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Genetic Diversity and Differentiation of Sand Crab (*Albunea symmysta*) (Crustacea: Decapoda: Hippoidea) from Java and Papua, Indonesia

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ABSTRACT

In Indonesia, the sand crab *Albunea symmysta* distribution includes Java, Sumatra, and Moluccas. Populations are assumed to be differentiated between western and eastern Indonesia due to the Wallace line; however, no information on the genetic diversity and differentiation of *A. symmysta* in Indonesia is available. This study was conducted to clarify the genetic diversity and differentiation of *A. symmysta* in Indonesia. During the sampling campaign, *A. symmysta* specimens were found only in Java and Papua. Genetic analysis based on the 643-bp fragment of the partial COI gene from 32 individuals revealed significant genetic differentiation between the Java and Papua populations (F_{ST} = 0.94, $p < 0.005$). The haplotype connectivity of the five *A. symmysta* sampling sites revealed a two-clade network. Based on analysis of molecular variance, most of the variation was found among populations (94.21%) rather than within populations (5.79%). Tajima's D and Fu's FS values indicated a population expansion. Overall, the findings support a high level of differentiation between the Java and Papua *A. symmysta* populations, suggesting the separation of population stocks due to low connectivity.

1. Introduction

The crab superfamily Hippoidea consists of three families: Hippidae, Blepharipodidae, and Albuneidae. Hippoid species spend part of their life cycle as pelagic larvae, with different species spending as little as 2 weeks (Stuck and Truesdale 1986) and up to 2–3 months (Knight 1970; Sastre 1990) in the pelagic larval stage. For instance, within the family Albuneidae, the larval development period lasts roughly 30 days (Rodrigues *et al.* 2020). The duration of the pelagic larval stage influences overall dispersal potential, geographic distribution, and connectivity among distant populations, as well as species' ecological, genetic, and evolutionary processes (Dawson *et al.* 2011; Sanvicente-Añorve *et al.* 2018).

The sand crab *Albunea symmysta* (family: Albuneidae) is distributed from the east coast of India throughout southwest Asia to Taiwan (Boyko 2010) and has also been found in Japan (Miyake *et al.* 1962) and Australia (Boyko 2002). In Indonesia, *A. symmysta* has been recorded in Moluccas (Boyko 2002), Sumatra, and Java (Mashar *et al.* 2015). Indonesia is an archipelago flanked by the Indian Ocean to the west and the Pacific Ocean to the east. Each ocean has distinct characteristics and currents (Mustikasari *et al.* 2015) that influence population connectivity within Indonesia. Although ocean currents may assist long-range dispersal and genetic homogeneity throughout ocean systems (Roberts 1997), currents have also been proven to inhibit larval dispersal and genetic connectivity (Jackson *et al.* 2014). A study on hippoid crabs (*Hippa ovalis*) in Indonesia (Putri *et al.* 2023) reported genetic mixing among populations in Sulawesi, Java, and Sumatra because the crabs could disperse over a vast area during their larval stage via ocean currents that connected the sampling areas. However, there are no studies on the genetic diversity and differentiation of *A. symmysta* in Indonesia.

In the present study, we investigated the genetic diversity and differentiation of *A. symmysta* in

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Indonesia using the partial cytochrome c oxidase subunit I (COI) gene. We analyzed samples from Java Island, representing the Indian Ocean population, and Papua Island, representing the Pacific Ocean population (Figure 1). We expected to observe patterns in the *A. symmysta* populations similar to those previously found for hippoid crabs in Indonesia.

2. Materials and Methods

2.1. Sample Collection

We performed haphazard sampling to collect A. symmysta specimens on Indonesian beaches in 2017–2022 (Table 1). The collected specimens were euthanized in 70% ethanol in the field and stored in 96% ethanol for long-term preservation. Specimen vouchers were deposited in the Animal Physiology and Function Laboratorium in the Department of Biology, IPB University (Dramaga, Indonesia).

2.2. DNA Extraction, Amplification, and Sequencing

Genomic DNA was extracted from each sample using a Tissue DNA Mini Kit (Geneaid Biotech, New Taipei City, Taiwan). A COI fragment was amplified using the primers and PCR conditions defined by Wardiatno *et al.* (2015). PCR product quality was assessed by agarose gel electrophoresis and FloroSafe DNA Stain and visualized using an ultraviolet transilluminator. Single, clear bands of PCR products were sent for Sanger sequencing to 1st Base, Singapore.

2.3. Data Analysis

Thirty-three partial COI sequences were obtained to generate multiple alignments of the edited sequences in MEGA 7 (Kumar *et al.* 2016).

Table 1. Information on the *Albunea symmysta* sampling sites in Indonesia

Site ID	Location	Number of specimens collected	Sampling date
1	Pelabuhan Ratu, West Java, Java Island	4	March 2019
2	Manokwari, West Papua, Papua Island	8	September 2020
3	Cilacap, Central Java, Java Island	10	October 2020
4	Carita, Banten, Java Island	5	July 2022
5	Jayapura, Papua, Papua Island	8	August 2022

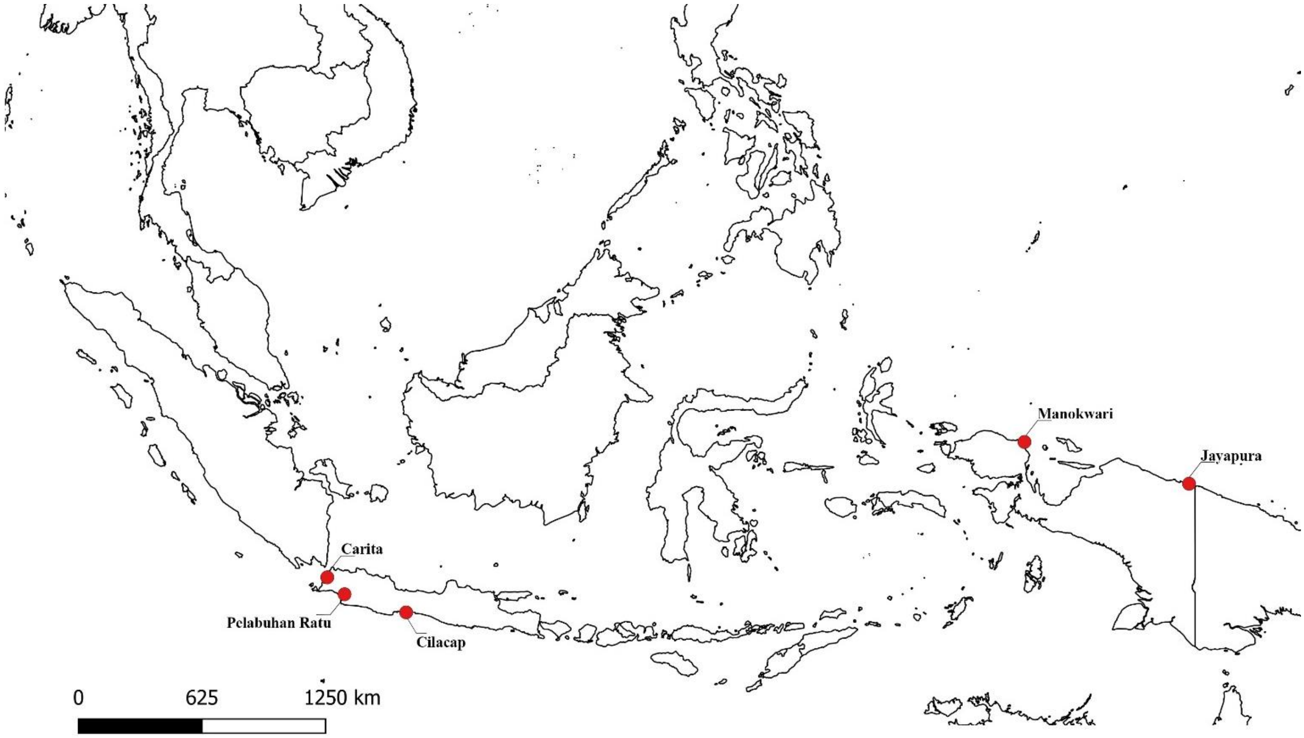

Figure 1. *Albunea symmysta* sampling locations in Java and Papua, Indonesia

Genetic distance was calculated using the Kimura two-parameter model in MEGA 7. The number of haplotypes (N*h*) and haplotype diversity (*Hd*) were analyzed using DnaSP ver. 6. Genetic diversity was determined from Nh, *Hd*, and nucleotide diversity (π) using DnaSP ver. 6 (Rozas *et al.* 2017). A median-joining network (Bandelt *et al.* 1999) was constructed in Network 10.2 (www.fluxusengineering.com) based on the haplotype data to investigate the phylogenetic relationships among haplotypes. The population structure was estimated using Wright's fixation index (F_{ST}) and analysis of molecular variance (AMOVA). Pairwise F_{ST} values were calculated as the genetic distance based on population differences, and population equilibrium was analyzed with Tajima's D (1989) and Fu's FS (1997) using Arlequin ver. 3.5 (Excoffier and Lischer 2010).

3. Results

We obtained 33 partial COI sequences approximately 643 bp in length from Java and Papua. From the obtained sequences, we identified 52 variable nucleotide sites and 16 haplotypes (Table 2). The Hd of all populations was high (mean = 0.89962), whereas the observed π was low (range: 0.001–0.003) (Table 3). The median-joining network revealed two clusters within *A. symmysta* separated by 37 mutational steps: one along the Indian Ocean coast of southern Java, and another along the Pacific Ocean coast of northern Papua (Figure 2). The pairwise F_{ST} values ranged from −0.04702 to 0.96914 across the populations (Table 4). The F_{ST} value for the *A. symmysta* populations used in this study is 0.94210, indicating segregating populations (Table 5).

Table 2. Nucleotide variation of *A. symmysta* haplotypes

ID	Haplotype	Position of nucleotide variants																	
		19	28	47	61	71	76	88	94	100	103	151	157	184	194	203	214	232	253
1	H 1	A	A	C	C	C	C	A	C	T	T	T	G	C	C	C	A	T	A
2	H 2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.
3	H 3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
4	H 4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
5	H 5	.	.	T	.	T	A	.	T	.	C	C	A	T	T	.	.	.	G
6	H 6	.	.	T	.	T	A	.	T	.	C	C	A	T	T	.	.	.	G
7	H 7	G	.	T	.	T	A	.	T	.	C	C	A	T	T	.	.	.	G
8	H 8	.	.	T	.	T	A	.	T	.	C	C	A	T	T	.	.	.	G
9	H 9	.	.	T	.	T	A	.	T	.	C	C	A	T	T	.	.	.	G
10	H 10	.	.	T	.	T	A	.	T	.	C	C	A	T	T	.	G	.	G
11	H 11	.	.	T	.	T	A	.	T	.	C	C	A	T	T	.	.	.	G
12	H 12	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.
13	H 13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	C	.
14	H 14	.	.	.	T	.	.	G	.	.	.	.	.	.	.	.	.	.	.
15	H 15	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.

Table 2. Continued

ID	Haplotype	Position of nucleotide variants																	
		259	263	265	295	301	307	310	316	331	334	337	349	352	364	367	376	385	415
1	H 1	A	C	A	G	G	G	G	G	A	T	T	A	A	C	T	A	T	G
2	H 2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
3	H 3	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.
4	H 4	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.
5	H 5	G	T	.	.	A	A	A	A	G	A	C	.	.	T	A	G	C	A
6	H 6	G	T	.	.	A	A	A	A	G	A	C	.	.	T	A	G	C	A
7	H 7	G	T	.	.	A	A	A	A	G	A	C	.	.	T	A	G	C	A
8	H 8	G	T	G	A	A	A	A	A	G	A	C	.	.	T	A	G	C	A
9	H 9	G	T	.	.	A	A	A	A	G	A	C	.	.	T	A	G	C	A
10	H 10	G	T	.	.	A	A	A	A	G	A	C	.	.	T	A	G	C	A
11	H 11	G	T	.	.	A	A	A	A	G	A	C	.	.	T	A	G	C	A
12	H 12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
13	H 13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
14	H 14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
15	H 15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 2. Continued

ID	Haplotype	Position of nucleotide variants															
		418	421	463	508	532	547	550	565	571	578	580	610	613	622	640	643
1	H 1	G	T	A	G	T	A	G	T	A	C	G	C	C	A	C	C
2	H 2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
3	H 3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
4	H 4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
5	H 5	A	A	G	A	C	T	A	A	G	T	A	T	T	G	A	.
6	H 6	.	A	G	A	C	T	A	A	G	T	A	T	T	G	G	.
7	H 7	.	A	G	A	C	T	A	A	G	T	A	T	T	G	G	.
8	H 8	.	A	G	A	C	T	A	A	G	T	A	T	T	G	A	.
9	H 9	.	A	G	A	C	T	A	A	G	T	A	T	T	G	A	.
10	H 10	.	A	G	A	C	T	A	A	G	T	A	T	T	G	G	.
11	H 11	A	A	G	A	C	T	A	A	G	T	A	T	T	G	A	T
12	H 12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
13	H 13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
14	H 14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
15	H 15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 3. Genetic diversity among Indonesian populations of *Albunea symmysta*

Population	n	N*h*	*Hd*	π	Tajima's *D*	Fu's F_S
Cilacap	10	4	0.711	0.001	−0.657	−0.657
Pelabuhan Ratu	4	3	0.833	0.001	0.592	0.592
Carita	5	5	1.000	0.003	−0.562	−0.562
Jayapura	6	4	0.800	0.003	−0.826	−0.826
Manokwari	8	5	0.857	0.002	0.283	0.283

N: number of samples, N*h*: number of haplotypes, *Hd*, haplotype diversity, π: nucleotide diversity, *significant at p<0.05

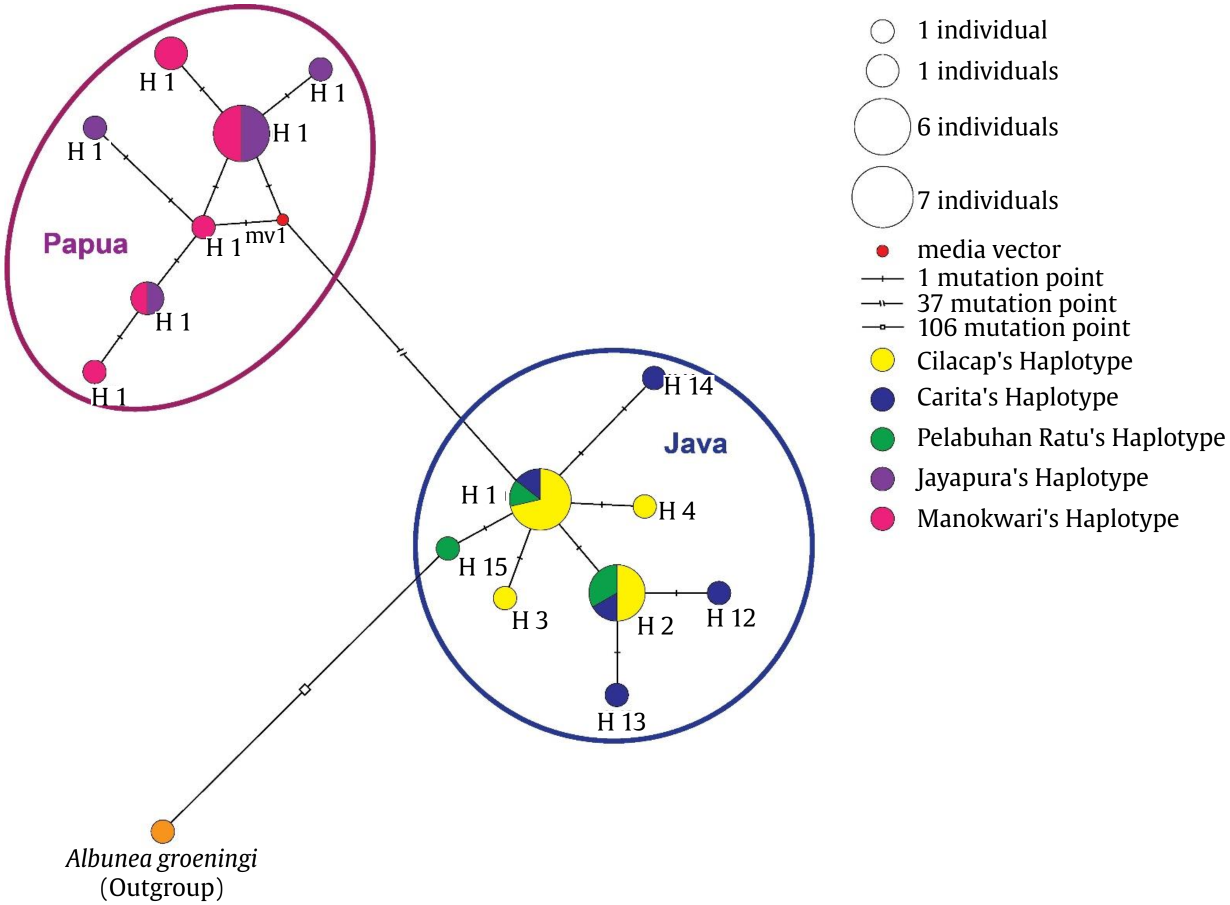

Figure 2. Haplotype network of *Albunea symmysta* in Papua and Java, Indonesia

Table 4. Pairwise FST values between *Albunea symmysta* populations from five locations in Indonesia

	Cilacap	Pelabuhan Ratu	Carita	Jayapura	Manokwari
Cilacap	–				
Pelabuhan Ratu	−0.04702	–			
Carita	0.05789	−0.10215	–		
Jayapura	0.96867*	0.95936*	0.94970*	–	
Manokwari	0.96914*	0.96197*	0.95383*	−0.05024	–

*significant at p<0.05

Table 5. Analysis of molecular variance based on *Albunea symmysta* haplotype frequencies

Source of variation	df	Variation (%)	F_{ST}	p
Among population	4	94.21	0.94210	0.00
Within population	28	5.79		
Total	34			

The haplotype network revealed recent demographic processes; however, the small sample sizes limited our ability to observe intermediate haplotypes, which were inferred to exist in the network. Moreover, while the Tajima's D and Fu's FS values were suggestive of population expansion, they were not significant; we suspect that the lack of significance was the result of the small sample size.

4. Discussion

Our result showed the Hd of all populations was high, whereas the observed π was low indicated that the *A. symmysta* populations experienced a bottleneck followed by rapid population growth and accumulation of mutations (Grant and Bowen 1998). The F_{ST} value between Java and Papua population approaches 1, indicating high genetic differentiation. When F_{ST} = 0, there is no differentiation between populations, whereas F_{ST} = 1 indicates complete differentiation (Bird *et al.* 2017). The F_{ST} value between Java and Papua population suggested marked differentiation between these two populations. The high subdivision between the Indian Ocean and Pacific Ocean populations supported the haplotype network results. These findings support high genetic differentiation and low population connectivity in *A. symmysta* in Indonesia. Overall, the relationship patterns at the mitochondrial DNA level indicated complex geographical structure; this might be due to separation of the Java and Papua populations.

Java Island is part of the Sunda Shelf and is surrounded by the Indian Ocean, whereas Papua Island is part of the Sahul Shelf and is surrounded by the Pacific Ocean. During the Pleistocene, a sea level drop of up to 130 m exposed the Sunda and Sahul shelves, which restricted waterways within the Indonesian archipelago and isolated Indo-Pacific marine populations (Voris 2000). Our study finding demonstrate that there are separations of Java (representing the Indian Ocean) and Papua (representing the Pacific Ocean) populations of *A. symmysta*. This finding aligns with the broader investigation into the genetic divergence and population distribution patterns of pelagic fishes across eastern and western Indonesia. The study focuses on understanding the potential influence of geographical features such as ocean current i.e. Halmahera and Mindanao Eddy (Figure 3), tectonic activity and sea level changes in pelagic larval retention in eastern Indonesia, as previously investigated by Jackson *et al.* (2014). The observed genetic divergence between eastern and western Indonesia is not exclusive to pelagic fishes, as demonstrated in crustacean species like the fiddler crab, *Austruca perplexa*, with a specific emphasis on the impact of the Indonesian Throughflow as a potential barrier to gene flow (Hardianto *et al.* 2022). This phenomenon extends beyond *A. perplexa*, as similar observations have been made in other marine species such as the giant tiger prawn *Penaus monodon* (Benzie *et al.* 2002) and the planktonic shrimp *Lucifer hanseni* (Noblezada *et al.* 2017). Furthermore, the documented separation of population distributions along the Wallace Line holds true for various marine species with large ranges throughout the Indo-Australian Archipelago, as reported in studies by Barber *et al.* (2000) and Lohman *et al.* (2011). Collectively, these studies shed light on the intricate interplay of geographic and oceanographic factors in shaping the genetic diversity and population structures of marine species in this region.

In *A. symmysta*, a low abundance and relatively short pelagic larval duration likely influenced the

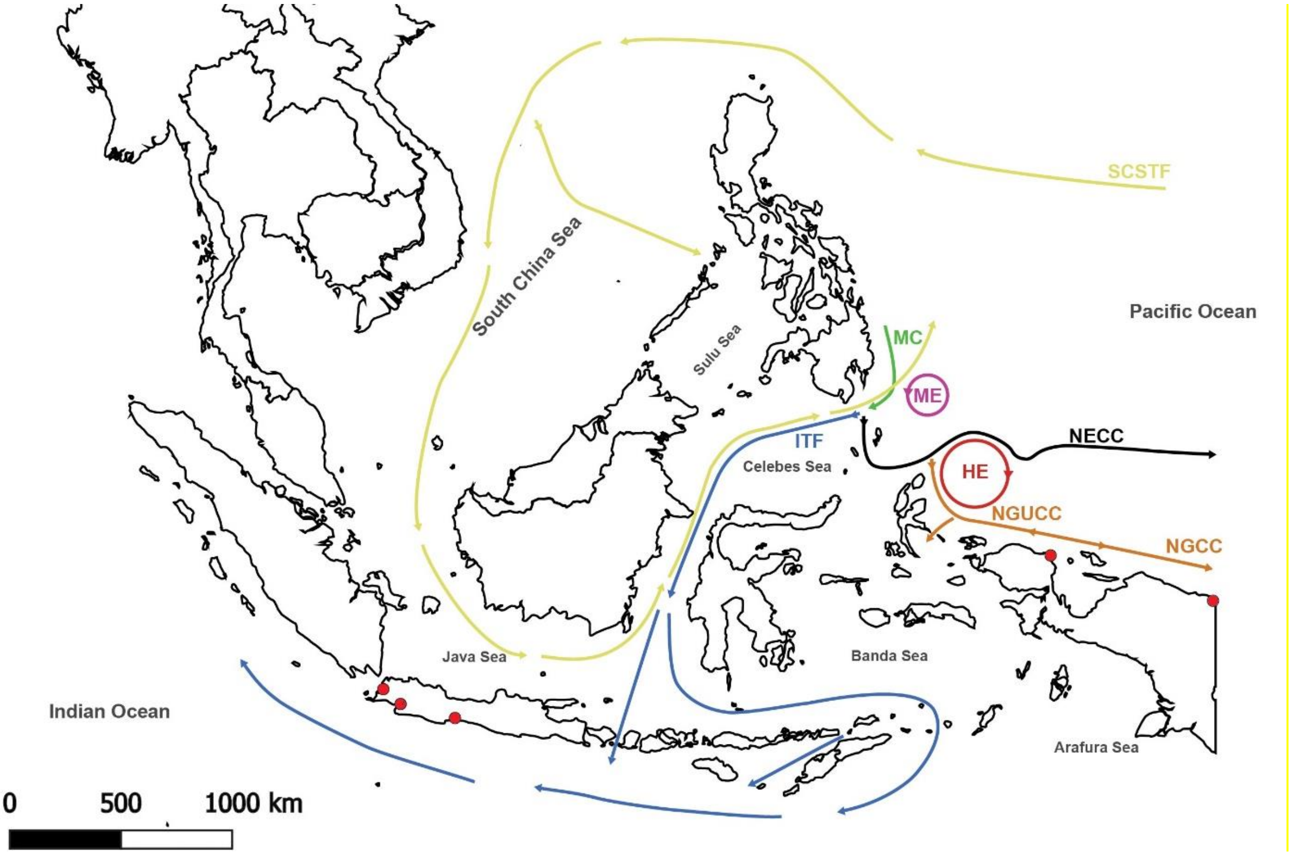

Figure 3. Map of ocean currents around Indonesia. ITF, Indonesian Through Flow; MC, Mindanao Current; NECC, North Equatorial Counter Current; NGCC, New Guinea Coastal Current; NGUCC, New Guinea Undercurrent (Fine *et al.* 1994; Makarim *et al.* 2019)

high differentiation and lack of genetic mixing between southern Java and northern Papua. Supporting this, Mashar *et al.* (2014) recorded a low abundance of *A. symmysta* (one specimen per 100 m^2). Furthermore, the period of time that larvae of marine species spend in the open ocean is thought to influence gene flow (Hedgecock *et al.* 2007); however, the pelagic larva duration of *A. symmysta* is expected to be shorter than that of other hippoid crabs. For instance, *Hippa* spp. have a pelagic larva duration of 50~80 days (Hanson 1969), which may explain why *Hippa ovalis* did not shows there are separation of population due to geographical structure (Putri *et al.* 2023), unlike *A. symmysta* in the present study.

The results of this study contribute to resolving the genetic diversity, differentiation, and distribution patterns of *A. symmysta* in Indonesia. Our findings strongly indicate the potential for population segregation between *A. symmysta* from Java and Papua, as supported by our results, likely attributed to larval retention influenced by geographical structures and its short pelagic larval duration. To enhance our comprehension of *A. symmysta*, future research endeavors should employ advanced population genetic analyses and broaden the geographic sampling scope across Indonesia.

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