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Research Article

The Genetic Diversity of Bali Sardinella (*Sardinella lemuru*) Caught at Bali Strait and Its Possible Relation to The Ocean Circulation

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Abstract

Sardinella lemuru is known as the native pelagic fish of the Bali Strait. However, its presence has recently become challenging to find. This study aimed to validate *S. lemuru* using molecular taxonomy and link it to water circulations for sustainable management. It is the first study of relatively complete sequence data on *S. lemuru* in the Bali Strait. A total of 47 sequences were amplified using the control region gene of mitochondrial DNA. Other *S. lemuru (n = 4) and Amblygaster sirm* (n = 12) sequences were retrieved from GenBank. Low sequence divergence is observed in clade-1 of *S. lemuru* across the Bali Strait, Manado-Sulawesi, and Kudat-Malaysia. This is probably due to its migration using the main Indonesian ThroughFlow (ITF). There is an evolutionary divergence between two groups of *S. lemurs,* measuring 35.3%±4.1. The first signs of these cryptic groups were found at Canggu and Prigi, with 87 base-pair differences between the two groups. This study also presents strong evidence that *A. sirm* prefers overlapping water mass conditions with *S. lemuru* in the Bali Strait but is morphologically and genetically distinct. Notably, three samples of *A. sirm* in Kedonganan-Bali are clustered with other *A. sirm* locations passed by the primary and secondary South China Sea throughflow. The high genetic diversity of *S. lemuru* among Bali Strait sites demonstrates its adaptive ability, with scattered single-frequency haplotypes. The adaptive ability traits of *S. lemuru* support its stock recovery. The stock recovery recommendation is based on finding *S. lemuru's* adaptive traits within their populations in suitable habitats and climatic conditions.

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1. Introduction

The Bali Strait is between Java and the Bali Islands of Indonesia, directly connected to the Java Sea in the north and the Indian Ocean in the south. The Bali Strait is well-known as fertile water due to the intensity of the upwelling process. As a result, it becomes a suitable habitat for pelagic fish (Himelda *et al*., 2011; Pranowo and Realino, 2006; Sartimbul *et al*., 2010; Suniada and Susilo, 2017; Wujdi *et al*., 2012), such as Bali Sardinella (*Sardinella lemuru* Bleeker 1853) (Himelda *et al*., 2011).

Bali Sardinella has high economic value for the people around the Bali Strait. They like to consume this fish due to its high nutritional value (Omega-3) and affordable cost (Arifan and Wikanta, 2011; Khoddami *et al*., 2009; Mahrus *et al*., 2012). The high demand for this commodity is a valuable source of income for seiners around the Bali Strait. In 1998, *S. lemuru* made a very high contribution of 98% to the total catch of the purse seine fleet in the Bali Strait. However, the production volume of *S. lemuru* fluctuates every year. The catch proportion of *S. lemuru* experienced the lowest production volumes (10–20% of the total catch) at the Bali Strait (Sartimbul *et al*., 2018b) in 2011-2012. This lowest production directly resulted from the excessive exploitation of *S. lemuru* resources in the Bali Strait (Buchary, 2010). In 2009, the maximum utilization rate of *S. lemuru* resources reached 105% per year (overexploited) (Setyohadi, 2009). Furthermore, an unusual trend in sea surface temperature and chlorophyll-a was found (Wijaya *et al*., 2020; Sambah *et al*., 2021a, 2021b) due to climate change, such as the El Niño Southern Oscillation (ENSO) (Hendiarti *et al*., 2005; Buchary, 2010; Sartimbul *et al*., 2010). The over exploitation and climate change impact make it necessary to have proper and sustainable management of *S. lemuru* in the Bali Strait.

Stock-based management is believed to be a crucial management concept in fisheries stock man agement efforts (Afifah *et al*., 2020; Hüssy *et al*., 2016). A lack of information on stocks can lead to failure in management and unsustainable use (Papasotiropoulos *et al*., 2007; Saeidi *et al*., 2014). Estimating fish stocks can be done through genetic diversity analysis (Hadi *et al*., 2020; Madduppa *et al*., 2021). Genetic diversity is causally related to fish resources and environmental conditions (Bramandito *et al*., 2018; Putri *et al*., 2022). Populations with large numbers tend to have higher genetic diversity than small populations (Hughes *et al*., 2008; Markert *et al*., 2010; Scribner *et al*., 2016). Nucleotide base substitution can have a lot of different outcomes depending on where the animal lives. For example, *S. lemuru* lives in the southern waters of East Java (Prigi-Trenggalek) and the coastal waters of Bali (Canggu). This happened because the *S. lemuru* population was mixed with another population of *S. lemuru* in Philippine waters (Winata *et al*., 2022; Sartimbul *et al*., 2023a).

Good quality data on the genetic diversity of the fish population is based on the same species. However, the term "*lemuru*" in Indonesia was used to address several species of sardines (Burhanuddin *et al*., 1974). In the annual publication of Indonesian Fisheries Statistics, "*lemuru*" consists of *Sardinella lemuru*, *S. longiceps* Valenciennes 1847, and *S. aurita* Valenciennes 1847 (Merta *et al*., 2000). Sardine is also attached to several species of the genus *Amblygaster* Bleeker 1849, which are closely related to the genus *Sardinella* Valenciennes 1847, such as *Amblygaster clupeoides* Bleeker 1849, *A. leiogaster* Valenciennes 1847, and *A. sirm* Walbaum 1792 (Carpenter and Niem, 1999). These species have very similar morphological features; therefore, they are routinely misidentified. Therefore, phylogenetics of sardine species caught in the Bali Strait is needed before genetic diversity analysis is done. A control region in mitochondrial DNA (mtDNA) can be used in genetic population analysis to find sequence divergence. This is because it is a non-coding area of mtDNA (Irmawati, 2016; Saeidi *et al*., 2014). The control region in mtDNA has a high degree of polymorphism. In addition, its mutation rate is faster than that of other loci segments, causing its nucleotide base arrangement to vary highly between individuals. This control region locus is appropriate for population genetic diversity analysis (Parker *et al*., 1998; Nicholls and Minczuk, 2014).

The largest *S. lemuru* fishing grounds around the Bali Strait are Kedonganan and Muncar waters, with Canggu waters serving as its seasonal catch peak during the southeast monsoon season. The study of the control region of mtDNA as a marker for sequence divergence of the *S. lemuru* population is still relatively limited in the Bali strait. All previous studies focused on partial data on morphological and genetic identification and population (Willette and Santos, 2013; Luceño *et al*., 2014). It is important to not lose the unique differences between species and mistakenly label *S. lemuru* as belonging to the genus Sardinella (*A. sirm*), which would lead to uncertainty about the fish stock. Hence, the research aimed to genetically determine the type of sardine with morphological characteristics identical to those of *S. lemuru*, especially caught at the fishing grounds of Kedonganan-Bali. Comparative genetic specimens were also collected in Muncar and Canggu waters (within the Bali Strait). Furthermore, several genetic diversity studies have also shown the role of ocean currents in reinforcing lineage divergence (Jackson *et al*., 2014). Not only have marine populations proven more closed than initially expected, but evidence has emerged to suggest that currents can inhibit larval dispersal and genetic connectivity (Ackiss *et al*., 2013; Labrador *et al*., 2022; Pata and Yñiguez, 2019). However, ocean currents can also help interconnected marine systems achieve genetic homogeneity and long-distance dispersal (Chan *et al*., 2013; Pedrosa-Gerasmio *et al*., 2015). To our knowledge, very few studies have been conducted concerning the migration route of biota through Indonesian ThroughFlow (ITF) will maintain its nucleotide variation between northern and southern latitudes (Sartimbul *et al*., 2023a; Wainwright *et al*., 2024). Measuring seawater-masses circulation, haplotype diversity, and its implications for Sardinella is an essential procedure in the scientific study of species.

The result of this study is expected to determine their genetic distance and diversity. Another expected result was that the phylogenetic tree of *S. lemuru* from the Bali Strait was linked to *S. lemuru* from other aquatic habitats, such as Kudat, Malaysia, and Manado, Indonesia. This was followed by a study of the genetic diversity of *S. lemuru*, especially at the three sites in the Bali Strait and including sequences from *S. lemuru* found in southern East Java (Prigi). Outgroup species sequences in the tree were retrieved from GenBank and isolated from the Lombok Strait, Taiwan Waters, and the Andaman Sea. Modeling of oceanographic conditions and circulation was carried out to answer the possible relationship between the genetic connectivity of Bali Strait Sardinella specimens with other waters supported by circulation and the characteristics of water masses across waters. This study addresses a current research gap related to the complete sequence data of *S. lemuru* based on higher polymorphism markers. It provides a relatively longer and relatively new sequence of control region markers of *S. lemuru* than previous studies of *S. lemuru* in Philippines waters (Labrador *et al*., 2021; Pedrosa-Gerasmio *et al*., 2015). This approach will be a foundation for future studies in Bali Strait.

2. Materials and Methods

2.1 Materials

2.1.1 The equipments

The equipment used in this study included an incubator bacteria (MCO-5AC, Panasonic, USA), 2720 thermocycler (Applied Biosystems, Veriti), gel electrophoresis unit with power supply, DNA imaging system using DNAzure® Blue Nucleic Acid Gel Stain (Biotium, USA), refrigerated centrifuge, precision micropipettes (Eppendorf, Germany), insulated cooler boxes, and computers equipped with MEGA11, DnaSP v6.12.03, NETWORK v10.2.0.0, PAST 3.1, MATLAB, and Ocean Data View software.

2.1.2 The materials

The materials used were 95% ethanol (Smartlab, Germany), Chelex 10% resin, dNTPs (8 mM), $MgCl_2$ (25 mM), 10X PCR Buffer, Amplitaq DNA Polymerase (ThermoFisher Scientific, 5 U/µL), agarose gel 1% (Promega, USA), CR primers (CRK and CRE), DNA ladder, TE buffer, ddH_2O, and 1.6 mL Eppendorf tubes.

2.1.3 Ethical approval

This experiment was performed based on approval by the laboratory animals using the research ethics committee of the faculty of veterinary medicine [4387/UN10.F6/TU/2024], Universitas Brawijaya, Indonesia.

2.2 Methods

2.2.1 Morphological Identification

Since multiple institutions collaborated on this project, no special permits were needed for sampling. *S. lemuru* specimens were collected during the southeast monsoon and the second transitional inter-monsoon season in 2019 (June-August and September-October, respectively) at Bali-Indonesia (i.e., Kedonganan fishing ground and Canggu fishing ground). At Kedonganan, two-boat system purse seiners caught *S. lemuru*, and at Canggu a small beach trawl operated by one diver caught *S. lemuru* (Figure 1). We used a two-boat system of purse seiners to collect *S. lemuru* specimens at the Muncar fishing ground in June 2017 (Figure 1). Artisanal fishermen only catch fish in waters 22–25 km from fishing ports because of their small boats, limited refrigeration, and expensive fuel costs. We will consider this spatial range surrounding fishing ports as distinct sampling locations for subsequent analyses. Notably, the average fish caught by fishermen who landed at the Kedonganan Fish Landing originates from around the Waters of Jimbaran Hills and the southern part of the Bali Strait (Figure 1). The fishing activity in Kedonganan waters is unique because the fishing grounds are very close and only take one night trip to the Kedonganan Landing Site (Rini *et al*., 2017).

We collected specimens that had been previously identified morphologically as *S. lemuru*. La beled specimens of *S. lemuru* are placed inside insulated cooler boxes to extend cold chain times. In this

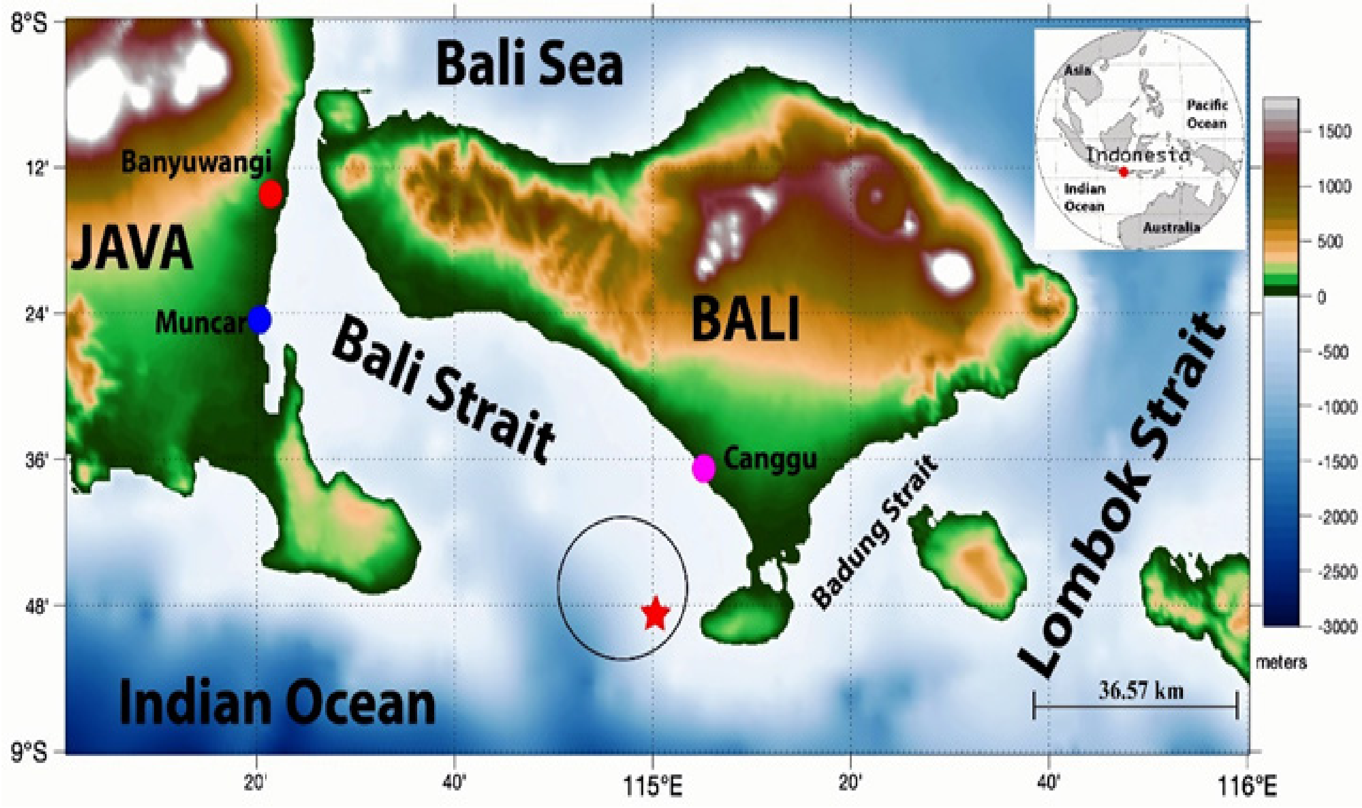

Figure 1. Map of the Bali Strait showing the fishing grounds area of *S. lemuru* at the Waters of Jimbaran Hills (black circle) and the Kedonganan (KD) sampling site (*). Moreover, other sites are located at Canggu (CGU) and Muncar (MCR).

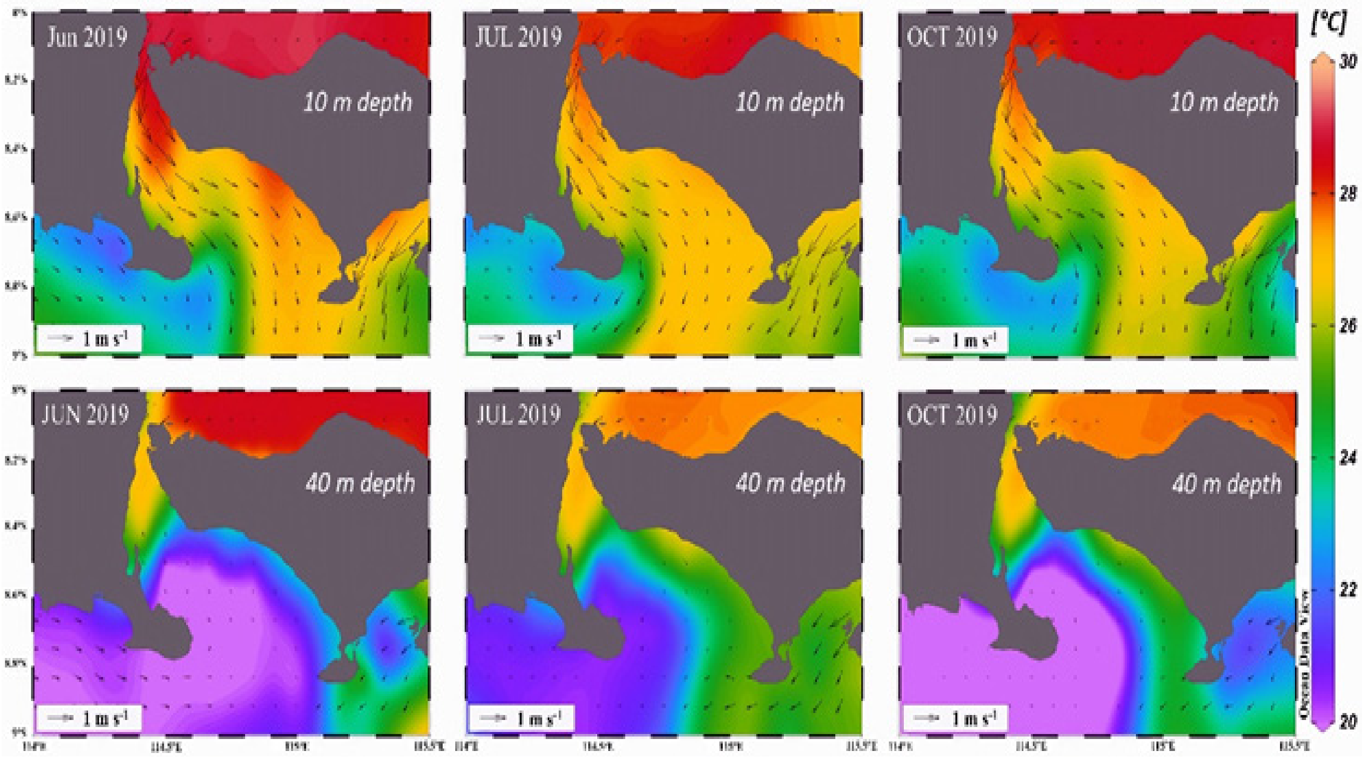

Figure 2. Ocean temperature (color) overlaid with current (arrows) at a depth of 10 meters (top panels) and 40 meters (bottom panels) during June, July, and October 2019.

study, the total number of samples collected was 47 individuals, which were distributed in 2017 and 2019. The forty individuals in Canggu and Kedonganan within several months in 2019 comprise June (n = 7), July (n = 12), August (n = 10), September (n = 5), and October (n = 6). Moreover, seven other specimens were caught at Muncar.

Table 1. Morphometric characteristics of *Sardinella* specimens caught at Kedonganan Fishing Grounds (KD2019).

No. ID	TL	SL/ TL^{d}	FL/ TL^{d}	PAL/ TL^{d}	PDL/ TL^{d}	PVL/ TL^{d}	PPL/ TL^{d}	BD/ TL^{d}	HdL/ TL^{d}	Eye/ HL^{d}	POL/ HL^{d}	RC
SL108	22.4	85.7	89.8	63.1	36.3	43.5	22.3	21.3	18.4	22.9	30.2	2.5
SL109	19.4	85.8	89.9	63.3	36.5	43.1	22.3	21.3	18.9	22.6	30.2	2.4
SL110	19.7	85.6	89.3	64.6	36.3	42.3	22.6	21.7	18.9	22.2	30.9	2.5
SL111	19.5	85.7	89.9	64.0	36.4	42.2	23.3	21.1	18.9	22.6	30.5	2.1
SL112	20.3	85.7	89.8	63.4	36.3	43.9	22.4	21.3	19.0	22.2	30.7	2.5
SL113	21	85.7	90.0	63.6	36.9	44.0	22.8	21.1	19.0	22.8	30.1	2.6
SL114	21.5	86.0	89.2	63.7	36.5	43.5	22.2	21.7	18.9	22.8	29.8	2.6
SL115	19.9	86.0	89.8	64.4	36.9	43.0	22.5	21.8	18.1	22.8	29.6	2.4
SL116	20.4	85.7	89.5	63.8	36.8	43.4	22.0	21.5	18.7	22.2	30.2	2.5
SL117	20.7	85.7	89.9	63.8	37.1	43.5	22.2	22.1	18.1	22.9	30.4	2.6
SL118	20.3	86.0	89.2	63.5	36.9	43.5	22.3	21.5	18.9	21.9	29.9	2.3
SL119	13.2	85.7	89.7	63.9	36.7	42.9	22.4	21.7	18.4	22.8	29.9	2.4
SL120	13.7	85.8	89.2	63.4	36.8	42.8	23.0	21.0	19.0	22.0	29.4	2.5
SL121	13	85.6	89.7	64.1	36.7	42.8	22.7	21.9	18.5	21.8	30.0	2.5
SL122	12.8	85.7	89.8	63.6	37.0	42.9	22.9	21.4	18.6	22.2	30.1	2.5
SL123	12.3	85.9	89.8	63.5	35.6	43.1	22.2	21.4	18.7	22.7	30.6	2.4
SL124	12.9	86.0	88.3	63.6	36.5	43.0	22.0	21.3	18.9	22.5	30.2	2.6
SL125	19.1	85.3	91.4	66.3	39.6	42.9	18.6	17.8	19.2	28.1	32.2	1.6
SL126	22.6	85.1	90.8	66.1	40.2	43.3	18.4	17.3	19.2	28.6	32.4	1.7
SL127	22.3	85.6	91.4	65.2	39.8	39.2	18.2	17.0	19.2	28.1	32.4	1.7

Description: No. (ID, sample code), SL108-SL118 and SL125-SL127 (southeast monsoon: June, July), SL119-SL124 (second transitional inter-monsoon season: October), d (the measured ratio from a specific body part length), and RC (ratio aspect of caudal fin).

The following morphological characteristics were measured on labeled specimens: total length (TL), forked length (FL), standard length (SL), pre-anal length (PAL), predorsal length (PDL), pre-ventral length (PVL), pre-pectoral length (PPL), body depth (BD), head length (HL), eye diameter (EyeL), pre-orbital length (pre-OrbL) (Sartimbul *et al.*, 2018a). In addition, the identification of meristic features and other supporting morphological markers are caudal fin ratio, number of fin spines, or rays of each fin were based on Sartimbul *et al.* (2018a) and Froese and Pauly (2024). We calculated the similarity index value based on several morphometric and meristic ratios (i.e., Kedonganan specimens) for morphological identification. We used PAST 3.1 software (Hammer *et al.*, 2001) for similarity index analysis based on the clustering method with Bray-Curtis similarity index coefficient (Bray and Curtis, 1957), with bootstrap 1000 iterations.

2.2.2 Extraction, PCR, electrophoresis, and sequencing

We stored the pectoral fin with attached muscle tissue samples in 1.6 mL Eppendorf tubes containing 95% ethanol (Smartlab, Germany). We extracted genomic DNA from tissue samples using the Chelex 10% protocol (Walsh *et al.*, 2013). We then amplified a 400 – 800 base pair (bp) of mtDNA fragments at the control region (CR) locus with the PCR method using forward primer (CRK: 5'-AGC TCA GCG CCA GAG CGC CGG TCT TGT AAA – 3') and reverse primer (CRE: 5' – CCT GAA GTA GGA ACC AGA TG – 3') (Lee *et al.*, 1995; Pertiwi *et al.*, 2015). The Polymerase Chain Reaction (PCR) was geared to a final volume of 25 µL containing 1.25 µL of CRK (10 µM), 1.25 µL CRE primer (10 µM), 2.5 µL of dNTPs (8 mM), 0.125 µL of Amplitaq DNA Polymerase (ThermoFisher Scientific, 5 U/µL), 14.5 µL of ddH2O, 2 µL of $MgCl_2$ (25 mM), 2.5 µL of 10X PCR Buffer, and modifications to the template DNA volume of 2 µL (Allen *et al.*, 2017). The reactions were run in a 2720 thermocycler (Applied Biosystems, USA) with initial denaturation at 94°C for 15 seconds, followed by 38 cycles of denaturation at 94°C for 30 seconds, annealing at 50°C for 30 seconds, extension at 72°C for 45 seconds, and final extension at 72°C for 5 minutes at the end of the 38th cycle. The results of PCR amplification products were seen visually using the electrophoresis method with 1% agarose gel (Promega, USA) and DNAzure® Blue Nucleic Acid Gel Stain (Biotium, USA). We sequenced the purified PCR products using the Sanger method (Sanger *et al.*, 1977) at the DNA Sequencing Facility, Genetika Science Indonesia, Jakarta. The CR mtDNA sequences for *S. lemuru* caught at three sites in the Bali Strait were deposited in GenBank with the following accession numbers: ON843782-ON843825. We also sequenced *A. sirm*, a species that is closely related to *S. lemuru* and was found in Kedonganan-Bali. The GenBank accession numbers for these species are ON843826–ON843828.

2.3 Analysis data

2.3.1 Molecular identification and genetic diversity

We obtained CR sequences mtDNA from *Sardinella* specimens of Bali Strait collected at Kedonganan in 2019 (n = 20), Canggu in 2019 (n = 20), and Muncar in 2017 (n = 7). We retrieved additional CR sequences of *S. lemuru* (n = 4) with several NCBI accession numbers (i.e., KF255108.1, KF255056.1 (Pedrosa-Gerasmio *et al.*, 2015), ON572219, ON572221 (Sartimbul *et al.*, 2023a). We utilized MEGA11 for molecular identification of the sequencing results of CR mtDNA (Tamura *et al.*, 2021). These CR specimens were matched with the CR nucleotide database on the Genbank page (National Center for Biotechnology Information: https://blast.ncbi.nlm.nih.gov/Blast.cgi) using the Basic Local Alignment Search Tool (Mega-BLASTn).

We used the neighbor-joining (NJ) method (Saitou and Nei, 1987) to look at the phylogenetic relationships between sequences from only water locations that ITF passed through. We used the Kimura-2 parameter substitution model and pairwise deletion in the phylogenetic analysis and genetic distance (Kimura, 1980). The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (9936 replicates) (Felsenstein, 1985) are shown only above the branches with a probability value ≥ 50%. We reconstructed a phylogenetic tree with an outgroup from ten CR sequences of *A. sirm* caught in 2017 from East Lombok waters (Figure 7A: ON572227-ON572236) (Sartimbul *et al.*, 2023a), comprising *A. sirm* from Taiwan (AP017948.1), and Andaman Sea (AP017949.1) (Lavoué *et al.*, 2017).

It was DnaSP v6.12.03 (Rozas *et al.*, 2003) we used to find the genetic diversity, and NETWORK v10.2.0.0 (Akbar and Aris, 2018; Chandrasekar *et al.*, 2019) to make the haplotype distribution. Its analysis was aimed at determining the diversity of haplotype (gene) (Hd) (Nei, 1987) and nucleotide (π) (Lynch and Crease, 1990; Pertiwi *et al.*, 2015). In addition, we collected several scientific publications related to genetic diversity data from various species in the genus Sardinella in other waters and compared them with *S. lemuru* from Bali Strait.

2.3.2 Ocean temperature, salinity, and circulation of water mass

We analyzed secondary data, such as sea temperature, salinity, and currents, to provide an overview of the circulation conditions of the water mass in the Bali Strait and its surroundings (8°S - 9°S and 114°E - 115.5°E) as habitat for *S. lemuru*. We obtained salinity and daily current data from the E.U. Copernicus Marine Services Information Archive (CMEMS: https://doi.org/10.48670/moi-00021) for 2019 (June, July, and October) at depths of 10 and 40 meters. The data had a spatial resolution of 1/12° arc-degree. We used World Ocean Atlas 2013 (WOA13: https://www.nodc.noaa.gov/OC5/woa13/woa13data.html (Locarnini *et al.*, 2013; Zweng *et al.*, 2013) climatological data (1955-2012) of temperature, salinity, and pressure to derive potential temperature (θ) and potential density (σ), and characteristics of the seawater-mass (T-S diagram). These three outputs (θ, σ, and T-S diagram) were analysed by neglecting teleconnection influences, such as ENSO and IOD

(Emery and Meincke, 1986; Purba *et al*., 2021). To generate a map of the Bali Strait (Figure 1), We extracted and plotted bathymetry data 30 arc-sec from The General Bathymetric Chart of the Oceans (https://gebco.net). We plotted and analysed various types of oceanographic data using MATLAB and Ocean Data View (Schlitzer, 2020).

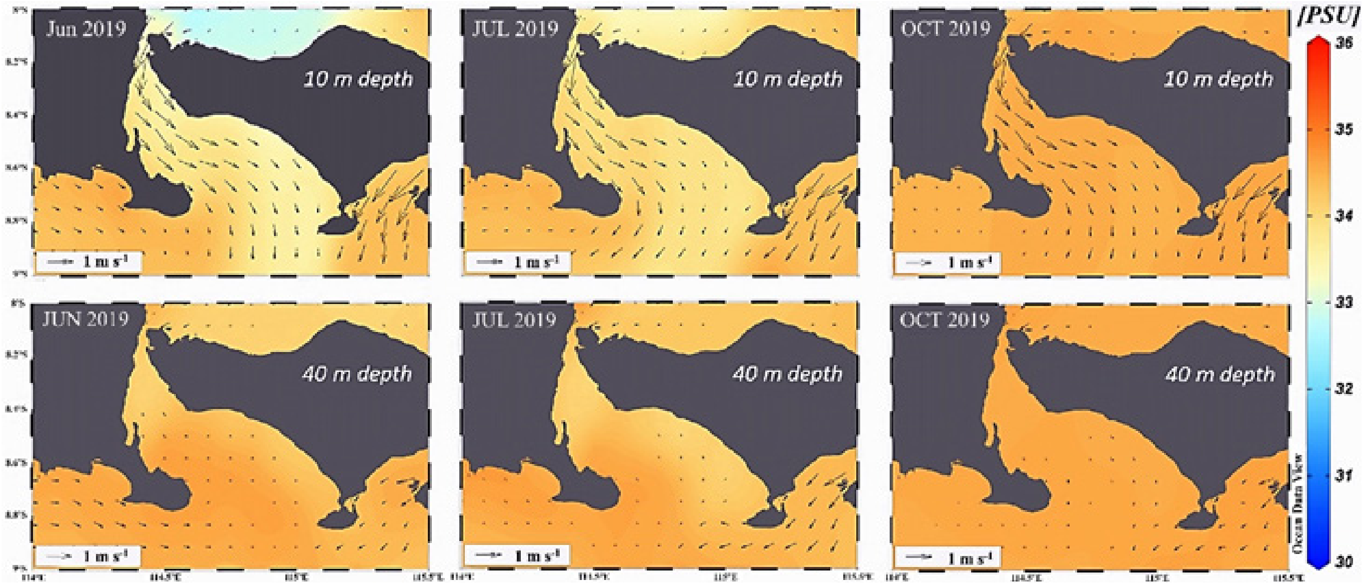

Figure 3. Salinity (color) overlaid with current (arrows) at a depth of 10 meters (top panels) and 40 meters (bottom panels) during June, July, and October 2019.

3. Results and Discussion

3.1 Results

3.1.1 Seawater-masses circulation in the Bali strait

The Bali Strait is a distinctive marine environment that borders the Indian Ocean in the south and the Bali Sea in the north. The northern mouth of the Bali Strait is much narrower than the southern mouth. Consequently, there is a strong flow from the north (Java or Bali Sea). There is no 'Sill' on the border between the Bali Strait and the Indian Ocean, as on the Lombok Strait border with the Indian Ocean (Figure 1). The configuration without the 'Sill' causes the mass flow of water to flow freely into the Bali Strait through the south mouth, either from the south (Indian Ocean), east (south of Lombok), or west (south of Java). It follows that upwelling water masses from the south mouth of the Bali Strait are also highly likely to enter (Pranowo *et al*., 2005b; Pranowo and Realino, 2006).

3.1.2 Upwelling events and salinity mixing

June, July, and October 2019 were periods of upwelling (Mandal *et al*., 2022; Susanto *et al*., 2001; Wirasatriya *et al*., 2020). The condition of the warm water mass in the Bali Strait (26-28°C) at a depth of 10 m was thought to be the result of mixing two water mass flows, namely: warmer water mass (28-30°C, 10 m depth) coming from the north (Bali Sea), then a mass of cold water (20-22°C, 40 m depth) coming from the deep layers of the Indian Ocean (Figure 2). This assumption was confirmed by the salinity conditions of the Indian Ocean (34-35 PSU) mixed with salinity from the internal waters of the Bali Sea (32-33 PSU), so makes the salinity in the Bali Strait around 33-35 PSU (Figure 3).

3.1.3 Water mass suitability for sardinella

This mixture makes the Bali Strait a habitat for *S. lemuru* to grow and mature, with a comfortable water mass (26-28°C, 33-35 PSU). The biological traits of *S. lemuru* are in line with two research reports (FAO-FIGIS, 2005; Pauly *et al*., 1996) which found that the sardine species of *S. lemuru* prefers depths of 15-100 meters, sea temperatures of 20.96-28.83°C, and salinity of 30.61-36.78 PSU. Furthermore, the sardine species of *A. sirm* prefer similar conditions at the same depth, with a temperature range of 25.58-29.8°C and salinity of 31.60-36.00 PSU (Burhanuddin *et al*., 1974; Whitehead, 1985).

3.1.4 Teleconnection and current dynamics

The condition of the water mass in the Bali

Strait is influenced strongly by the teleconnection between the Indian Ocean and the Pacific Ocean. Southward flows (originating from the Java Sea and Makassar Strait) with warmer water dominated the circulation in the Bali Strait in the top 10 m. At a depth of 40 m, its teleconnection can be indicated from the flow of seawater temperature (Figure 2). Comparatively, in June 2019, cold-water masses and current arrow vectors seemed stronger when entering the Bali Strait from Southern East Java (Muncar). The water mass comes clearly from the Indian Ocean.

Table 2. Meristic characteristics of *Sardinella* at fishing grounds of Kedonganan-Bali.

Sample ID	D_ hard	D_ soft	P_ hard	P_ soft	V_ hard	V_ soft	A	C_ hard	C_ soft	Ct	S
SL108	2	15	2	13	1	8	17	4	17	Forked	Gold
SL109	2	15	2	15	1	8	15	4	16	Forked	Gold
SL110	2	15	2	13	1	8	16	4	16	Forked	Gold
SL111	2	15	2	13	1	8	17	3	16	Forked	Gold
SL112	2	14	2	12	1	8	16	4	16	Forked	Gold
SL113	2	14	1	14	1	8	15	4	16	Forked	Gold
SL114	2	15	1	14	1	8	17	3	17	Forked	Gold
SL115	2	14	1	14	1	8	15	4	16	Forked	Gold
SL116	2	13	1	14	1	8	14	4	16	Forked	Gold
SL117	2	14	1	14	1	8	14	4	16	Forked	Gold
SL118	2	13	1	14	1	8	16	4	16	Forked	Gold
SL119	2	13	1	14	1	8	14	4	16	Forked	Gold
SL120	2	15	1	14	1	8	16	4	16	Forked	Gold
SL121	2	15	1	14	1	8	15	4	16	Forked	Gold

Description: D (dorsal fin), P (pectoral fin), A (anal fin), V (ventral fin), C (caudal fin). Ct (Caudal type), and S (Spotted).

3.1.5 Water mass entry from adjacent straits

The difference was observed in July 2019 because the mass of cold water and the arrow vector of the current entering the Bali Strait were rather intense from the direction of the Badung and Lombok Strait. The seawater mass of Lombok Strait was dominated by Indonesian ThroughFlow (ITF) seawater mass during the June-October period from the Pacific Ocean (Gordon *et al.*, 2008, 2010; Sprintall *et al.*, 2009; Susanto *et al.*, 2012, 2021). Its consequence could then affect the presence of the *S. lemuru* population in the Bali Strait. As suggested by Sartimbul *et al.* (2010) and (2018b), Sambah *et al.* (2021a, 2021b), and Setyohadi *et al.* (2021), the sea temperature variability correlated with ENSO and IOD, with generating upwelling phenomenon significantly affects the number of *S. lemuru* in the Bali Strait.

3.1.6 Pacific water mass contribution

Based on the result, it can be seen that there are two types of Pacific Ocean water masses flowing into the Indian Ocean, namely Western North Pacific Central Water (WNPCW) and Western South Pacific Central Water (WSPCW) (Figure 4). There are two

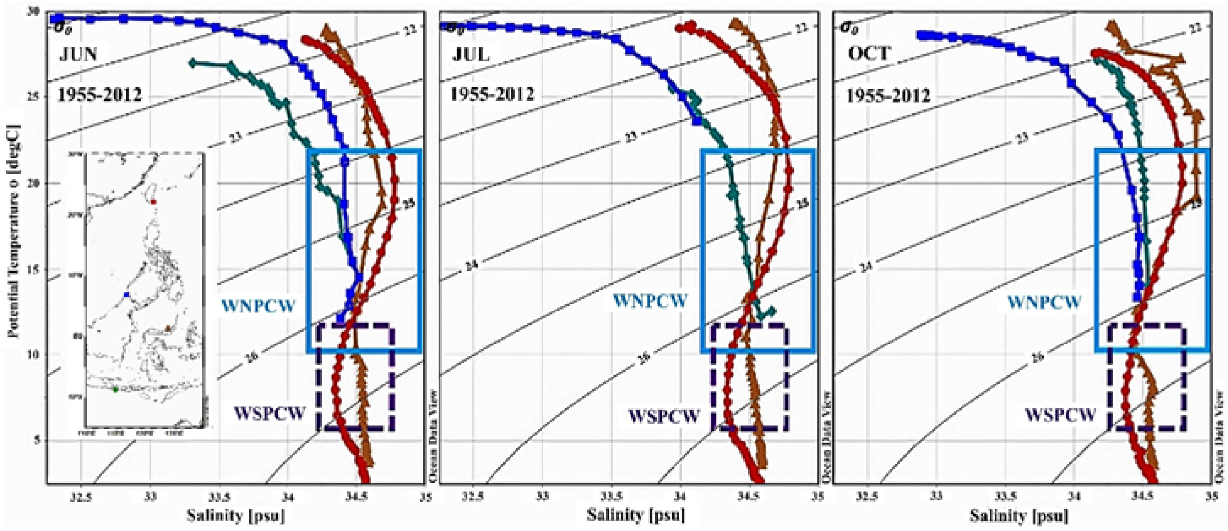

Figure 4. Temperature-Salinity Diagram for June, July, and October derived from climatological data (1955-2012) water mass characteristics in Taiwan (red dot), Kudat-Malaysia (blue rectangle), Manado (brown triangle), and Bali Strait (green diamond) stations.

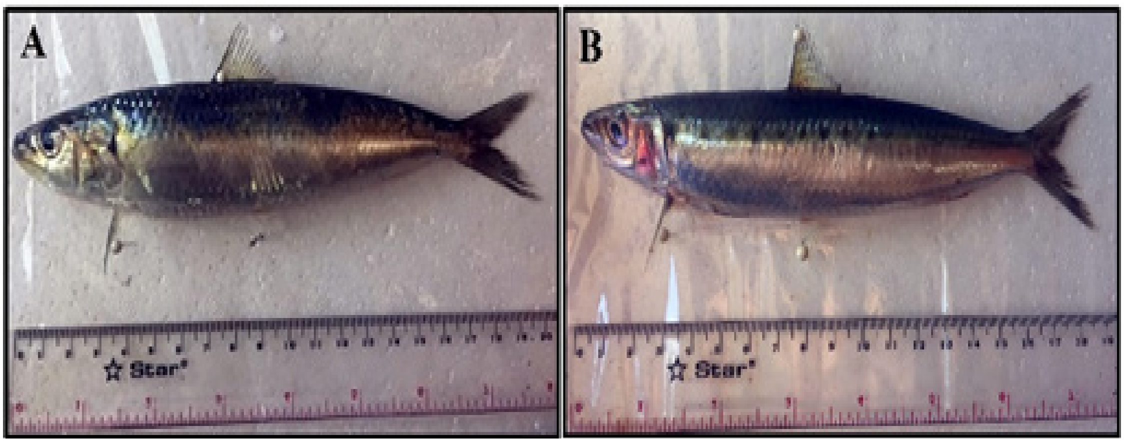

Figure 5. *Sardinella* specimens taken from Kedonganan Fishing Grounds. Specimen based on morphology identification of [A] *S. lemuru* and [B] *A. sirm.*

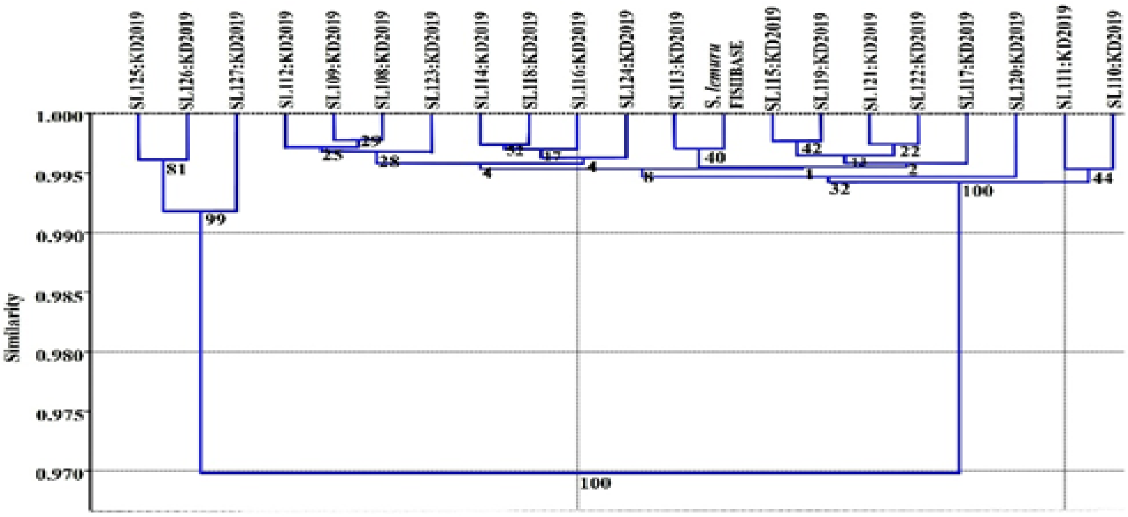

Figure 6. The dendrogram is based on morphometric-meristic characteristics of the Sardinella of Kedonganan samples, using the Bray-Curtis similarity matrix. For each node, the % confidence level of clustering was shown.

Table 3. BLAST analysis result of *Sardinella* from Bali Straits with the % identity around 97.01-98,72%. In addition, there are two unique sequences of *S. lemuru* (Sample ID: SL16 and SL17).

Sample ID	Species	Identity of the NCBI reference	% QC	% Ident	E- value	Sequence Length
SL1:CGU072019	*S. lemuru*	MK579664.1^{a}	67%	98.47%	0.0	582
SL2:CGU072019	*S. lemuru*	MK579584.1^{a}	65%	97.96%	0.0	602
SL3:CGU072019	*S. lemuru*	MK579752.1^{a}	65%	97.70%	0.0	599
SL4:CGU072019	*S. lemuru*	MK579652.1^{a}	67%	97.96%	0.0	582
SL5:CGU072019	*S. lemuru*	MK579801.1^{a}	67%	98.47%	0.0	580
SL6:CGU82019	*S. lemuru*	MK579645.1^{a}	65%	98.21%	0.0	597
SL7:CGU082019	*S. lemuru*	MK579689.1^{a}	66%	98.47%	0.0	586
SL8:CGU082019	*S. lemuru*	MK579742.1^{a}	67%	98.47%	0.0	584
SL9:CGU082019	*S. lemuru*	MK579777.1^{a}	68%	98.45%	6.00E^{-163}	630
SL10:CGU08019	*S. lemuru*	MK579717.1^{a}	68%	97.70%	0.0	575
SL11:CGU082019	*S. lemuru*	MK579777.1^{a}	65%	97.96%	0.0	596
SL12:CGU082019	*S. lemuru*	KM518973.1^{a}	77%	97.62%	0.0	675
SL13:CGU082019	*S. lemuru*	MK579839.1^{a}	68%	98.21%	0.0	573
SL14:CGU082019	*S. lemuru*	MK579633.1^{a}	65%	98.47%	0.0	595
SL15:CGU082019	*S. lemuru*	MK579790.1^{a}	66%	97.46%	0.0	591
SL16:CGU092019	*S. lemuru*	MK579773.1^{a}	37%	78.42%	9.00E^{-53}	869
SL17:CGU092019	*S. lemuru*	MK579773.1^{a}	37%	77.74%	7.00E^{-49}	866
SL18:CGU092019	*S. lemuru*	MK579583.1^{a}	65%	97.96%	0.0	603
SL19:CGU092019	*S. lemuru*	MK579799.1^{a}	66%	98.47%	0.0	588
SL20:CGU092019	*S. lemuru*	MK579675.1^{a}	66%	98.47%	0.0	591
SL76:MCR2017	*S. lemuru*	MK579583.1^{a}	69%	97.96%	0.0	566
SL77:MCR2017	*S. lemuru*	MK579733.1^{a}	67%	98.21%	0.0	584
SL78:MCR2017	*S. lemuru*	MK579787.1^{a}	68%	98.47%	0.0	569
SL79:MCR2017	*S. lemuru*	MK579787.1^{a}	74%	98.47%	0.0	523
SL80:MCR2017	*S. lemuru*	MK579787.1^{a}	74%	98.47%	0.0	528
SL81:MCR2017	*S. lemuru*	MK579733.1^{a}	68%	97.96%	0.0	571
SL82:MCR2017	*S. lemuru*	MK579733.1^{a}	68%	98.21%	0.0	572
SL108:KD2019	*S. lemuru*	MK579634.1^{a}	65%	98.47%	0.0	594
SL109:KD2019	*S. lemuru*	MK579668.1^{a}	67%	98.72%	0.0	579
SL110:KD2019	*S. lemuru*	MK579584.1^{a}	66%	97.96%	0.0	593
SL111:KD2019	*S. lemuru*	MK579665.1^{a}	66%	98.47%	0.0	587
SL112:KD2019	*S. lemuru*	MK579787.1^{a}	66%	98.47%	0.0	593
SL113:KD2019	*S. lemuru*	MK579652.1^{a}	65%	97.96%	0.0	600
SL114:KD2019	*S. lemuru*	MK579839.1^{a}	65%	97.96%	0.0	602
SL115:KD2019	*S. lemuru*	MK579799.1^{a}	67%	98.47%	0.0	584
SL116:KD2019	*S. lemuru*	MK579614.1^{a}	66%	97.70%	0.0	592
SL117:KD2019	*S. lemuru*	MK579795.1^{a}	65%	98.72%	0.0	603
SL118:KD2019	*S. lemuru*	MK579742.1^{a}	65%	98.47%	0.0	594
SL119:KD2019	*S. lemuru*	MK579746.1^{a}	66%	98.21%	0.0	586
SL120:KD2019	*S. lemuru*	MK579720.1^{a}	65%	98.21%	0.0	594
SL121:KD2019	*S. lemuru*	MK579822.1^{a}	66%	97.96%	0.0	592
SL122:KD2019	*S. lemuru*	MK579651.1^{a}	75%	98.47%	0.0	518
SL123:KD2019	*S. lemuru*	MK579765.1^{a}	66%	97.45%	0.0	588
SL124:KD2019	*S. lemuru*	KM518973.1^{a}	82%	97.53%	0.0	590
SL125:KD2019	*A. sirm*	AP017948.1^{b}	100%	97.01%	0.0	536
SL126:KD2019	*A. sirm*	AP017948.1^{b}	100%	98.09%	0.0	523
SL127:KD2019	*A. sirm*	AP017948.1^{b}	100%	98.02%	0.0	506

Description: a (*S. lemuru* isolate control region, partial sequence of mitochondrial (387 bp)), and
b (*A. sirm* mitochondrial DNA, complete sequence (17049 bp)), and QC (Query Cover).

Table 4. Genetic diversity of *Sardinella* around the world. The nucleotide base length of *S. lemuru* in this study was different between Table 3 and Table 4. This was because of the genetic diversity analysis using *S. lemuru* sequences from the NCBI (i.e., Pedrosa-Gerasmio *et al*. (2015): 305 bp).

Species	Location	Locus	bp	n	Hd	References
Sardinella lemuru	Kedonganan-Bali	Control Region	309	17	1 ± 0.020	This study
	Canggu-Bali		303	20	1 ± 0.016	
	Muncar-East Java		309	7	0.81 ± 0.130	
Sardinella lemuru	Puger-East Java	Control Region	600	20	1.000	Lestari (2017)
	Prigi-East Java		600	20	1.000	
Sardinella lemuru	Probolinggo-East Java	Control Region	693	20	1.000	Listiyaningsih (2017)
	Prigi-East Java		693	20	1.000	
Sardinella lemuru	Prigi-East Java	Control Region	651	9	1.00	Ikhsani (2017)
	South Malang-East Java		651	5	0.7	
	Puger-East Java		651	6	1.00	
Sardinella lemuru	Madura Strait-East Java	COI	600-800	5	0.0	Noviasri *et al.* (2016)
	Bali Strait		600-800	5	0.7	
	Southern waters of East Java		600-800	5	0.7	
Sardinella lemuru	Palawan-Philippines	Control Region	305	40	0.9987	Pedrosa-Gerasmio *et al.* (2015)
	Zamboanga-Philippines		305	50	0.9984	
	Kudat-Malaysia		305	49	10.000	
	Manado-Indonesia		305	48	0.9981	
	Tawi-Tawi-Philippines		305	44	0.9984	
Sardinella fimbriata	Northern waters of East Java	COI	680	4	1.000	Syahidah (2017)
	Bali Strait		680	4	0.83	
Sardinella fimbriata	Prigi-East Java	COI	698	3	0.667	Ekawati (2017)
	Madura Strait		698	4	n.a.	
Sardinella longiceps	India	Control Region	758	287	0.9933	Sukumaran *et al.* (2016)
		COI	576	291	0.8257	
Sardinella albella	Sea of Oman (Jask), Iran	Control Region	500	13	0.96515	Rahimi *et al.* (2016)
	Strait of Hormoz (Qeshm), Iran		500	12	0.9848	
	The Persian Gulf (Lengeh), Iran		500	14	0.8952	
Sardinella hualiensis	Taiwan	Control Region	433	6	1.000	Chan *et al.* (2019)
	Cagayan-Philippines		433	6	0.833	
Sardinella tawilis	Batangas-Philippines	Control Region	433	18	0.778	Chan *et al.* (2019)
Sardinella zunasi	Northwestern Pacific	Control Region	686	77	0.994	Wang *et al.* (2008)
Sardinella aurita	Bermuda Aquarium Museum and Zoo dock in Flatts (BAMZ)-USA	COI	781	2	1.000	Goodbody-Gringley *et al.* (2019)
Sardinops sagax	Vancouver Island-Canada	Cyt b	481	32	0.897	Lecomte *et al.* (2004)

Description: Hd (Haplotype diversity), n (number of specimens), n.a. (not available).

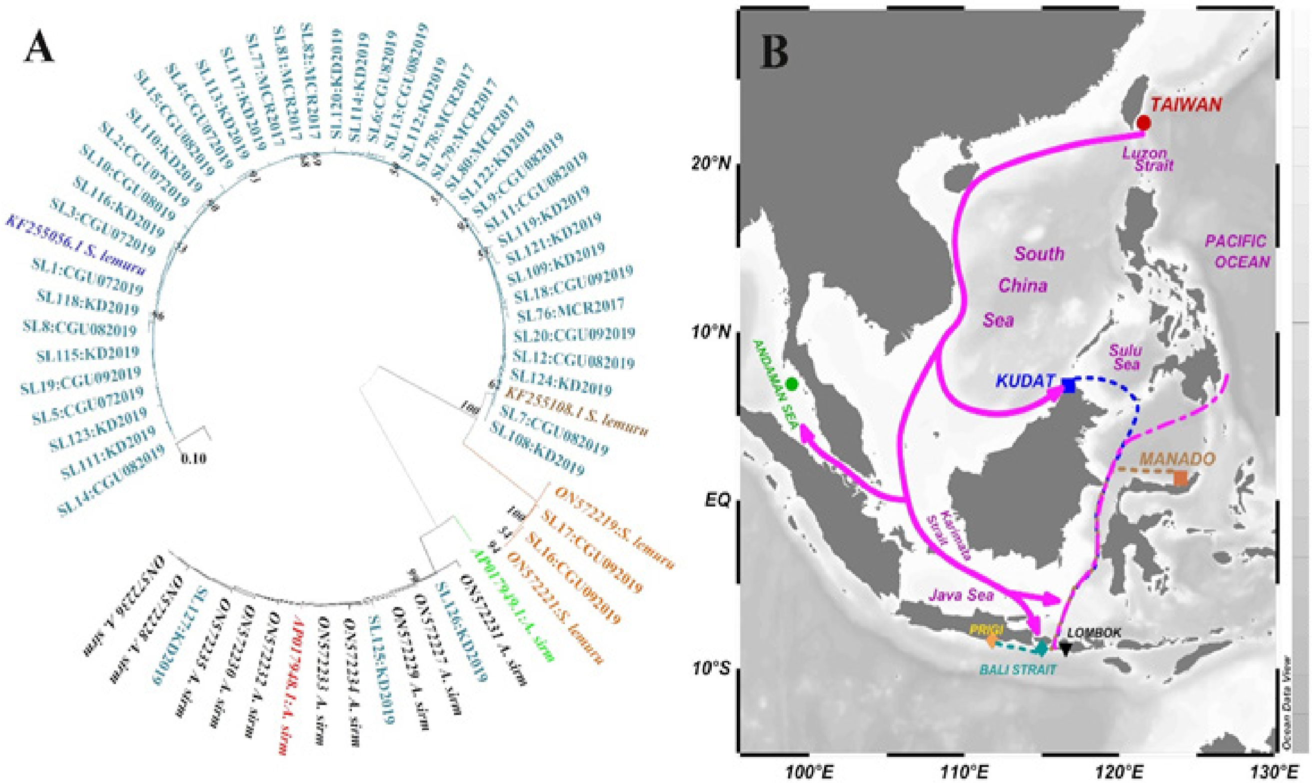

Figure 7. [A] Phylogenetic tree of *Sardinella* from Bali Strait based on 320 bp control region that longer than the findings of Pedrosa *et al.* (2015) and Labrador *et al.* (2021). The reconstruction of the phylogenetic tree is formed by three clades: Clade-1 (*S. lemuru* from three sites of Bali Strait, Kudat, and Manado), Clade-2 (*S. lemuru* Canggu and Prigi), and outgroup clade (*A. sirm* of Kedonganan-Bali Strait, Taiwan, and the Andaman Sea). The numbers above the nodes are bootstrap proportions (in percent). [B] Main Indonesian ThroughFlow pathways: Pacific – Sulawesi Sea – Makassar Strait – Lombok Strait – Indian Ocean, and SCSTF (Pacific – Luzon Strait – Karimata Strait – Java Sea – Bali/Lombok Strait – Indian Ocean) and secondary via the Sulu Sea.

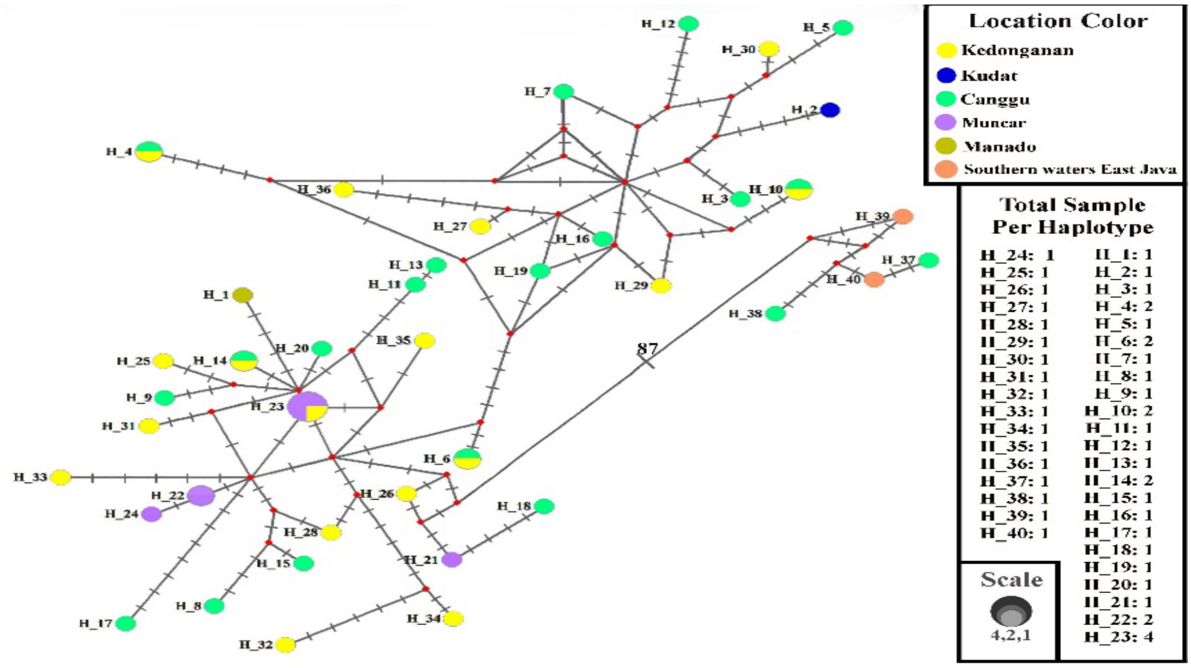

Figure 8. A haplotype network of 313 bp of *S. lemuru* from Bali Strait (Kedonganan, Canggu, Muncar) and other locations based on the mtDNA control region marker. Vertically small bars represent step changes between haplotypes, with the number of mutation bases.

routes of seawater mass flow (Figure 4). The first route is ITF (Gordon *et al*., 2008, 2010; Susanto *et al*., 2012), while the second route is known as the South China Sea Through-Flow (SCSTF) (Fang *et al*., 2010; Susanto *et al*., 2010, 2013, 2016; Wei *et al*., 2015, 2019; Wang *et al*., 2019; Xu *et al*., 2021). The SCSTF's main route is from the Western Pacific into the Luzon Strait, South China Sea, Karimata Strait, and Java Sea, and then in combination with the main ITF from Makassar Strait to exit to the Indian Ocean via the Sunda and Bali Straits, and straits along the Nusa Tenggara Island chain (Susanto *et al*., 2016). There is a secondary SCSTF from the South China Sea into the Sulu Sea and then into the Sulawesi Sea that merged with the main ITF in the Makassar Strait (Qu *et al*., 2009; Gordon *et al*., 2010; Sprintall *et al*., 2012). The main water flow in the Lombok Strait is towards the Indian Ocean. However, there are branching and turning through the Badung Strait. The mass of water that comes out of the Lombok Strait and Badung Strait outlets flows into the Bali Strait (Pranowo *et al*., 2005a; Theoyana *et al*., 2015).

3.1.7 WSPCW Pathways into the SCSTF System

The water mass from the WSPCW passes only through the Mindanao Strait (brown triangle) and Luzon Strait (red dots) (Figure 4). When the WSPCW entered the South China Sea via the Luzon Strait, it did not appear to turn to the Balabac Strait (blue rectangle). It most likely entered through the main western route of SCSTF through the Karimata Strait (e.g., Supplementary Figure of Susanto *et al*. (2010)).

3.2 Discussions

3.2.1 Morphological identification of sardinella

All samples collected had a compressed body shape, with a mouth near the nose (terminal) and a forked tail type. The body color was similar to the silvery color on the ventral side of all samples, with some differences in each dorsal. There was a turquoise dorsal in a total of 44 individuals (Figure 5A), that are in line with the diagnostic features of *S. lemuru* reported in previous studies (Froese and Pauly, 2024 ; Sartimbul *et al*., 2018a; Willette and Santos, 2013). Besides that, the other dorsal color tends to be dark black (n = 3) rather than turquoise (Figure 5B).

The Kedonganan sample (KD) morphometric ratios between KD1–17 and other samples (KD18–20) were different in almost all of the morphometric traits (Table 1). In addition, the measurement result of meristic characteristics shows prominent differences, especially in the total number of ventral fin spine and rays. The number of ventral fin spines and rays is nine in each KD1-17 specimen, while eight ventral fin spines and rays are observed in each KD18-20 specimen (Table 2). Indications of differences in morphometric and meristic characters in the Kedonganan specimens may occur. Aquatic environmental factors and sample treatment during the fishing process influence their morphometric-meristic characteristics.

The findings of previous studies show the S. lemuru fins consist of anal fins, a pair of ventral fins with nine rays and a spine (soft and hard), pectoral fins pair, a fork-shaped caudal fin, and a single dorsal fin (without additional fins). The head section of the S. lemuru species has a black spot on its gill cover frame and its posterior operculum accompanied by a golden spot (Mahrus *et al*., 2012; Willette and Santos, 2013; Sartimbul *et al*., 2018a; Froese and Pauly, 2024). On the other hand, A. sirm is a type of sardine fish from the family Clupeidae in Indonesia. *A. sirm* has different characteristics from *S. lemuru* because it has several black spots or bumps along its lateral line. These spots became the basis for the identification of *A. sirm*. Nevertheless, these spots can fade or vanish and shift from golden to black when dead (Rajan *et al*., 2013; Saleh *et al*., 2017) (Figure 5B).

Based on morphometric and meristic characteristics, the dendrogram shows that there are two groups of trees on the fishing grounds of Kedonganan-Bali (Figure 6). Seventeen samples were in clade-1 with S. lemuru samples from FishBase, and their similarity value was high (≥ 98.62%) (Supplementary 1). Meanwhile, the other three individuals had a smaller similarity value (≤ 96.89%) than *S. lemuru* of FishBase (Supplementary 1). The separation between clade-1 and clade-2 may indicate a different species (Willette and Santos, 2013; Lestari, 2017).

3.2.2 Molecular identification and phylogenetic relationship of sardinella

The molecular identification method can cover the limitations of morphological identification. The genetic data is considered relatively more stable in the evolutionary process using the control region of mtDNA as the informative gene locus. In addition, environmental influence can change the morphological characteristics. Further consequences result in inaccurate identification. Molecular identification is needed in the authentication of species and genetic diversity estimation of exploited fish populations (Dharmayanti, 2011; Ardura *et al*., 2013; Willette and Santos, 2013; Samsi *et al*., 2019).

Supplementary 1. Similarity indexes based on morphological characteristics from the Kedonganan fish specimens against the *S. lemuru* from FishBase.

Sample ID	Similarity indexes with *S. lemuru* of FishBase
SL108:KD2019	98.81%
SL109:KD2019	98.89%
SL110:KD2019	99.93%
SL111:KD2019	98.76%
SL112:KD2019	98.95%
SL113:KD2019	98.81%
SL114:KD2019	98.94%
SL115:KD2019	98.77%
SL116:KD2019	98.73%
SL117:KD2019	98.62%
SL118:KD2019	98.94%
SL119:KD2019	98.71%
SL120:KD2019	98.89%
SL121:KD2019	98.69%
SL122:KD2019	98.78%
SL123:KD2019	98.75%
SL124:KD2019	99.25%
SL125:KD2019	96.81%
SL126:KD2019	96.74%
SL127:KD2019	96.89%

This is the first study with relatively complete sequence data for S. lemuru in the Bali Strait. The sequence length (bp) of the control region (CR) ranges from 506 to 869 bp (Table 3). The sequence length is quite similar to the CR sequences of S. lemuru (693 bp) found by Listyaningsih (2017) in East Java. Similar results were also found with the CR sequence length of S. lemuru (463-862 bp) in the Southern Waters of East Java (Sartimbul *et al.*, 2023a). It is longer than the CR sequences of S. lemuru found in Philippine waters (Zamboanga, Tawi-Tawi, and Palawan), Indonesian waters (Manado), and Malaysian waters (Kudat), with a length of 305 base pairs (Pedrosa-Gerasmio *et al.*, 2015).

From mega-BLASTn results, most samples of *Sardinella* of Bali Strait were identified as species of *S. lemuru*, with a similarity percentage of 97.45-98.72% (Table 3). Interestingly, two unique CR sequences of S. lemuru from Canggu were identified with relatively lower identity percentages and longer CR sequence lengths. Meanwhile, the other three samples were identified as A. sirm, with a high rate of similarity in their identities of 97.01-98.09% (Table 3). The reconstructed phylogenetic tree (Figure 7A) and genetic distance confirmed the consistency of BLASTn results.

Three clades formed between the *Sardinella* samples (Figure 7A). *S. lemuru* of Bali Strait is clustered with *S. lemuru* isolated from Kudat and Manado (clade-1). In clade-2, samples originating from Canggu are mixed with cryptic species of *S. lemuru* in the southern waters of East Java. Another clade (clade-3) is an outgroup species of *A. sirm*. A similar identity of *S. lemuru* between waters occurred because the overall average genetic distance presents low sequence divergence (8 ± 0.8 %) over all sequence pairs. Notably, this value was relatively lower in *S. lemuru* sequences in clade-1 (2.9 ± 0.5 %). The moderate genetic distance between *S. lemuru* clade-1 and *S. lemuru* clade-2 presents evolutionary divergence (35.3 ± 4.1 %). Bi-parentally inherited genetic markers are suggested to confirm this cryptic clade (clade-2) (Figure 7A). Solid evidence of cryptic species was demonstrated for *Sardinella gibbosa* Bleeker 1849 in Philippines waters, with a genetic distance estimation of 10 to 40 % (Thomas *et al.*, 2014). Similar patterns were reported in multiple taxa of Mormyridae (Lavoué *et al.*, 2003). In addition, both bi-parentally inherited genetic markers revealed significant genetic differentiation between one unique Schizothorax waltoni Regan 1905 population in the Eastern Yarlung Tsangpo River. In contrast, its genetic homogeneity was observed among three central populations in the western Yarlung Tsangpo River (Guo *et al.*, 2019).

The genetic distance of *S. lemuru* between locations in clade-1 is shown in Figure 7A. The pairwise sequence divergence value of the Kedonganan and Muncar samples is the highest. This is followed by the Canggu and Muncar samples, which have the lowest difference. Finally, Canggu and Kedonganan samples have the highest genetic distance, at 3.2 ± 0.6. We also found that the average number of base substitutions across all sequence pairs in Muncar is one-third of the average evolutionary divergence across all sequence pairs in other places (i.e., sequence divergence in% within Muncar, Canggu, and Kedonganan, respectively: 1.1 ± 0.38, 3.2 ± 0.64, and 3.3 ± 0.61).

The suggested connectivity map (Figure 7B) comes from looking at the water mass circulation analysis (Figure 4), the native range map for *S. lemuru* modeled by IPCC RCP8.5 emissions scenario (AquaMaps, 2019), and the phylogenetic tree analysis (Figure 7A). *S. lemuru* sequences between Muncar and Manado are relatively closer than *S. lemuru* between Muncar and Kudat (i.e., the genetic distance between location groups (%) is 1.2 ± 0.5, 2.4 ± 0.8, respectively). This relatively closer relationship between *S. lemuru* localities is probably due to *S. lemuru* using the main ITF (i.e., Pacific Ocean-Sulawesi Sea-Makassar Strait-Lombok Strait-Bali Strait and the Indian Ocean) as its migration route. Moreover, all samples of *S. lemuru* in clade-1 remain closely related. Hence, there is no significant difference (single species) because the bootstrap value is less than 99% in each node of clade-1 (Figure 7A).

Single species of *S. lemuru* across waters imply a low geographic barrier reported in the previous study of *S. lemuru* between Canggu and the Philippines Waters (Winata *et al*., 2022). Its dispersal connection was strengthened (i.e., translocated to the southern latitude from Philippines waters) with ITF circulation and local seawater mass-circulation model of southern waters of East Java (Sartimbul *et al*., 2023a). *S. lemuru* distribution is broad across the Eastern Indian Ocean and Western Pacific region. Subsequently, is tagged Bali *Sardinella* based on the FAO name because it was first identified as having abundant catches in the Bali Strait. Unequivocally, reports of its appearance in Philippine waters were made in 2013. However, the limited research findings on *S. lemuru's* migratory route and behavior have yet to determine its origins (Labrador *et al*., 2021). Moreover, *S. lemuru* has different peak spawning periods, such as in the South China Sea (March-May), Sulu Sea (October-December), and Bali Strait (December-January). Their peak spawning period occurs in chronological order because it is influenced by water circulations (Figure 7B). However, *S. lemuru* also spreads its range northward from the Philippines to China and southern Japan (Whitehead, 1985; Willette *et al*., 2011; Willette and Santos, 2013). Hence, more in-depth studies are needed, with more complete datasets in one cycle of a year or another alternative tool, such as environmental DNA (eDNA).

The phylogenetic tree analysis (Figure 7A) also illustrates that the three samples of Kedonganan are identically single species as *A. sirm* caught from the Taiwan waters, Lombok Strait, and the Andaman Sea. The overall average genetic distance of *A. sirm* sequences in clade-3 indicates a low divergence (5.4 ± 0.7 %). Compared to other locations, *A. sirm* isolated from the Andaman Sea is unequivocally a unique variation (i.e., the bootstrap value in Figure 7A is 100%, and the genetic distance is 21.9 to 25.2%). Meanwhile, *A. sirm* from three locations (Kedonganan, Lombok Strait, and Taiwan) had a low difference in genetic distance (1.3 to 5%) due to the mixing variation process through high gene flow. The high gene flow of *A. sirm* from three locations is probably due to the secondary ITF western route (SCSTF) as a potential driver for its wide-range distribution (i.e., South China Sea (SCS) – the Sulu Sea - Sulawesi Sea that merged with the main ITF in the Makassar Strait).

We looked at the cytochrome b and COI genes of mtDNA in *A. sirm* genetic populations in the SCS region from 2014 to 2018 in places like Kudat, Kuching, and Kuantan in Malaysia, Muara in Brunei, and Songkhla in Thailand. This region includes the Java Sea in Indonesia and the Andaman Sea in Thailand. *A. sirm* collected in the Java Sea shares the major haplotypes (single stock) with several regions of the SCS, but *A. sirm* of the Andaman Sea is identified as a cryptic species. This cryptic species needs further genetic population study (Saleh *et al*., 2017; Wahidah *et al*., 2019). In addition, based on a complete mitogenome analysis of two specimens, *A. sirm* from Taiwan and the Andaman Sea is in the same position in the phylogenetic tree of Clupeoidei (Lavoué *et al*., 2017). These genetic similarities of *A. sirm* in different bodies of water are in line with the main routes of the SCSTF, which are Luzon, the SCS, the Karimata Strait, the Java Sea, the Bali Sea, or the Lombok Strait (Figure 7B). After that, some SCS water flows to the Malacca Strait and the Andaman Sea. There aren't any CR sequences of *S. lemuru* in Genbank from Taiwan, the Andaman Sea, the South China Sea, or the Java Sea. However, there is a close genetic relationship between *S. lemuru* from the Bali Strait and *S. lemuru* from the Philippines, the South China Sea, China, and the Taiwan Strait. This can be inferred in two ways: COI sequences (Kartika *et al*., 2017) and the species' biologically wide distribution and catch production trends in FishBase (AquaMaps, 2019). More genetic research should be done on *S. lemuru* in Indo-Pacific waters (e.g., SCS, Andaman Sea, Taiwan) using the control region gene, microsatellites, and eDNA.

In the interclade, the genetic distance of *S. lemuru* and *A. sirm* is shown in Figure 7A, with a high divergence of 102–123%. Three different types of trees—one based on morphometric-meristic dendrogram (Figure 6), one based on CR sequences (Figure 7A), and the first one based on 13 protein-coding genes of mtDNA (Jiang *et al*., 2018)—all agree with each other. It's similar to how *S. lemuru* (clade-1 and clade-2) and *A. sirm* (clade-3) are different species (Figure 7A). In the Philippines, *S. lemuru* and *A. sirm* are very different in 16S rRNA mtDNA and the nuclear gene of the S7 intron (37% to 60%) (Thomas *et al*., 2014). A similar pattern with moderate genetic distance also occurs for *S. lemuru* against *S. longiceps*, with a divergence of 35.4% based on another genetic locus (cytochrome b) (Willette and Santos, 2013). Moreover, highly migratory big pelagic fish (genera *Thunnus* South 1845) had a moderate genetic distance (12.5%) reported between *T. albacares* Bonnaterre 1788 and *T. thynnus* Linnaeus 1758 (Wijana and Mahardika, 2010). In contrast, a low genetic distance (2%) was observed based on the COI marker between anchovies of the southern waters of Lombok and *Spratelloides delicatulus* Bennett 1832 from Australia, so clustered together in clade-4 (Mahrus *et al*., 2022). This low genetic distance means no geographical barrier from one to another water facilitated by ocean circulation for larval dispersal and influences adult migration (Pata *et al*., 2021; Sartimbul *et al*., 2023a). However, despite high gene flow, locally adaptive variation is maintained by selective forces influenced by environmental heterogeneity (Labrador *et al*., 2022).

3.2.3 Genetic diversity consequence for S. lemuru adaptive traits

Through genetic diversity analysis, 44 Bali Strait samples have been identified as *S. lemuru* through morphological and molecular identification. The haplotype diversity (Hd) and the number of haplotypes (h) of *S. lemuru* were high at the three sites of Bali Strait (Table 4, Figure 8). Interestingly, in Muncar waters, the nucleotide diversity (Pi Jukes and Cantor) of *S. lemuru* is relatively lower than in other locations (i.e., 0.01 ± 0.004 in Muncar, 0.03 ± 0.003 in Kedonganan, and 0.09 ± 0.027 in Canggu). Notably, the number of polymorphic sites in Canggu waters is higher compared with Kedonganan and Muncar (i.e., 105, 38, and 10 bases, respectively). Many haplotypes with single sequences are closely related to each other in intraclade-1 (Figure 8). Plotting nucleotide diversity and polymorphic sites against the spread distribution of the haplotype network demonstrates this. Still, some inter-water haplotypes in the Bali Strait share identical haplotypes, especially between Canggu and Kedonganan, followed by Muncar and Kedonganan. There are 87 base-pair differences between two types of *S. lemuru* from Canggu and other types of *S. lemuru* in the Bali Strait. However, there are not many differences between them and Prigi samples in clade-2 (Figure 8).

It was seen that *S. lemuru* populations in the Sulu-Celebes region had high Hd values and little difference between haplotypes in the CR mtDNA marker (Pedrosa-Gerasmio *et al*., 2015) (Table 4). The high number of polymorphic sites (i.e., 33-65 bases across Philippine sites) influenced the pattern of high value of Hd and low differentiation among haplotypes. Even so, its polymorphic sites globally counted as many as 107 of 299 bp (Labrador *et al*., 2021). Furthermore, the divergence haplotypes of Sardinella gibbosa clade-1 and clade-2 were found to be the same in three molecular markers that changed at different speeds. In particular, the CR marker has 96 different base pairs, which is a lot of evidence for cryptic species of *S. gibbosa* living in the waters around the Philippines (Thomas *et al*., 2014). Another pattern similar to the cytochrome b marker was found in the haplotype network of *A. sirm* from the Andaman Sea in Thailand (Wahidah *et al*., 2019).

The genetic diversity of various Sardinella species has been summarized to serve as comparison data in this study (Table 4). *Sardinella* is a genus of tropical and subtropical sardines (Parrish, 1989; Checkley *et al*., 2017). *Sardinella* is found not only in Indonesian waters but also in Malaysia, the Philippines, and Iran (Pedrosa-Gerasmio *et al*., 2015; Rahimi *et al*., 2016). In other waters, the genetic diversity level of *Sardinella* commodities was reported in the high category, including *S. lemuru* (Table 4).

The observed value of genetic diversity was high in several *Sardinella* species (Table 4). Previous studies illustrated diverse gene sequences in sardine commodities, with the number of haplotypes found varied (Smith and Chesser, 1981; Sakai *et al*., 2001; Kusuma *et al*., 2016; Sukumaran *et al*., 2016; Akbar and Aris, 2018). The high value of genetic diversity in a population can occur for two reasons. First, the size and number of stocks are still relatively large in fertile oceanic and local waters. Second, these species have high migratory abilities.

The genus *Sardinella* belongs to the Clupeidae group, which likes to wander to search for food sources and optimal environmental conditions for spawning (Himelda *et al*., 2011). *Sardinella* is found in large numbers in productive coastal areas or upwelling areas in waters, such as the waters around the Philippines (Palawan, Zamboanga, and Tawi-Tawi) (Skogen, 2005). Moreover, Kudat Waters in the City of Sabah-Malaysia showed a high value of genetic diversity in S. lemuru, with a very fertile bay and a variety of corals. This fertile bay is also influenced by an upwelling phenomenon generating the water masses movement for nutrient enrichment (blooming plankton) (Ho *et al*., 2013; Manjaji-Matsumoto *et al*., 2017).

Sardinella is a genus of plankton feeder fish.

Its habitat in fertile waters is one of the determinants of its large numbers (Sartimbul *et al*., 2010, 2018b; Rahimi *et al*., 2016; Checkley *et al*., 2017). A recent study found that *S.lemuru* tends to be an opportunistic and omnivorous feeder, with a feeding target on both phytoplankton and zooplankton. Phytoplankton is the dominant diet of *S. lemuru* during Southeast monsoon, inter-monsoon 1 and 2, while zooplankton is a diet of *S. lemuru* during Northwest monsoon (Sartimbul *et al*., 2023b). In Indonesian waters, the fertile area with the highest exploitation rate for *S. lemuru* is the Bali Strait (Pet *et al*., 1997; Sartimbul *et al*., 2018a, 2018b).

The fertile conditions of the Bali Strait are also very popular with *Sardinella*, especially for larval rearing and spawning *S. lemuru*. The nursery ground of *S. lemuru* in this strait is precisely located in ten zones (e.g., Sembulungan, Anyir, Watu Layar, Sekeben, Senggong, Klosot, Prepat, Lampu Kelip, Kapal Pecah, and Pangpang Bay). Then, the spawning ground zone of *S. lemuru* was observed in four areas (e.g., Bukit, Benoa, Jimbaran, and Pemancar) (Wujdi *et al*., 2013). *S. lemuru* also prefers shallow waters (Pauly *et al*., 1996). The bathymetry of this strait is known to be shallow in the north, while in the south, it is classified as deep waters (Figure 1). In addition, the flow in and out of the Bali Strait water mass tends to be a surface water mass, so the water mass (i.e., the water column layer) is trapped with a high nutrient content (Rintaka and Priyono, 2020).

Upwelling intensity increased in the southeast monsoon (June–August) because of easterly winds induced from Australia. Water that is rich in nutrients moves up from the bottom of the mixed layer to the euphotic zone. This gives sardine populations in any part of the Bali Strait food chain (Susanto *et al*., 2001, 2006; Hendiarti *et al*., 2004, 2005; Susanto and Marra, 2005; Rintaka and Priyono, 2020; Siswanto *et al*., 2020; Wirasatriya *et al*., 2020; Mandal *et al*., 2022). In addition, the high dissolved oxygen (7-8 ppm) in Bali Strait is a suitable condition for *S. lemuru* (Sartimbul *et al*., 2018a). The Bali Strait is also one of the ITF routes, which causes these waters to be nutrient-rich for phytoplankton productivity. When the phytoplankton abundance is high, phytoplankton tends to be the primary food for *S. lemuru* (Pranowo *et al*., 2005b; Sartimbul *et al*., 2018a; Sartimbul *et al*., 2023b).

The migration of *S. lemuru* for reproductive activity and foraging can allow breeding and gene mixing between populations. As a result, single-frequency unique haplotype composites are discovered. Stocks with high genetic diversity have a potential for high adaptability to environmental conditions. This condition happens because the genetic composition of a particular individual is significantly diverse, with each of its genes having a different response to environmental conditions (Sakai *et al*., 2001; Akbar and Aris, 2018), as well as happens to the S. lemuru populations in the Bali Strait (Table 4).

One form of high adaptability in *S. lemuru* can be seen at the first size when gonad maturity occurs. In 2012, the first matured size of females on average was 18.9 cm in fork length (FL), while the male was 17.78 cm FL (Wujdi *et al*., 2012). The size of the first maturity of this gonad decreased to 16.8 cm FL in 2015. This condition can happen because *S. lemuru* adapts to maintain the sustainability of its population from continuous fishing pressure (Wujdi and Wudianto, 2015).

The excessive catch of *S. lemuru* has caused its stock in the Bali Strait to decline. Moreover, the size of *S. lemuru* caught is decreasing yearly (Wujdi and Wudianto, 2015). The catch volume of *S. lemuru* tremendously reduced in 2011-2012, contributing to only 10-20% of the total catch in the Bali Strait (Sartimbul *et al*., 2018b). This significantly differs from the previous years (1987-1993) because this fish can contribute 80-90% of the total catch production volume (Pet *et al*., 1997). The number of *S. lemuru* caught in the Bali Strait is going down, so scads (*Decapterus* spp.) have taken their place, especially in 2011 and 2012 (Sartimbul *et al*., 2018b).

The *S. lemuru* commodity always shows fluctuating volumes of catches. Numerous assessments conducted since 1950 have revealed that excessive utilization rates and climatic change are the reasons for fluctuations in *S. lemuru* commodities (Willette *et al*., 2011; Checkley *et al*., 2017). Therefore, the nature of this sardine commodity in finding suitable habitats and climatic conditions can be the basis for sustainable management.

Based on the high genetic diversity of *S. lemuru* in the Bali Strait, this fish can survive if adequate management efforts support its catching. One strategy might be to close or prohibit *S. lemuru* from fishing for a set time to solve the decreasing fish production and enable a more productive spawning season. For example, the Philippines closed their sardine fishing season for three months each year from 2011 to 2014 (Rola *et al*., 2018). The management policies can also be figured out by looking at the *S. lemuru* itself, which is strongly affected by the months of upwelling, the amount of chlorophyll-a in the water, the temperature of the water, and the presence of food sources (Sartimbul *et al*., 2018a, 2018b).

4. Conclusion

The low sequence divergence of *S. lemuru* between the Bali Strait and the northern latitude indicated spatial genetic homogeneity due to the high genetic flow facilitated by the main ITF circulation. Some of *S. lemuru*'s biological traits include large effective population sizes, high migration rates, and strong dispersal abilities at both the larval and adult stages. These traits make the effects of gene flow more homogenizing and the effects of genetic drift less structuring. *S. lemuru*'s migration routes may allow all genes with adaptive features (i.e., nucleotide base substitution results) to mix at all locations. Subsequently, the genetic composition of each individual is significantly diverse, with each of its genes having a different response to environmental change. This different response to environmental change contributes to a higher rate of survival and recruitment success during migration, strengthened by the suitable characteristics of the mass circulation of water. It will maintain its nucleotide variation. Keeping this nucleotide variation means that *S. lemuru* have a lot of different single-frequency unique haplotype composites. However, it is still considered a single species (intraspecies variation). Furthermore, *S. lemuru* and *A. sirm* are morphologically and genetically distinct, suggesting that different stock management is needed. It is noteworthy that the water mass flow, both the primary and secondary routes of SCSTF, reinforces closely related sequences of *A. sirm* between waters other than the Andaman Sea.

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Authors' Contributions

All authors are the main contributors to the experimental genetics of *S. lemuru*, including their analysis. AS; Conceptualization, Funding acquisition, Investigation, Supervision, Validation, Writing-Review, and Editing. IGADH; Investigation (laboratory work), Visualization (DNA sequence data of *S. lemuru*), Writing-Original draft preparation. IWA; Validation, Writing-Review, and Editing. GRAK; Project administration, Validation, Writing-Review, and Editing. VAW; Laboratory work, designed the figures of DNA of *S. lemuru*, Writing-Review, and Editing. WSP; Data Curation, Computing resources, and Visualization (oceanographic data: T-S diagram, seawater-masses circulation, and Bali Strait bathymetry). RDS; Supervision, Writing-Review & Editing. ER; Mapping, Data Analysis, Writing review. NM; Validation, Writing-Review. DY; Writing-Review and Editing. FI; Data Curation, Writing-Review, and Editing. All authors discussed the results and contributed to the final manuscript.

Conflict of Interest

The authors declare that they have no competing interests.

Declaration of Artificial Intelligence (AI)

The author(s) affirm that no artificial intelligence (AI) tools, services, or technologies were employed in the creation, editing, or refinement of this manuscript. All content presented is the result of the independent intellectual efforts of the author(s), ensuring originality and integrity.

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