a juvenile planktonic phase resembling free-swimming hatchlings that lasts for weeks to months, typically ranging between 1 to 2 months (Hamad *et al*. 2023; Silas *et al*. 2023). During this stage, octopuses actively migrate both vertically and horizontally, following ocean currents in their

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hatching area (Roura *et al*. 2016). The duration of the larval and paralarval stages, combined with the migration behaviors in both phases, makes this octopus a highly dynamic species with a wide distribution (Chande *et al*. 2021). However, the larvae slow down upon reaching shallow waters and remain there until entering the settlement stage (Noegroho *et al*. 2023).

One of the marine areas with octopus habitats in the Indian Ocean, characterized by a cluster of islands, is in Northern Sumatra. Several island clusters, such as Nias Island, Banyak Island, Simeulue Island, Weh Island, and Aceh Island, surround this region. Marine waters consisting of island chains serve as sources of biogeographic diversity associated with genetic isolation, population differentiation, and individual speciation (Lee *et al*. 2022). Marine waters with many geographical barriers exhibit high genetic variation influenced by factors such as hydrographic structures and currents, which can act as both obstacles and pathways for larval dispersal of intertidal invertebrates (Ramanantsoa *et al*. 2018; Huyghe and Kochzius 2018).

The recruitment of octopus commodities serves as a reference for fisheries management or ecosystem-based fisheries management. This information is highly relevant for stock management, particularly given the increasing threat of overfishing in the northern Sumatra waters. In areas where local octopus populations are overexploited, other regions are expected to support recruitment through the Shared Stocks mechanism (Indriyani *et al.* 2025; Halimatussadiah *et al*. 2023). Designing an effective Shared Stocks network requires a clear understanding of connectivity between populations via larval dispersal (Hatmar *et al.* 2024), as this connectivity determines gene flow, resilience, and the capacity of populations to recover from anthropogenic pressures, especially overfishing (Chavez *et al*. 2021; Fontoura *et al.* 2024). Strengthening this ecological linkage highlights the urgency of implementing stock-based management to ensure the sustainability of *Octopus cyanea* populations in the study area. The systematics of octopuses and the understanding of their geographical range have been greatly facilitated by the use of molecular DNA (Ramadhaniaty *et al.* 2018). Molecular DNA has become a critical tool for identifying and understanding the genetic diversity of marine biota to date (Madduppa *et al*. 2014; Prehadi *et al*. 2015). It is widely used to answer questions that ecology alone cannot address (Dwinovantyo *et al*. 2016). The ability of populations to adapt to their environment is influenced by genetic diversity (Saleky and Dailami 2021).

This study will analyze the genetic diversity and population connectivity of *Octopus cyanea* in the northern waters of Sumatra. Oceanographic factors enable gene flow along this coastline, resulting in genetic structure and diversity, as observed in related studies (Ramadhaniaty *et al*. 2018). Genetic studies on octopuses have not been conducted previously in the Sumatra Northern area; however, similar research on shared stocks has been carried out for Lutjanidae commodities in Indonesia and Australia. These studies revealed that the two countries share stocks, leading to joint management being established in 1999 (Blaber 2007). A similar survey of squid in the Adriatic Sea found low genetic distances and homogeneous haplotypes among populations, recommending coordinated management across the waters (Garoia *et al*. 2004). Understanding the genotypic diversity and population structure of a species is a critical strategy for fisheries management, aiding in the establishment of conservation management units and providing valuable information for the management plans of commercially important species. To the best of our knowledge, this is the first study to investigate the genetic diversity and population connectivity of *O. cyanea* in northern Sumatra. This novelty provides essential baseline molecular data for an ecologically and economically important octopus species that has not been previously characterized in these waters, thereby contributing new insights for sustainable fisheries management and conservation strategies.

2. Materials and Methods

2.1. Time and Place of Implementation

This study was conducted over the course of one year, from January to December 2024. Octopus samples were collected from islands along the Aceh waters, including Aceh Island, Weh Island, Banyak Island, Simeulue Island, and Nias Island. (Figure 1). Morphological identification and molecular analysis were carried out at the Genetics and Aquatic Biodiversity Laboratory, Faculty of Marine and Fisheries, Universitas Syiah Kuala.

2.2. Sample Collection

A total of 21 octopus samples was collected from fish landing at the five research locations. Local fishermen caught the sample from the respective location. Before

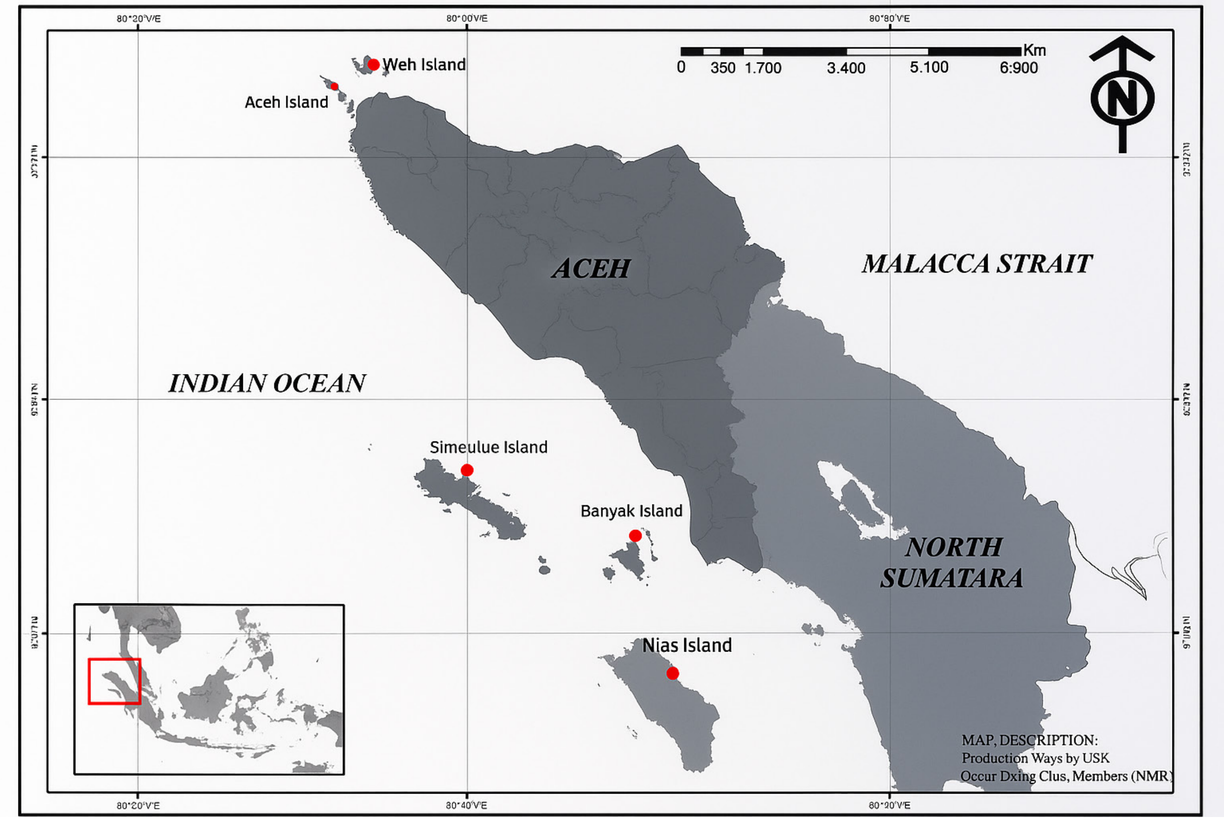

Figure 1. Research map of octopus in the Island Clusters of Northern Sumatra. The blue dots show the sampling location

collection, brief interviews were conducted regarding the capture locations to validate the source of the octopus. The octopus was identified morphologically based on references and previous research journals (Balansada *et al*. 2019; Hutagaol *et al*. 2019), and identification guides (Jereb and Roper 2005). Subsequently, a total of 1 cm fragment of the tentacle was cut off by sterile scissors and stored in an extraction tube containing 96% ethanol for further laboratory analysis.

2.3. Molecular Analysis

2.3.1. Extraction

Molecular analysis was conducted to obtain DNA fragments from octopus samples. DNA extraction was performed using tentacle tissues, following a modified CTAB (Cetyltrimethyl Ammonium Bromide) protocol as described by Bakar *et al*. (2018). This protocol was chosen for its efficiency in isolating high-quality DNA from marine organisms, effectively removing contaminants such as proteins, polysaccharides, and secondary metabolites. The extracted DNA was subsequently quantified and assessed for purity using the NP80 Implen Nanophotometer (https://www.implen.de/) and visualized through gel electrophoresis to ensure its quality and integrity for downstream analyses.

2.3.2. Amplification

Amplification of the extracted DNA was carried out using PCR techniques with a forward primer (L1987:5′-GCCTCGCCTGTTTACCAAAAAC-3′) and a reverse primer (H2609:5′-CGGTCTGAACTCAGATCACGT-3′), as described by Palumbi *et al*. (1991). The PCR reaction was performed in a total volume of 25 µL, which included 2 µL of DNA template, 8.5 µL of double-distilled water (ddH$_2$O), 1 µL of each primer (forward and reverse), and 12.5 µL of Red Mix. The PCR was amplified in a SensoQuest gradient Thermal Cycler (https://www.sensoquest.de/). The PCR profile consisted of the following steps: an initial pre-denaturation at 95°C for 2 minutes, followed by 30 cycles of denaturation at 94°C for 30 seconds, annealing at 49°C for 30 seconds, and extension at 72°C for 55 seconds. A final extension step at 72°C for 2 minutes was included to ensure complete amplification of the target DNA fragments (Melis *et al*. 2018).

2.3.3. Electrophoresis and Sequencing

DNA visualization was performed using electrophoresis with a 1.7% agarose gel containing 2 µL of Nucleic Acid Gel Stain (GelRed®) Red Stain. The gel electrophoresis was carried out at 100 V for 30 minutes to separate the DNA fragments based on size. A molecular weight marker (DNA ladder) was included to estimate the size of the amplified DNA fragments. DNA bands were visualized using a UVITEC Firereader (https://www.uvitec.co.uk/). Successfully amplified DNA samples were excised from the gel, purified to remove any residual contaminants, and sent to First Base Malaysia for sequencing. Base sequence analysis was conducted using the Sanger method (Sanger *et al*. 1977), a widely used and reliable approach for obtaining high-quality DNA sequences. The resulting sequences were analyzed and compared to reference databases to confirm species identity and assess genetic variation.

2.4. Data Analysis

The COI gene sequencing results were aligned using the Mega X software (Tamura *et al*. 2013). Species similarity will be determined by comparing the sequences with databases available on BLAST (http://www.ncbi.nlm.nih.gov/BLAST) and BOLD (www.boldsystems.org). Genetic distances will be calculated based on the Kimura 2-parameter (K2P) model using Mega X (Tamura *et al*. 2013). Phylogenetic tree reconstruction will be performed using the Maximum Likelihood method with the Hasegawa-Kishino-Yano model, with 1000 bootstrap replications (Kimura 1980; Hasegawa *et al*. 1985; Kumar *et al*. 2022).

Molecular population structure analysis will be conducted using AMOVA (Excoffier *et al*. 1992), calculating haplotype diversity using DNAsp (Librado and Rozas 2009), and then calculating haplotype diversity (Hd), nucleotide diversity (π), and population structure using the Arlequin program (Schneider *et al*. 2000). Population structure analysis will measure genetic distance subdivision differences between populations using the Fixation index (Fst) and Chi-square probability tests for population differentiation, using 1000 permutations from data estimated with DNAsp (Hudson *et al*. 1992). Population connectivity will be analyzed using the Network application with the Median-Joining method (Bandelt *et al*. 1999). The average ocean current patterns for 2023-2024 will be analyzed using Pyferret software, which is used to average data based on depth and time and visualize current data (Haditiar *et al*. 2024). This data is expected to help explain the biogeographic relationships through larval dispersal and connectivity between populations.

3. Results

A total of 21 octopus samples were collected from each fish landing site. However, only 21 sequences were successfully amplified and could be further analyzed. Molecular identification results confirmed through BLAST on the NCBI website and BOLD SYSTEMS can be used to match the sequencing results with the existing GenBank database. The EValue obtained from the study showed 0.0, and the identity value was high, ranging from 99 to 100%.

3.1. Phylogenetic Tree Reconstruction of *Octopus cyanea*

The phylogenetic tree shown in the figure illustrates the evolutionary relationship between individuals or populations of *Octopus cyanea* based on genetic data (Figure 2). This tree was constructed using the Neighbor-Joining (NJ) analysis method with 1000 × bootstrap replicates to assess the reliability of the branches, showing the genetic proximity between sequences. The outgroups used were *Loligo vulgaris* and *Sepia officinalis* from different families, and *Octopus vulgaris* from the same family and genus. All sequences from the five populations were grouped into one large clade, indicating the close relationship among all the samples. Simeulue Island sequence showed a distinct subclade, which was also reflected by another sequence being grouped with the Nias Island population.

3.2. Genetic Diversity

The sequence analysis of *Octopus cyanea* using the COI locus involved 21 sequences with a nucleotide length of 651 bp (base pairs). Genetic diversity showed a range of values 0.285-0.800 with the lowest value coming from the Banyak Island population. The number of haplotypes found in 5 populations was 11, with the same dominant distribution for all populations (Table 1). The average nucleotide composition was as follows: (A) Adenine = 30-30.1%, (C) Cytosine = 19.4-19.6%, (T) Thymine = 35.5-35.7%, and (G) Guanine = 14.8-14.9% (Table 2). The average GC content was lower, at 17.25%, while the AT content was 32.8%. The GC content decreased from the first, second, and third codon positions.

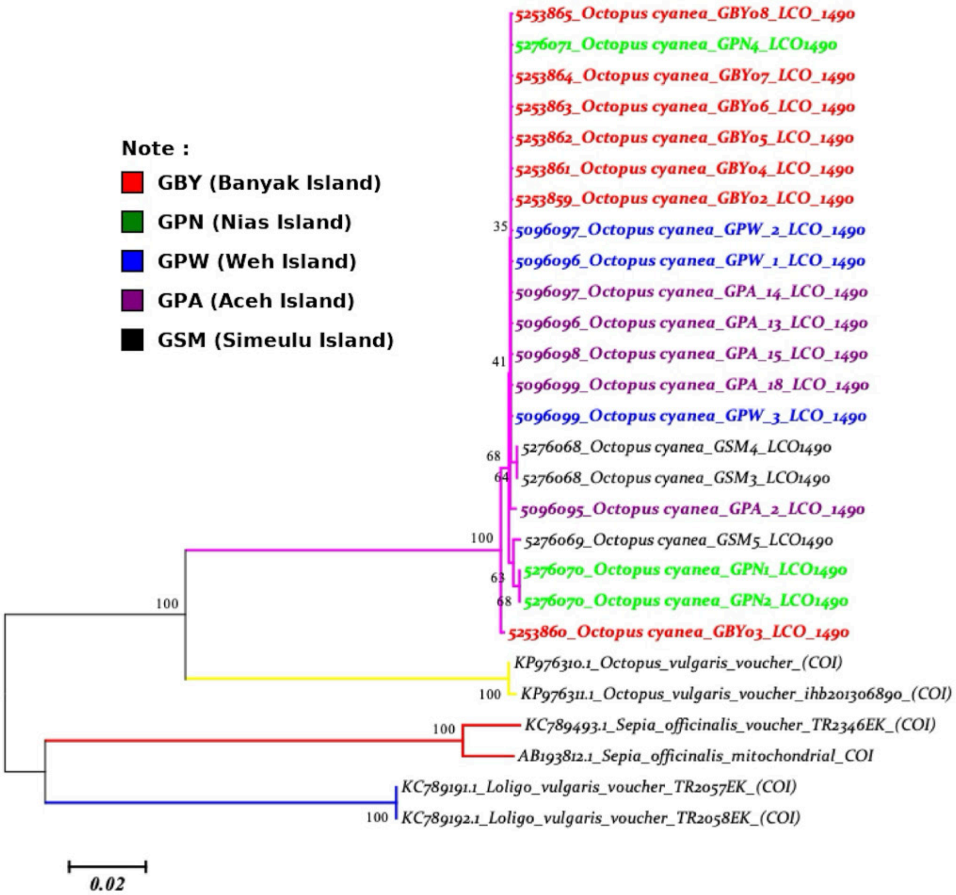

Figure 2. Phylogenetic tree of *Octopus cyanea* from five populations

3.3. Genetic Population Structure

The genetic distance calculation for the five populations ranged from 0 to 0.003 within populations and from 0 to 0.004 between populations. The population of Weh Island showed the lowest genetic distance, while Simeulu Island exhibited the highest genetic distance (Table 3). The pairwise distance test (Fst) for *Octopus cyanea* resulted in a value of 0.315, which is categorized as low (Table 4).

3.4. Haplotype Network and Population Connectivity

The haplotype network shows the genetic relationship between individuals in a population based on haplotype data. The dominant haplotype, Haplotype 1 (Hap 1), has the largest circle size, indicating that this haplotype is the most common among the populations analyzed. The haplotype diversity network shows seven haplotypes (Hap 1 to Hap 7), with some haplotypes being less frequently found (e.g., Hap 5 and Hap 6) (Figure 3).

The length of the red lines connecting the haplotypes represents the number of mutations or genetic differences between haplotypes. Haplotype pairs that are farther apart have more genetic differences. The color of the circles reflects the distribution of haplotypes at different locations (Figure 4). The pie charts at each location (Aceh Island, Weh Island, Banyak Island, Simeulu Island, Nias Island) show the proportion of haplotypes in each population. The distribution of haplotypes in the five populations is as follows: Aceh is dominated by Hap 1, Weh shows high haplotype diversity (Hap 1, Hap 2, Hap 4). Banyak Island is dominated by Haplotype 3, indicating local genetic differences. Simeulu Island and Nias Island show a combination of Haplotypes 1 and other haplotype.

4. Discussion

Octopus cyanea that were successfully amplified came from five populations spread across the waters of

Table 1. Genetic Diversity of *Octopus cyanea* in five populations

Population	N	Hd	II
Aceh Island	5	0.8	0.001
Weh Island	3	0.667	0.001
Banyak Island	7	0.285	0.009
Simeulu Island	3	0.667	0.003
Nias Island	3	0.667	0.002

Population	N	Hd	II	Hap
Aceh Island	5	0.8	0.001	3
Weh Island	3	0.667	0.001	2
Banyak Island	7	0.285	0.009	2
Simeulu Island	3	0.667	0.003	2
Nias Island	3	0.667	0.002	2

Table 2. Nucleotide composition of *Octopus cyanea* in five populations

Population	T (U)	C	A	G	Total
Aceh Island	35.5	19.6	30.0	14.9	628.6
Weh Island	35.5	19.6	30.1	14.9	628.3
Banyak Island	35.6	19.5	30.1	14.8	628.0
Simeulu Island	35.5	19.6	30.1	14.8	628.0
Nias Island	35.7	19.4	30.1	14.8	628.0

Table 3. Genetic distance of *Octopus cyanea* in five populations

Population	1	2	3	4	5
Aceh Island	0.001				
Weh Island	0.000	0.000			
Banyak Island	0.001	0.000	0.001		
Simeulu Island	0.002	0.002	0.003	0.003	
Nias Island	0.002	0.002	0.003	0.004	0.002

Table 4. Pairwise distance (Fst) of *Octopus cyanea* in five populations

Source of variation	d f	Value	Percentage of variation (%)
Among population	4	5.524	31.43
Within population	16	7.714	68.74
Total	20	13.238	100
FST			0.315

northern Sumatra. However, the number of sequences from each population was different, due to constraints in the sample amplification process. The parameters used in the reconstruction were Kimura 2 parameters (Tamura *et al.* 2013). This phylogenetic tree illustrates the genetic relationships among *Octopus cyanea* populations, showing that all sequences from the five populations clustered into a single major clade. Populations from Aceh Island, Weh Island, and Banyak Island exhibit genetic homogeneity, whereas Simeulue Island and Nias Island form distinct subclades, indicating higher genetic divergence. Overall, the phylogenetic tree shows that all populations are combined into one large clade, with several subclades including Simeulue Island and Nias Island. This subclade confirms the existence of different genetic variations between the populations of Nias Island and Simeulue Island. The visualization of this phylogenetic tree is in line with the genetic distance values between the five populations.

The range of genetic distance values of the five populations is 0-0.004. Based on these values, the most significant genetic distance was found between the populations of Nias Island and Simeulue Island (0.004). In contrast, the smallest distance was found between Weh Island and Aceh Island (0). Genetic distance values ranging from 0 to 1 indicate that the closer it is to 0, the closer the genetic relationship between populations. In general, the genetic distance values in all populations are relatively low, so it can be concluded that these populations have a very close kinship relationship with low genetic variation (Li *et al.* 2021). Genetic distance reflects the level of kinship between populations, where the smaller the genetic distance value, the more similar the genetic composition between populations. Geographic factors also affect the value of genetic distance (Antoro *et al.* 2006; Ramadhaniaty *et al.* 2023). Marine organisms that reproduce by producing many eggs and planktonic larvae can disperse long distances through extensive ocean currents (Ramadhaniaty *et al.* 2023; Ramadhaniaty *et al.* 2024). In addition, many adult organisms, such as nekton, often migrate across the ocean. Hence, marine organisms generally show low levels of genetic differentiation despite being distributed over large geographic areas, because ocean currents and the absence of physical barriers tend to favor gene flow (Bryan-Brown *et al.* 2017).

Genetic diversity (Hd) in *Octopus cyanea* populations from northern Sumatra reflects the genetic composition shaped by the species' adaptive capacity to cope with environmental pressures, including climate change, fishing intensity, and predation (Ord *et al.* 2023). Such variation has important implications for population persistence, as higher genetic diversity generally enhances adaptive capacity to environmental change (Frankham *et al.* 2014). In contrast, lower diversity can limit adaptive responses and increase the risk of local extinction. For instance, the Banyak Island population, with the lowest Hd (0.285), likely experiences restricted gene flow and a small population size. These conditions can accelerate the loss of rare alleles through genetic drift and reduce genetic diversity (Park & Xi 2021). Low

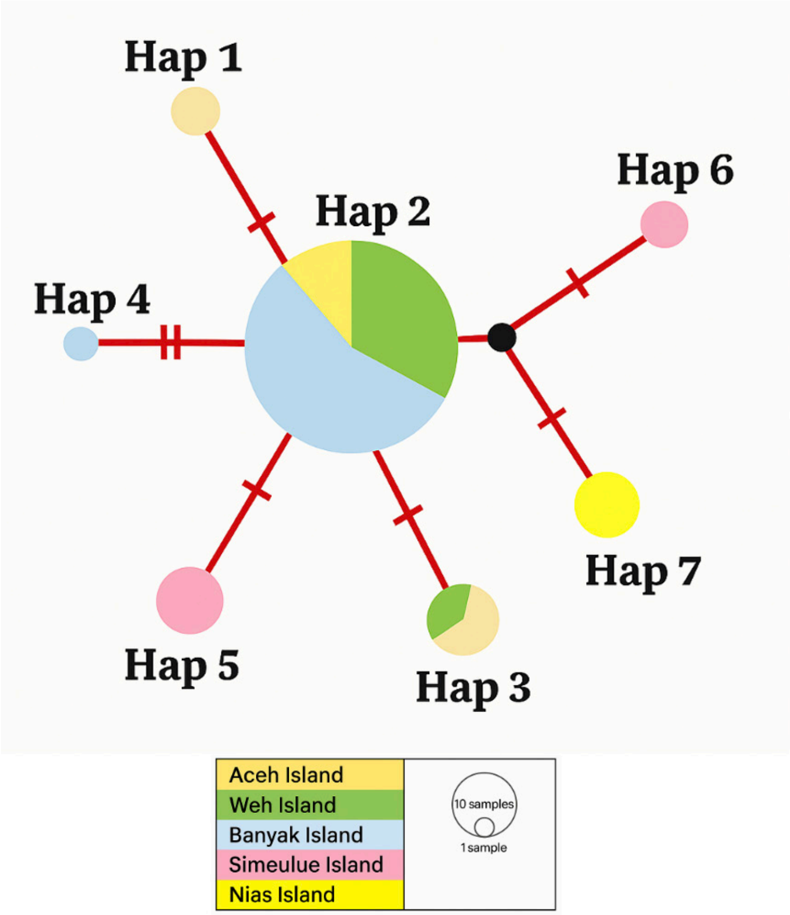

Figure 3. Haplotype network of *Octopus cyanea* from five populations

nucleotide diversity in specific populations reinforces the evidence of limited genetic variation, given the strong relationship between Hd and π as indicators of intraspecific variation (Petit-Marty *et al*. 2021). Genetic drift in small populations can rapidly erode genetic diversity, trigger inbreeding depression, and ultimately diminish adaptive potential. However, evolutionary models suggest that strong stabilizing selection may counteract drift and preserve adaptive variation even in small populations (Hedrick 1999).

The link between genetic diversity patterns and population structure is evident in the Fst value of 0.315, indicating that most genetic variation occurs within populations (68.74%) rather than among populations (31.43%). A relatively low Fst such as this reflects significant similarity among populations, suggesting that allele frequencies are largely homogeneous across sites. This pattern is typical in marine fish and invertebrates with planktonic larvae, where allele frequencies tend to remain uniform over large geographic areas (500-2000 km) due to larval dispersal (Cornwell *et al*. 2016). For *O. cyanea*, this low to moderate Fst highlights substantial inter-island genetic connectivity, consistent with the species' sedentary adult lifestyle combined with a planktonic larval stage that facilitates dispersal via ocean currents (Villanueva & Norman 2008; Treleven *et al*. 2024). Such homogeneity supports the management of these populations as a single stock unit. Nevertheless, local populations showing higher Fst values may still require targeted conservation strategies to maintain their unique genetic variation.

The pattern is further reflected in mitochondrial base composition, which shows dominance of adenine (A) and thymine (T) (30-30.1% and 35.5-35.7%) and a low GC content (17.25%). The high AT content in the *O. cyanea* sequence may indicate the influence of environmental adaptation or natural selection related to mitochondrial genome stability (Ramadhaniaty *et al*. 2018). The gradual decline in GC content from the first to the third codon position indicates selective pressure on codon usage, potentially influencing translational efficiency and molecular adaptation (Nakahigashi *et al*.

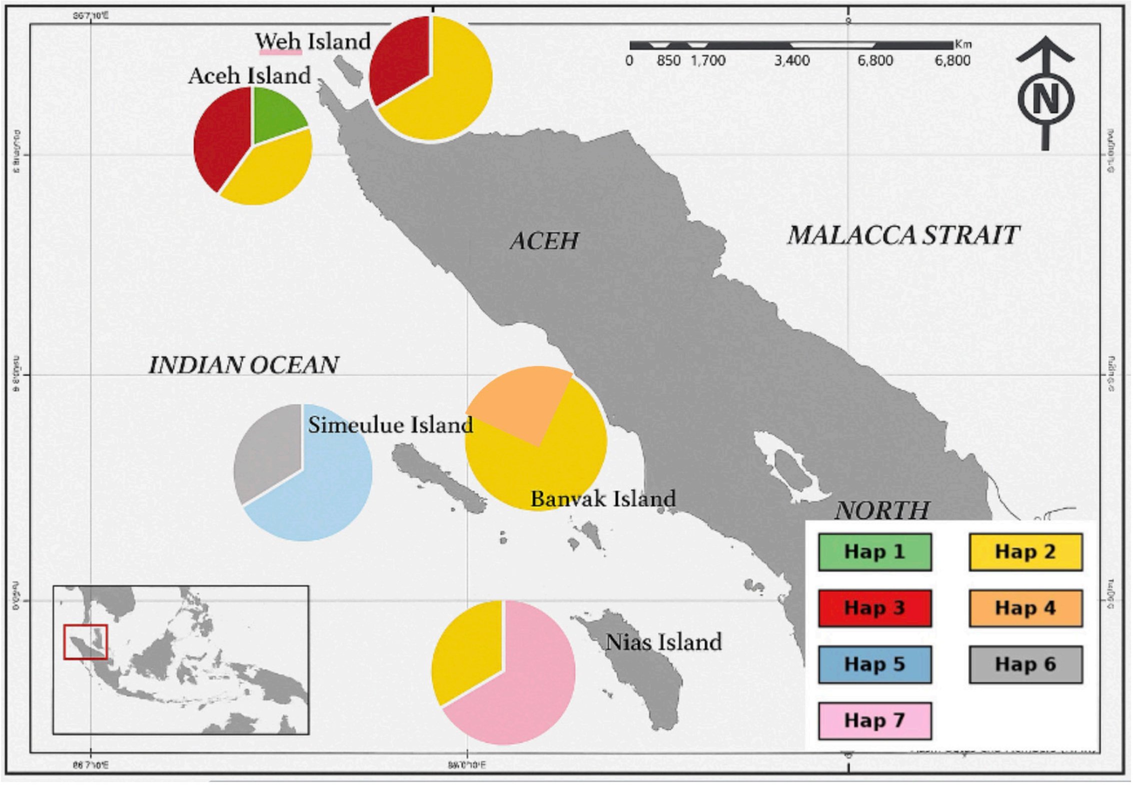

Figure 4. Population connectivity of *Octopus cyanea* from five populations

2014). Dominant AT content may also promote genetic homogeneity among populations through parallel or independent substitutions (Lopez-Marcano *et al*. 2021; Zhang *et al*. 2024). Overall, the genetic relationships between these populations can also be observed through the phylogenetic tree, which illustrates inter-population relationships and reveals both the strong connectivity and the limited genetic differentiation within *O. cyanea* populations in northern Sumatra, despite indications of gene isolation in specific subpopulations (Treleven *et al*. 2024).

The results of network analysis and connectivity maps show that the octopus's population on Island Simeulue does not share haplotypes with other populations. This finding indicates the presence of genetic or geographic barriers that limit gene flow between populations, as explained by Lopez-Marcano *et al*. (2021). Geographic isolation between islands, as evident in the distribution pattern on Island Simeulue, underscores the role of distance and physical barriers, such as ocean currents or habitat characteristics, in shaping the genetic patterns of this population (Bryan-Brown *et al*. 2017). This pattern is similar to that reported by Charles *et al*. (2024), which assumed different spawning times so that the recruitment process was periodic and varied, so that there was a gap between populations even though they were geographically close. In contrast, the other four populations had similarities in haplotype 2, while the populations on Aceh Island and Weh Island shared haplotype 3. This haplotype similarity can be attributed to the distribution of larvae, which allows gene transfer and inter-population mating, known as inbreeding. This process supports haplotype mixing, which results in increased genetic variation. Higher genetic variation is an essential element to maintain the adaptive capacity of species to various environmental pressures, such as climate change, human activities, or ecosystem dynamics. This high population connectivity is in line with research on *Octopus cyanea* in Tanzania (Treleven *et al*. 2024), where the relatively close geographical distance allows genetic interactions between populations. This factor is caused by octopus larvae that have a planktonic period of 30 days before settling, which makes their distribution range difficult to predict. As a result, genetic connectivity between populations in the surrounding area is high, even though there is a certain geographical isolation. The high genetic variation resulting from connectivity can provide evolutionary advantages to the population. Populations with higher genetic variation tend to have a better ability to adapt to environmental fluctuations, reducing the risk of extinction. In addition, this genetic connectivity pattern provides essential insights for various applications in marine science.

The results of connectivity and population structure analysis indicate that *Octopus cyanea* populations exhibit a relatively close genetic relationship. Although the Simeulue population shows the lowest genetic relatedness, it is still categorized as part of gene variation influenced by surrounding oceanic currents. These findings suggest that all populations along the northern waters of Sumatra can be managed as a shared stock. The life cycle of *Octopus cyanea*, which includes a larval phase, results in unpredictable geographic dispersal (Petit-Marty *et al*. 2021). Intensive fishing and extractive activities contribute to overfishing and stock depletion, allowing local populations to be replenished through recruitment from other populations. The high variability in stock abundance and migratory behavior poses significant challenges in the management of shared stocks. These share stocks play a crucial role not only in sustaining fisheries but also in mitigating the depletion of wild populations, which could lead to the extinction of *Octopus cyanea*, a species of high commercial value (Calò *et al*. 2013).

In conclusion, Species identification using DNA barcoding (COI gene) confirmed *Octopus cyanea* with a high similarity (99-100%) in the BLAST and BOLD SYSTEMS databases. The phylogenetic analysis revealed a single main clade with several subclades reflecting genetic differentiation among populations. Overall, populations from Aceh, Weh, and Banyak Islands showed high connectivity, indicating extensive gene flow likely facilitated by ocean currents and planktonic larval dispersal. In contrast, populations from Simeulue and Nias Islands exhibited apparent genetic isolation, suggesting restricted exchange with other islands. First analysis indicated a low to moderate population structure, with most of the genetic variation occurring within populations (68.74%). These results emphasize that while connectivity supports the concept of shared stock management among most populations, the isolation of Simeulue and Nias requires special consideration. Therefore, sustainable management of *O. cyanea* should combine strategies for shared stocks with targeted measures for isolated populations, ensuring both ecological resilience and protection against overexploitation.

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