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Thesis for the Degree of Master of Fisheries Science

**Mitochondrial Genome Analysis of *Selene dorsalis* (Gill 1863) from Eastern Atlantic:
Structural Organization and
Phylogenetic Analyses**

by

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KOICA-PKNU International Graduate Program of Fisheries Science

Graduate School of Global Fisheries

Pukyong National University

February 2025

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동부 대서양의 *Selene dorsalis* (Gill
1863)의 미토콘드리아 유전체 분석: 구조

및 계통발생학적 분석

Professor Hyun-Woo Kim

by

Emmanuel Ofosu Mireku Ewusi

A thesis submitted in partial fulfilment of the requirements
for the degree of

Master of Fisheries Science

in KOICA-PKNU International Graduate Program of Fisheries Science,
Graduate School of Global Fisheries
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February 21, 2025

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**Mitochondrial Genome Analysis of *Selene dorsalis* (Gill 1863)
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Abstract

This study offers an in-depth analysis of the mitochondrial genome of *Selene dorsalis* (Gill 1863), a species native to the Eastern Atlantic Ocean. The circular mitochondrial DNA molecule measures 16,541 base pairs and comprises 13 protein-coding genes (PCGs), 22 transfer RNA (tRNA) genes, two ribosomal RNA genes, and a control region (CR). The nucleotide composition exhibits a notable adenine-thymine (AT) bias, accounting for 53.13%, which aligns with other species in the Carangidae family. Most PCGs initiate with the ATG codon, with the exception of Cytochrome C oxidase subunit I, which starts with GTG. Analysis of relative synonymous codon usage reveals that leucine and serine are the most

prevalent amino acids in the mitochondrial genome of *Selene dorsalis* and its congeners (*Selene vomer* and *Selene setapinnis*). All tRNAs display the typical cloverleaf structure, though tRNA Serine (S1) lacks a dihydrouracil arm. Pairwise comparisons of synonymous and nonsynonymous substitutions for all PCGs yielded values below 1, indicating strong purifying selection. The CR spans 847 bp, representing 5.12% of the mitochondrial genome, and is characterized by high AT content (62.81%). It is situated between tRNA-Pro (TGG) and tRNA-Phe (GAA). The CR contains conserved sequence blocks, with CSB-1 being the longest at 22 bp and CSB-D the shortest at 18 bp. Phylogenetic analysis, using Bayesian and Maximum-likelihood trees constructed from concatenated PCGs across 72 species, successfully differentiates *Selene dorsalis* from other carangids. This study also explores how ocean currents and gyres might influence lineage diversification and parapatric speciation of *Selene* species between the Atlantic and Pacific Oceans. These results highlight the importance of the mitochondrial genome in elucidating the structural organization and evolutionary dynamics of *Selene dorsalis* and its relatives within marine ecosystems.

Keywords: Atlantic Ocean; marine fish; mitochondrial genome; evolutionary relationship; lineage diversification; conservation

Introduction

Proper fisheries resource management is essential to ensure sustainable exploitation of marine resources, to achieve such a profound and delegate objective it is crucial for proper applicable management policies tailored to the species level be enacted. Traditionally marine species identification has centered on taxonomic keys constituting body shape, head supination, melanophore patterns, and meristic count (Strauss and Bond, 1990). This method has proven to be successful. However, it is riddled with many challenges particularly when the studied species fall within the preflexion and flexion stage of development. With the current advances in mitogenomics, analysis of DNA (Deoxyribonucleic acid) which uniquely identifies an organism has been used by scientists to assist in the accurate identification of organisms to the species level to infer on genetic diversity and evolutionary lineage, specifically using mitochondrial DNA sequences such as cytochrome C oxidase I (COI) (Palumbi and Benzie, 1991; Ward et al., 2005; Vrijenhoek, 2009; Crampton-Platt et al., 2016).

The mitochondrial genome, plays a vital role in all eukaryotic organisms to infer the ancient evolutionary relationships (Boore, 1999). Within vertebrates, the mitochondrial genome is highly compacted, typically measuring around 16 to 17 kilobase pairs in length, and demonstrates remarkable conservation in the assortment of genes they harbor (Anderson et al., 1981). The mitogenome predominantly encodes 13 protein-coding genes

(PCGs), two ribosomal RNAs (rRNAs), and 22 transfer RNAs (tRNAs), alongside one noncoding gene known as the control region (CR) (Iborra et al., 2004). Furthermore, mitochondrial genes exhibit a high level of conserved genetic traits across different taxa especially bilaterian metazoans, demonstrating unique similarities in both size and base composition (Gissi et al., 2008). These genes are a crucial element within the genetic arsenal of eukaryotic cells facilitating their use in evolutionary studies (Dowling and Wolff, 2023). Therefore, it is essential to elucidate the configuration and variability of the mitogenome in every organism in order to grasp its functionalities and possible genetic alteration arising from mutations (Guo et al., 2023). Furthermore, beyond the mitochondrial and nuclear partial genes, the complete mitochondrial genomes have been successfully used to study various aspects in biodiversity research (Rubinoff, 2006; Johnstone et al., 2007; Tang et al., 2014; Margaryan et al., 2021).

1. Systematic status and distribution of *Selene* species

The family Carangidae, within the order Carangiformes, encompasses a diverse group of marine species commonly referred to as jacks, trevallies, scads, amberjacks, queenfishes, runners, pilot fish, and pompanos. These species are widely distributed across tropical and subtropical marine ecosystems, where they occupy various ecological niches (Amponsah et al., 2021). Carangids are essential to coastal pelagic fish communities, contributing

significantly to global fisheries due to their economic value. Their broad distribution and commercial importance underscore their role in marine biodiversity and highlight their impact on global seafood markets (Reuben et al., 1992). This taxonomic order comprises a total of 1103 valid species under 198 genera throughout the world with most species' rich families being Bothidae (169 species), Carangidae (153 species), Cynoglossidae (168 species) and Soleidae (179 species). The family Carangidae is represented by 39 genera under four subfamilies Caranginae, Naucratinae, Scomberoidinae and Trachinotinae (Fricke et al., 2024). Compared to other subfamilies, the Caranginae comprises 104 valid species under 29 genera. The moonfish genus *Selene* is one of the unique members of the subfamily Caranginae with six valid species distributed globally. Among them, five species (*Selene brevoortii*, *Selene brownii*, *Selene peruviana*, *Selene setapinnis*, and *Selene vomer*) are distributed in Eastern Pacific and Western Atlantic oceans. However, a single species the African Moon fish (*Selene dorsalis*) is distributed from Eastern Atlantic to Southwestern Mediterranean Sea (Vella and Deidun, 2009; Panda et al., 2012).

The African moon fish (*Selene dorsalis*) is an economically important fish species native to the Atlantic Ocean (Portugal south to South Africa, including Madeira, Cape Verde Islands and São Tomé and Príncipe). (Efe et al., 2019). Beyond its native range, *Selene dorsalis* has also been reported from the Central Mediterranean Sea near Munxar Reef, situated in the shallow waters off the southeastern coastline of the island of Malta (Vella and Deidun, 2009; Panda et al., 2012; Amponsah et al., 2021). This unparalleled distribution could be as a result of introduction or migration of the species into colder

regions due to ongoing warming oceanic temperatures in the Gulf of Guinea (Odekunle and Eludoyin, 2008) . In addition, according to the United Nations Food and Agriculture Organization (FAO), the African moon fish is a common component of the ichthyofauna of the Gulf of Guinea and a highly demanded species in Ghana contributing to the annual per capita consumption of 25kg . Furthermore, a recent study estimates that the exploitation rate of the African moon fish is greatly harvested within the tropical fishing zones (Amponsah et al 2021). Despite the extensive anthropogenic pressure, the International Union for Conservation of Nature (IUCN) Red List categorized the conservation status of all *Selene* species under 'Least Concern'. (www.iucnredlist.org).

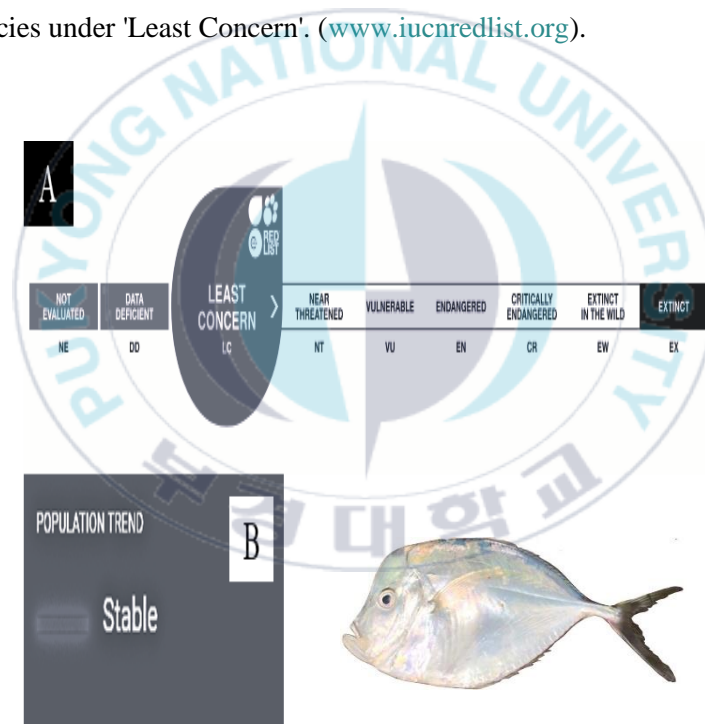
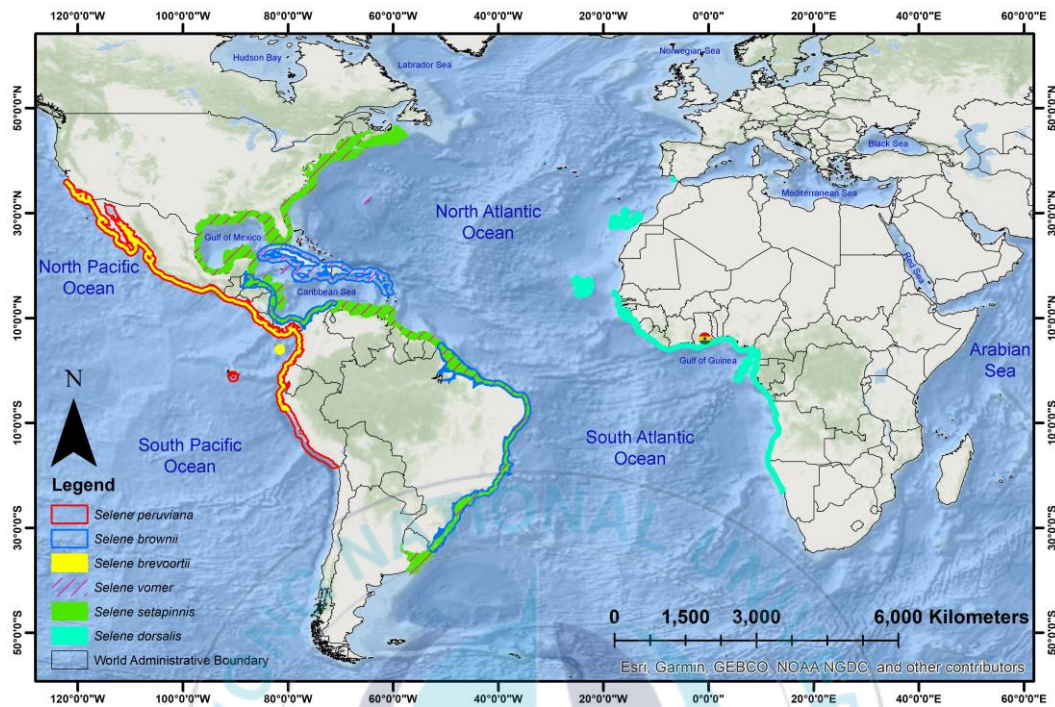


Fig. 1. *Selene dorsalis* IUCN Red list status (A) and population trend status (B).



Sampling location in Ghana

Fig. 2. Geographical distribution range of six *Selene* species (*Selene brevoortii*, *Selene brownii*, *Selene peruviana*, *Selene setapinnis*, *Selene vomer*, and *Selene dorsalis*).

1.1 Taxonomy of *Selene dorsalis*

The taxonomical classification of *Selene dorsalis* is as follows (Froese and Pauly., 2024)

Kingdom: Animalia

Phylum: Chordata

Class: Actinopterygii (ray-finned fishes)

Order: Carangiformes

Family: Carangidae

Genus: *Selene*

Species: *Selene dorsalis*

1.2 Morphological characteristics

Selene dorsalis, commonly known as the African moonfish or lookdown, is named for its distinct head profile, eye placement, and unique body structure which is horizontally compressed with a deep, rounded profile (Vella and Deidun, 2009). This distinctive morphology, including the flattened, almost disk-like body, is a characteristic trait observed across other species within the *Selene* genus of the Carangidae family, suggesting a shared evolutionary adaptation among these carangids (Reed et al., 2001).

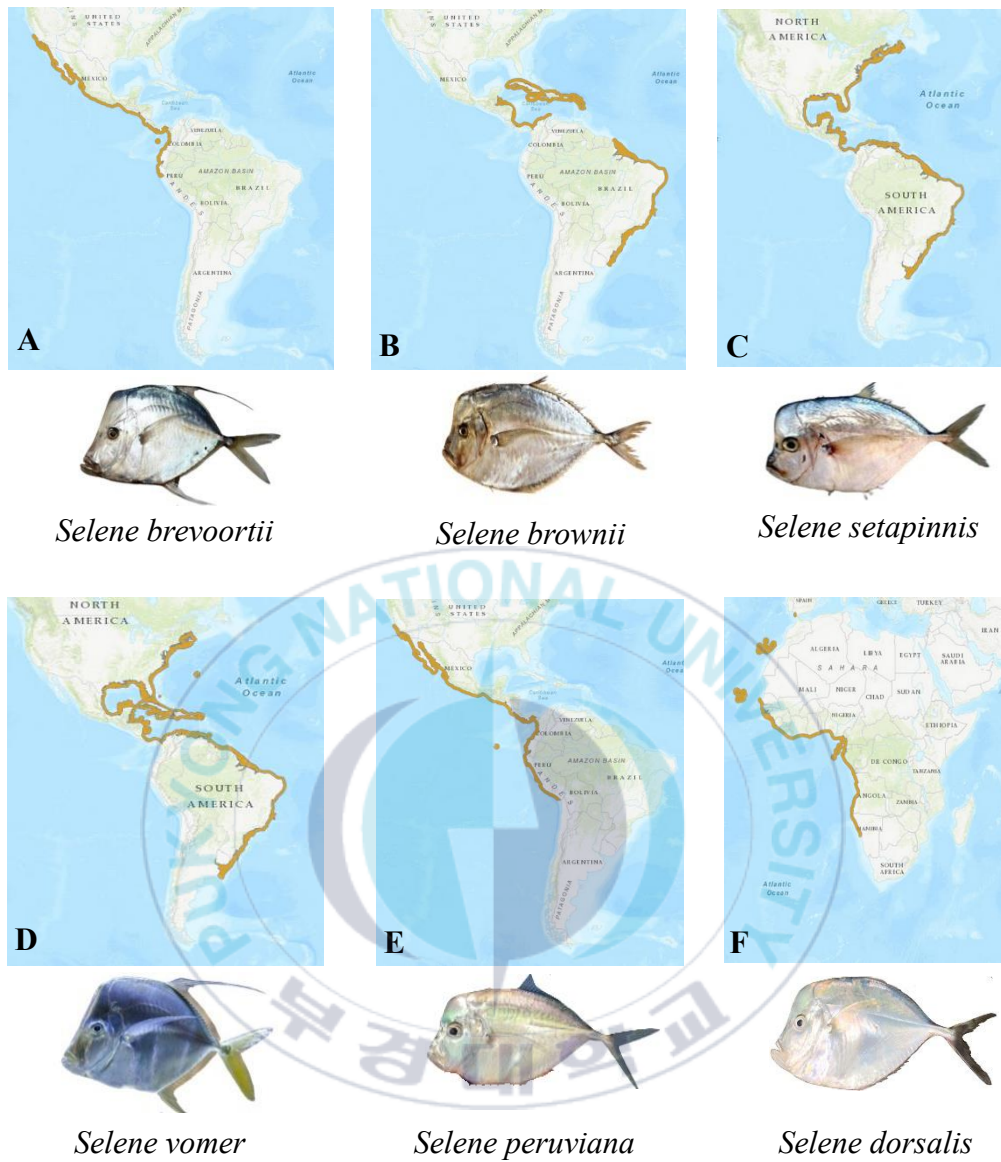


Fig. 3. Distribution map and images of all 6 members of the Selene genus.

1.3 Research advancements and gap in carangid systematics

Research on the African moonfish (*Selene dorsalis*) has predominantly addressed its biology, ecology, and taxonomy (Vella & Deidun, 2009; Arra et al., 2018; Amponsah et al., 2021). Since genetic and physiological changes are closely linked to a species' ecological role, genetic information from native and expanded ranges is vital (Massuti & Stefanescu, 1992; Biro et al., 2007). Detailed genetic data, such as mitochondrial genomes, are crucial for understanding taxonomic classification, evolutionary history, and population structure, which inform effective management policies (Moritz, 1994; Rubinoff, 2006). In Carangidae species, molecular studies have been prioritized due to their variable morphological traits and frequent taxonomic revisions (Kimura et al., 2022). Early genetic studies on *Selene* species focused on mitochondrial Cytb gene analysis to clarify species classification (Reed et al., 2001). Recent investigations include the nuclear RNF213 marker and multi-gene studies to resolve acanthomorph phylogeny and carangid taxonomy (Li et al., 2009; Damerau et al., 2018). Furthermore, mitochondrial DNA barcoding of *Selene* species supports fish identification for management, ornamental trade, and regulatory databases (Yancy et al., 2008; Steinke et al., 2009). Studies have analyzed partial mitochondrial genes across various ecosystems, such as São Paulo, the Caribbean, and the North Atlantic, enhancing genetic diversity understanding (Ribeiro et al., 2012; Weigt et al., 2012). The incorporation of *Selene* sequences in phylogenetic analyses aids in mapping bony fish classification and evolutionary pathways (Betancur et al., 2013; Sanciangco et

al., 2016). Beyond taxonomy and evolutionary studies, *Selene* DNA sequences contribute to a reference library for DNA-based fish and seafood identification, predator-prey dynamics, and environmental DNA research (Deeds et al., 2014; Aguilar et al., 2017). In recent past, the complete mitochondrial genomes of two *Selene* species, *Selene setapinnis* and *Selene vomer*, were sequenced (Hoban et al., 2022; Alvarenga et al., 2024). However, prior studies have not thoroughly analyzed the structural organization or genetic variability within these mitogenomes, which is essential for understanding gene features, structural variability, and maternal phylogenetics (Sato et al., 2016; Kundu et al., 2024). Moreover, both sequenced species are found in the Western Atlantic, including the Gulf of Mexico and the Caribbean, leaving a significant gap in research concerning the evolutionary relationships and diversification patterns of *Selene* species in the Eastern Atlantic, such as *Selene dorsalis*.

The objectives of this study are:

1. To generate the DNA barcode region (Mt COXI) to confirm morphology-based species identification.
2. To generate the complete mitochondrial sequences through next-generation sequencing (NGS) and illuminating structural features compared to other congeners.
3. To elucidate the mitogenomic phylogeny for evaluating the evolutionary position of *Selene dorsalis* compared with other carangids and illuminating their lineage diversification and dispersal pattern in the Atlantic Ocean.

Materials and Methods

1. Sample collection and species identification

A single specimen of moonfish was collected from the Atlantic Ocean at (5.611389 N 0.044444 W) on 22nd February 2024. The studied species was identified to be *Selene dorsalis* using taxonomic keys as described by previous studies (Wirtz et al. 2013; Kimura et al. 2022) followed by the preservation of specimen with novel voucher number (GH1) at the Fisheries Scientific Survey Division of Ghana. Under aseptic conditions, about 20g of tissue from the apical muscle was extracted and preserved in 95% molecular grade ethanol in a 2 ml centrifuge tube and stored in a -20°C freezer. The tissue sample was forwarded to the Molecular Physiology laboratory at Pukyong National University, South Korea under the same voucher code 'GH1' for downstream molecular experiments. The distribution data of *Selene dorsalis* and other *Selene* species were obtained from IUCN (<https://www.iucnredlist.org/>) and mapped to understand their unique biogeographic distribution in both eastern and western Atlantic and Pacific Ocean. The fish was caught by local fishermen and the dead individuals collected by the researcher, hence the sample does not involve any act of animal ethics. Further, the molecular data generation and analyses were approved by the host institution Pukyong National University (PKNUIACUC-2022-72) and confirms that the use of biological material in the

experiments adhered to ethical standards.



Fig. 4. Sampling location of *Selene dorsalis* in the Eastern Atlantic Ocean (5.611389 N 0.044444 W) Ghana.

1.1 Genomic DNA (gDNA) extraction and partial gene sequencing

The AccuPrep® Genomic DNA extraction kit (Bioneer, Republic of Korea) was employed to extract the genomic DNA following the manufacturer's standard protocols. The quality of the extracted DNA was systematically determined using NanoDrop spectrophotometer (Thermo Fisher Scientific D1000). In detail, 30 mg tissue of the target

specimen was subjected to homogenization in 600 µl 1X lyse buffer, making use of a mechanized Tissue Lyser II (Qiagen, Hilden, Germany) for 60 seconds. The sodium dodecyl sulfate (SDS) (100 µl) and proteolytic enzyme proteinase k (20 µl) were introduced to disrupt cell membrane and degrade proteins, this was followed by an incubation period on a heat block at 60°C for 12 hours. Consequently, 500 µl of GC buffer and 300 µl of isopropanol were appended to the mixture to facilitate precipitation of target DNA, this was later transferred into a column tube and centrifuged at 8,000 rpm for one minute. The application of washing buffers 1 and 2 assisted in eradicating any residual biomolecular substances, and finally 50 µl of TE buffer was applied to elute the target DNA.

Subject to the DNA extraction, polymerase chain reaction (PCR) was conducted utilizing the universal primers FISH-BCH (5'-TAAACTTCAGGGTGACCAAAAATCA) and FISH-BCL (5'-TCAACYAATCAYAAAGATATYGGCAC) to amplify the partial Cytochrome C oxidase subunit I (COI) for preliminary DNA sequence-based species confirmation (Baldwin et al., 2009). The PCR was performed by Takara PCR thermal cycler in a 30 µL reaction mixture constituting 1 µl each of forward and reverse primers, 0.9 µl dimethyl Sulfoxide (3% DMSO), 19.9 µl sterilized deionized water, 3 µl of 10X ExTaq Buffer, 0.2 µl Ex Taq HS enzyme, 3 µl dNTPs and 1 µl of target DNA template (1/10 diluted) with the thermal profile of an initial denaturation temperature of 94°C for 3 minutes followed by 40 cycles of denaturation at 94°C (30 seconds), annealing at 50°C (30 seconds), extension at 72°C (1 minute) and one cycle of final extension at 72°C for 5 minutes. The purification of the PCR product was accomplished using AccuPrep® PCR/Gel purification kit (Bioneer,

Republic of Korea) and sequenced bi-directionally in 96 capillaries automated ABI PRISM 3730XL Analyzer at Macrogen (<https://dna.macrogen.com/>) (Daejeon, Republic of Korea). The noisy part from the bi-directional chromatograms results were removed by using SeqScanner version 1.0 (Applied Biosystems Inc., CA, USA). Subsequently, the generated COI sequence of the targeted species was determined by confirming through nucleotide BLAST search (<https://blast.ncbi.nlm.nih.gov>) in global GenBank database.

Table 1. Composition of PCR reaction mixture

Name	Volume
Forward primer	1 μ L
Reverse primer	1 μ L
Dimethyl Sulfoxide (3% DMSO)	0.9 μ L
Sterilized deionized water	19.9 μ L
10X ExTaq Buffer (TaKaRa Bio, Inc.)	3 μ l
Ex Taq HS enzyme (TaKaRa Bio, Inc.)	0.2 μ l
Deoxynucleotide triphosphates (dNTPs) mixture (2.5 μ l Takara, Japan)	3 μ l
DNA template (1/10 diluted)	1 μ l

Table 2. A PCR thermal profile

	Temperature	Time
Initial denaturation	94°C	3 minutes
Denaturation	94°C	30 seconds
Annealing	50°C	30 seconds
Extension	72°C	1 minute
Final extension	72°C	5 minutes
4°C	4°C	∞

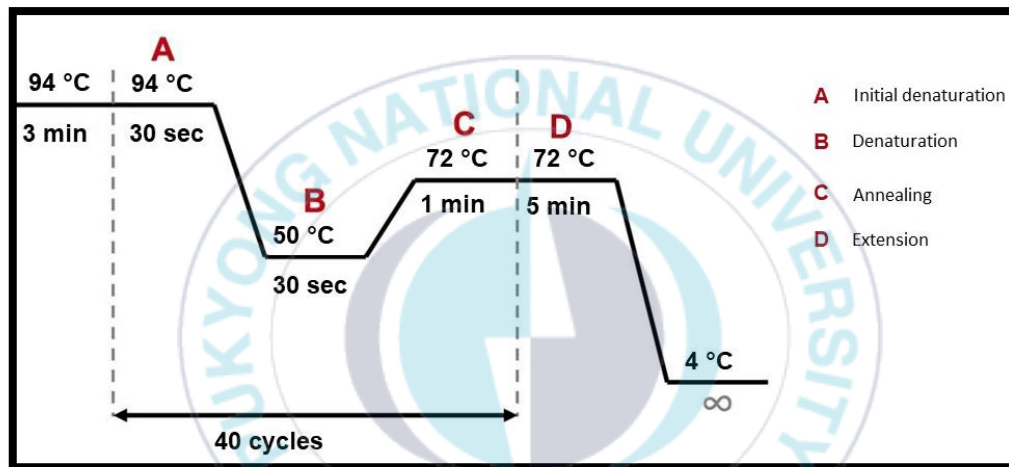


Fig 5. PCR temperature profile graph depicting the denaturation, annealing and extension temperatures.

1.2 Mitogenome sequencing and assembly

To obtain the complete mitogenome of *Selene dorsalis*, the paired-end (2×150 bp) next-generation sequencing (NGS) procedure was carried out on NovaSeq platform at Macrogen (Illumina, Inc., San Diego, CA, USA). Sequencing libraries were prepared according to the manufacturer's specifications for the TruSeq Nano DNA High-Throughput Library Prep Kit (Illumina, Inc., San Diego, CA, USA). The 100 ng of genomic DNA underwent fragmentation utilizing adaptive focused acoustic technology (Covaris, Woburn, MA, USA), resulting in double-stranded DNA molecules with blunt ends and 5'-phosphorylation. Following the end-repair step, DNA fragments were size-selected using a bead-based method, modified with the addition of a single 'A' base, and ligated with TruSeq DNA UD Indexing adapters. The products were purified and enriched through PCR to generate the final DNA library. Library quantification was carried out using qPCR, following the qPCR Quantification Protocol Guide (KAPA Library Quantification Kits for Illumina Sequencing Platforms), and a quality assessment was performed using Agilent Technologies 4200 TapeStation D1000 screentape (Agilent Technologies, Santa Clara, CA, USA). The Geneious Prime v2023.0.1 was employed to assemble high-quality NGS sequences and mapped with the reference mitogenome (*Selene vomer* Accession No. PP033011) (Kearse et al., 2012). Through the utilization of conventional mapping procedures, the verification of PCGs was conducted by aligning overlapping regions using MEGA X software followed by the confirmation of the boundaries and directions of other

genes using MITOS Galaxy web server (<http://mitos.bioinf.uni-leipzig.de>) and MitoAnnotator (<http://mitofish.aori.u-tokyo.ac.jp/annotation/input/>) (Bernt et al., 2013; Iwasaki et al., 2013; Tamura et al., 2021). Additionally, the boundaries of each PCGs were further confirmed through Open Reading frame (<https://www.ncbi.nlm.nih.gov/orffinder/>) after translation into respective amino acids. The final mitogenome of *Selene dorsalis* was submitted to Genbank database to acquire the unique accession number.

1.3 Characterization and comparative analyses

To generate a three-dimensional representation of the generated mitogenome, MitoAnnotator was employed. The primary aim for the detailed analyses of the obtained sequences was to fully characterize the mitogenome, and determine profound variations in comparison with two existing mitogenomes of the genus *Selene* (*Selene vomer*: PP033011 and *Selene setapinnis*: OR575618). The intergenic spacers between contiguous genes along with overlapping regions were manually calculated. Nucleotide compositions of 13 PCGs, two rRNAs, 22 tRNAs, and CR were determined using MEGA X (Kumar et al., 2018). Through a sliding window approach, an examination of the nucleotide diversity (P_i) was determined employing a window size of 200 bp and a step size of 25 bp, executed in DnaSP6.0 (Rozas et al., 2017). Base composition skews were determined using the established formulas: $AT\text{-skew} = [A - T]/[A + T]$ and $GC\text{-skew} = [G - C]/[G + C]$ (Perna and Kocher, 1995). With the application of DAMBE6, the AT and GC skew in addition to

the saturation codon of the PCGs based on transition (s) and transversion (v) were illustrated (Xia., 2017). The initiation and termination codon for each PCG in adherence to the vertebrate mitochondrial genetic code was determined using MEGAX in conjunction with MITOS. Further analyses involved the precise calculation of the relative frequency of amino acids, relative synonymous codon usage (RSCU), and pairwise comparisons for synonymous (Ks) and nonsynonymous (Ka) substitutions between *Selene dorsalis* and two other *Selene* species through DnaSP6.0. Consequently, tRNAscan-SE Search Server 2.0 in combination with ARWEN 1.2 was used to validate the boundaries of rRNA and tRNA genes (Laslett and Canbäck, 2008; Chan and Lowe, 2016). The identification of structural domains in the control region was attained through the execution of CLUSTAL X alignments aligned with previous research (Thompson et al., 1997, Satoh et al., 2016; Kundu et al., 2023).

1.4 Dataset preparation and phylogenetic analyses

To explicate the matrilineal phylogenetic relationship within the Carangidae family, a total of 72 mitogenomes (one generated and 71 from GenBank) of 72 species from the four subfamilies were combined to construct a dataset (Table S1). The mitogenomes of two species under the family Coryphaenidae (*Coryphaena equiselis*, PP032965 and *Coryphaena hippurus*, OR582674), *Rachycentron canadum* (FJ154956) from the family Rachycentridae, and *Nematistius pectoralis* (ON838225) from the family Nematistiidae,

and four species (*Remora albescens*, OP057074; *Remora brachyptera*, OR546234; *Remora osteochir*, OR575559; and *Echeneis naucrates*, AB355905) under the family Echeneidae were designated as the outgroup following the previous studies (Santini and Carnevale 2015, Glass et al., 2023). The iTaxoTools 0.1 was used to build the concatenated datasets of 13 PCGs to elucidate the evolutionary relationships among the carangids, with highlights on *Selene* species within the subfamily Caranginae (Vences et al., 2021). Each PCG was separated to determine the best-fit model 'GTR+G+I' with lowest BIC scores of the dataset, using PartitionFinder 2 and JModelTest v2 (Miller et al 2015; Lanfear et al., 2017). The Bayesian (BA) tree was constructed utilizing Mr. Bayes 3.1.2, integrating a probability distribution algorithm known as metropolis-coupled Markov chain Monte Carlo (MCMC) with nst = 6. This process run over 10,000,000 generations, with samples collected at each 100th generation, of which 25% were considered discarded in burn-in (Ronquist and Huelsenbeck, 2003). The generated tree was subjected to visualization through the iTOL v4 web server for better visualisation (Letunic et al., 2007).

Results and Discussion

1. Mitogenome structure and organization

In this study, the mitogenome of *Selene dorsalis* was sequenced, revealing a length of 16,541 bp (GenBank accession PP857611) and comprising 13 protein-coding genes (PCGs), 22 transfer RNAs (tRNAs), two ribosomal RNAs (rRNAs), and an AT-rich control region. Notably, *S. dorsalis* exhibited the shortest mitogenome among documented *Selene* species, with *S. vomer* measuring 16,558 bp (GenBank PP033011). Gene organization showed that 28 genes (12 PCGs, 14 tRNAs, and two rRNAs) are located on the heavy strand, while the ND6 PCG and eight tRNAs are housed on the light strand. The mitogenome of *S. dorsalis* displayed an AT content of 53.13%, with nucleotide frequencies of 27.48% A, 25.66% T, 30.18% C, and 16.69% G. AT and GC skews were 0.034 and -0.288, respectively, similar to skews observed in *S. vomer* and *S. setapinnis*. *S. dorsalis* contained 19 overlapping regions totaling 40 bp, the longest being a 10 bp overlap between ATP6 and ATP8. Three PCG overlaps consistent across *Selene* species were identified, including ND4L (7 bp), ND5 (4 bp), and ATP8 (10 bp), while tRNA-Asn exhibited the longest intergenic spacer at 37 bp. These findings on mitogenomic structure and variability in *Selene* species provide valuable insights into evolutionary mechanisms, gene function, and metabolic adaptations, aligning with similar trends observed in other teleost fish

(Brown, 2008). This study thus adds critical knowledge to the mitogenomic features and functional genetics within the *Selene* genus.



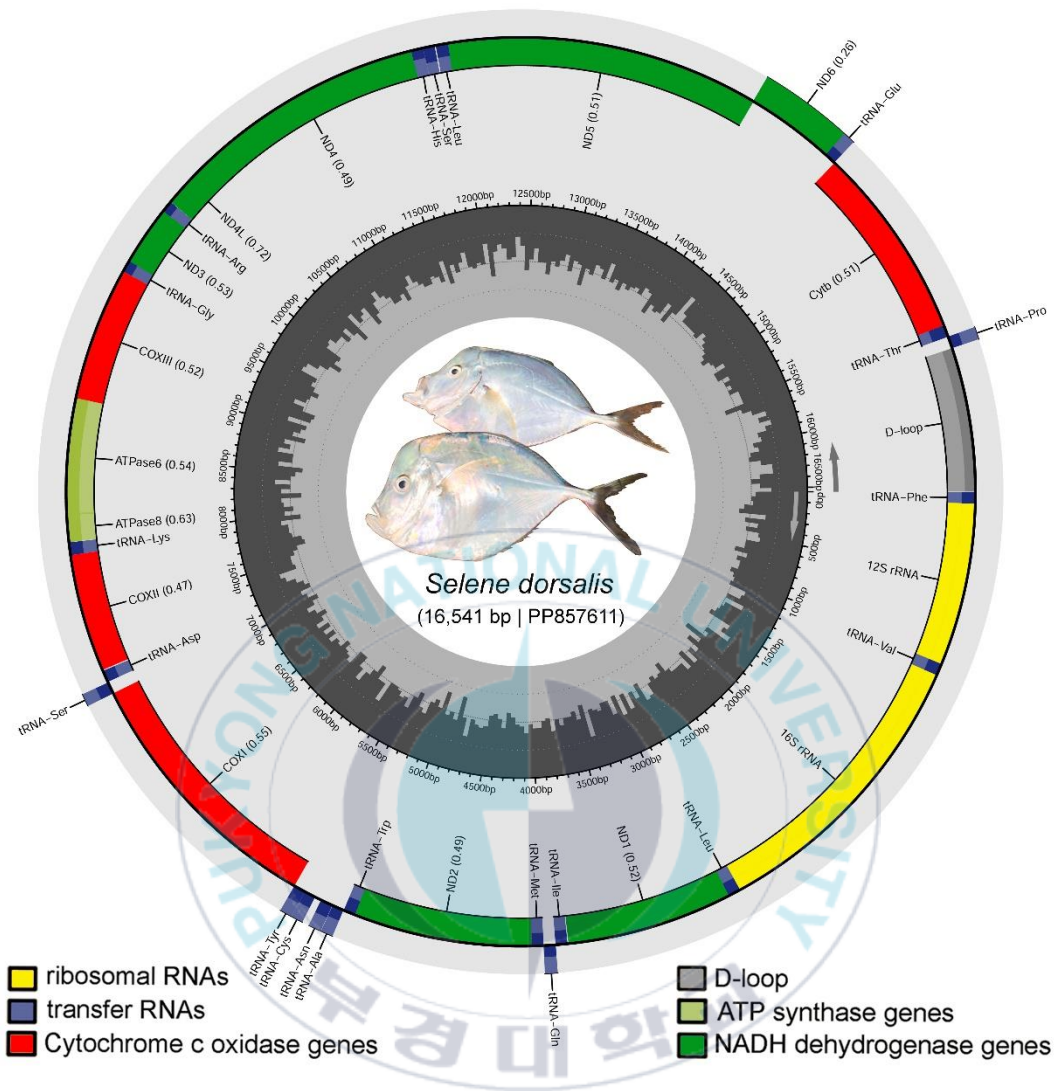


Fig. 6. The circular mitochondrial genome of *Selene dorsalis* is represented and annotated using the MitoAnnotator online server. Different color arcs indicate different PCGs, rRNAs, tRNAs, and CR. Species.

Table 3. List of annotated mitochondrial genes, including their boundaries, sizes, and intergenic nucleotides (IN) for *Selene dorsalis*

Genes	Start	Stop	Size (bp)	Strand	IN	Start codon	Stop codon	Anti-codon
<i>tRNA-Phe (F)</i>	1	68	68	+	-1			GAA
<i>12S rRNA</i>	68	1022	955	+	-1			
<i>tRNA-Val (V)</i>	1022	1094	73	+	0			TAC
<i>16S rRNA</i>	1095	2809	1715	+	-1			
<i>tRNA-Leu (L2)</i>	2809	2883	75	+	0			TAA
<i>ND1</i>	2884	3858	975	+	4	ATG	TAA	
<i>tRNA-Ile (I)</i>	3863	3933	71	+	-2			GAT
<i>tRNA-Gln (Q)</i>	3932	4003	72	-	-2			TTG
<i>tRNA-Met (M)</i>	4002	4072	71	+	0			CAT
<i>ND2</i>	4073	5117	1045	+	-1	ATG	T--	
<i>tRNA-Trp (W)</i>	5117	5188	72	+	0			TCA
<i>tRNA-Ala (A)</i>	5189	5258	70	-	0			TGC
<i>tRNA-Asn (N)</i>	5259	5332	74	-	37			GTT
<i>tRNA-Cys (C)</i>	5370	5437	68	-	-1			GCA
<i>tRNA-Tyr (Y)</i>	5437	5507	71	-	1			GTA
<i>COI</i>	5509	7059	1551	+	-1	GTG	TAA	
<i>tRNA-Ser (S2)</i>	7059	7130	72	-	2			TGA
<i>tRNA-Asp (D)</i>	7133	7203	71	+	7			GTC
<i>COII</i>	7211	7901	691	+	-1	ATG	T--	
<i>tRNA-Lys (K)</i>	7901	7976	76	+	1			TTT
<i>ATP8</i>	7978	8145	168	+	-10	ATG	TAA	
<i>ATP6</i>	8136	8818	683	+	0	ATG	TA-	
<i>COIII</i>	8819	9603	785	+	-1	ATG	TAA	
<i>tRNA-Gly (G)</i>	9603	9673	71	+	0			TCC
<i>ND3</i>	9674	10022	349	+	-1	ATG	T--	
<i>tRNA-Arg (R)</i>	10022	10091	70	+	1			TCG
<i>ND4L</i>	10093	10389	297	+	-7	ATG	TAA	
<i>ND4</i>	10383	11763	1381	+	-1	ATG	T--	
<i>tRNA-His (H)</i>	11763	11835	73	+	-1			GTG
<i>tRNA-Ser (S1)</i>	11835	11903	69	+	5			GCT
<i>tRNA-Leu (L1)</i>	11909	11982	74	+	0			TAG
<i>ND5</i>	11983	13821	1839	+	-4	ATG	TAA	
<i>ND6</i>	13818	14339	522	-	-1			
<i>tRNA-Glu (E)</i>	14339	14408	70	-	3			TTC
<i>CYTb</i>	14412	15552	1141	+	-1	ATG	TAA	
<i>tRNA-Thr (T)</i>	15552	15624	73	+	-2			TGT
<i>tRNA-Pro (P)</i>	15623	15694	72	-	0			TGG
<i>Control region</i>	15695	16541	847	+	-16542			

Table 4. Nucleotide composition of mitochondrial genomes across different *Selene* species

Species Name	Size (bp)	A%	T%	G%	C%	A+T%	AT-Skew	GC-Skew
Complete mitogenome								
<i>Selene dorsalis</i>	16541	27.48	25.66	16.69	30.18	53.13	0.034	-0.288
<i>Selene vomer</i>	16558	27.79	25.56	16.20	30.44	53.35	0.042	-0.305
PCGs								
<i>Selene dorsalis</i>	11427	25.83	26.63	15.29	32.25	52.46	-0.015	-0.357
<i>Selene vomer</i>	11428	26.29	26.33	14.77	32.61	52.62	-0.001	-0.377
<i>Selene setapinnis</i>	11427	25.11	27.04	16.12	31.73	52.15	-0.037	-0.326
tRNAs								
<i>Selene dorsalis</i>	1576	30.65	24.37	19.92	25.06	55.01	0.114	-0.114
<i>Selene vomer</i>	1556	30.59	24.23	20.18	25.00	54.82	0.116	-0.107
<i>Selene setapinnis</i>	1415	27.63	27.56	23.89	20.92	55.19	0.001	0.066
rRNAs								
<i>Selene dorsalis</i>	2670	31.161	21.12	21.31	26.40	52.28	0.192	-0.107
<i>Selene vomer</i>	2669	31.285	21.06	21.06	26.60	52.34	0.195	-0.116
CRs								
<i>Selene dorsalis</i>	847	32.59	30.22	14.64	22.55	62.81	0.038	-0.213
<i>Selene vomer</i>	862	32.60	32.02	12.99	22.39	64.62	0.009	-0.266
<i>Selene setapinnis</i>	718	34.68	30.50	14.35	20.47	65.18	0.064	-0.176

Table 5. Comparison of intergenic nucleotides of three different *Selene* species mitogenomes

Genes	<i>Selene dorsalis</i>	<i>Selene vomer</i>	<i>Selene setapinnis</i>
<i>tRNA-Phe (F)</i>	-1	0	-1
<i>12S rRNA</i>	-1	0	-1
<i>tRNA-Val (V)</i>	0	0	0
<i>16S rRNA</i>	-1	0	0
<i>tRNA-Leu (L2)</i>	0	0	0
<i>ND1</i>	4	5	5
<i>tRNA-Ile (I)</i>	-2	-1	-1
<i>tRNA-Gln (Q)</i>	-2	-1	-1
<i>tRNA-Met (M)</i>	0	0	0
<i>ND2</i>	-1	0	0
<i>tRNA-Trp (W)</i>	0	1	1
<i>tRNA-Ala (A)</i>	0	1	1
<i>tRNA-Asn (N)</i>	37	38	38
<i>tRNA-Cys (C)</i>	-1	0	0
<i>tRNA-Tyr (Y)</i>	1	1	1
<i>COI</i>	-1	0	0
<i>tRNA-Ser (S2)</i>	2	3	3
<i>tRNA-Asp (D)</i>	7	7	7
<i>COII</i>	-1	0	0
<i>tRNA-Lys (K)</i>	1	1	1
<i>ATP8</i>	-10	-10	-10
<i>ATP6</i>	0	-1	-1
<i>COIII</i>	-1	0	0

<i>tRNA-Gly (G)</i>	0	0	0
<i>ND3</i>	-1	0	0
<i>tRNA-Arg (R)</i>	1	1	1
<i>ND4L</i>	-7	-7	-7
<i>ND4</i>	-1	0	0
<i>tRNA-His (H)</i>	-1	0	0
<i>tRNA-Ser (S1)</i>	5	6	6
<i>tRNA-Leu (L1)</i>	0	0	0
<i>ND5</i>	-4	-4	-4
<i>ND6</i>	-1	0	0
<i>tRNA-Glu (E)</i>	3	4	3
<i>Cyt b</i>	-1	0	0
<i>tRNA-Thr (T)</i>	-2	-1	-1
<i>tRNA-Pro (P)</i>	0	0	-1
<i>Control region</i>	-	-	-

1.1 Protein-coding genes

The mitogenome of *Selene dorsalis* encompassed 13 PCGs amassing a total length of 11,427 bp representing 69.10 % of the total mitogenome. The shortest length was observed in *ATP8* (168 bp) and the longest in *ND5* (1839 bp). Two species, *Selene dorsalis* and *Selene setapinnis* demonstrated similar lengths of PCGs of 11,427 bp, contrasting with *Selene vomer* which displayed the lengthiest PCGs at 11,428 bp. Out of the 13 PCGs, 12 PCGs of the mitogenome of *Selene dorsalis* exhibited an initiation code of ATG (Methionine) in contrast to GTG for *COI*. The typical termination codon TAA was

observed in (*ND1, ND4L, ND5, COI, and ATP8*) except for (*ND2, ND3, ND4, COII, COIII, ATP6 and CYTB*) with incomplete termination codons, these incomplete termination codons detected could possibly be terminated with TAA through the process of polyadenylation during RNA maturation (Ojala et al., 1981). Comparative analyses of the protein coding genes (PCGs) of the *Selene* species revealed AT-skews ranging from -0.015 (*Selene dorsalis*), -0.001 (*Selene Vomer*) and -0.037 (*Selene setapinnis*). Additionally, GC-skew ranged from -0.357 (*Selene dorsalis*), -0.377 (*Selene vomer*) and -0.326 (*Selene setapinnis*). Results from nucleotide diversity studies employing a sliding window analysis on concatenated PCGs, revealed a nucleotide diversity value (P_i) of 0.07357. The detected genetic modifications could potentially result in the independent preferential adoption, positive selection and the evolution in amino acids of PCGs (Consuegra et al., 2015; Hill et al., 2019). These PCGs are accountable for encoding proteins needed in the electron transport pathways, performing essential functions in oxidative phosphorylation and adenosine triphosphate (ATP) synthesis. Hence, the examination of additional mitogenomes from different *Selene* species can be conducted to reveal differences in energy metabolism and protein expression profile.

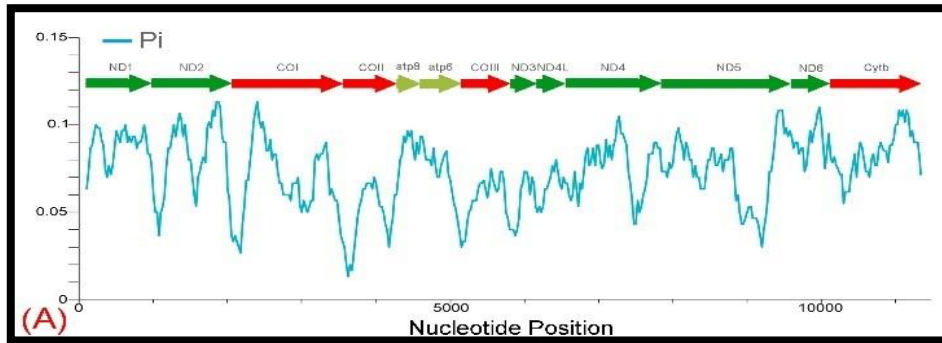


Fig 7. Genetic diversity (Pi) of mitochondrial PCGs highlighting variation among *Selene dorsalis* and Its congeners.

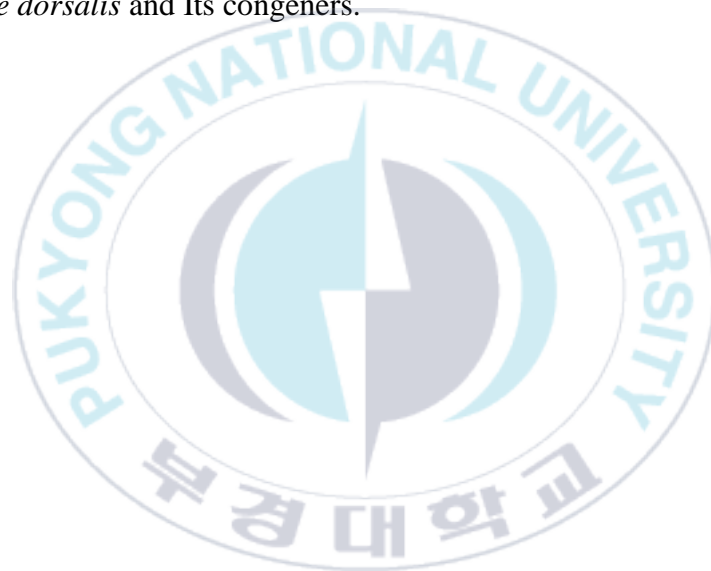


Table 6. Comparison of the start and stop codons of the PCGs across three *Selene* mitogenomes

Genes	<i>Selene dorsalis</i>		<i>Selene vomer</i>		<i>Selene setapinnis</i>	
	Start	Stop	Start	Stop	Start	Stop
<i>ND1</i>	ATG	TAA	ATG	TAA	ATG	TAA
<i>ND2</i>	ATG	T--	ATG	T--	ATG	T--
<i>COI</i>	GTG	TAA	GTG	TAA	GTG	TAA
<i>COII</i>	ATG	T--	ATG	T--	ATG	T--
<i>ATP8</i>	ATG	TAA	ATG	TAA	ATG	TAA
<i>ATP6</i>	ATG	TA-	ATG	TAA	ATG	TAA
<i>COIII</i>	ATG	TA-	ATG	TA-	ATG	TA-
<i>ND3</i>	ATG	T--	ATG	T--	ATG	T--
<i>ND4L</i>	ATG	TAA	ATG	TAA	ATG	TAA
<i>ND4</i>	ATG	T--	ATG	T--	ATG	T--
<i>ND5</i>	ATG	TAA	ATG	TAG	ATG	TAG
<i>ND6</i>	ATG	TAG	ATG	TAG	ATG	TAG
<i>Cyt b</i>	ATG	T--	ATG	T--	ATG	T--

1.2 Codon usage and substitution pattern

The utilization frequency of amino acids between the target species *Selene dorsalis* and its congeners *Selene vomer* and *Selene setapinnis* exhibited similarities with Leucine, Serine and Proline recording the highest abundance across all species while aspartic acid, cysteine and glutamic acid recorded the least abundance (Fig. 6).

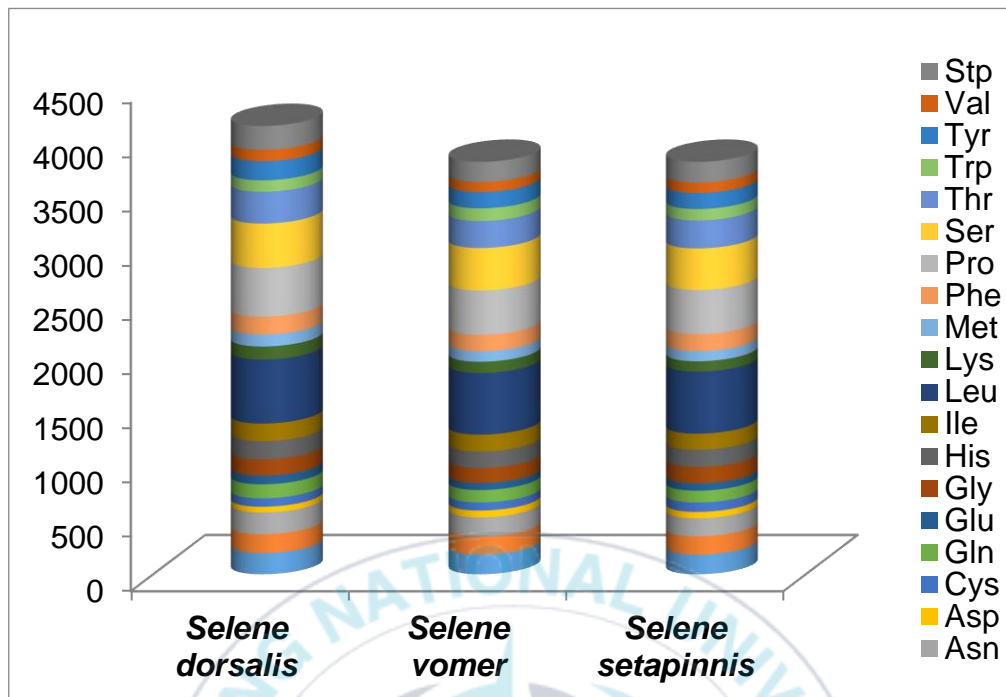


Fig. 8. Amino acid abundance of three *Selene* species (*Selene dorsalis*, *Selene vomer* and *Selene setapinnis*).

Analysis of RSCU revealed a collective count of codon transcriptions for the 20 amino acids, 3,912 counts were observed for *Selene dorsalis*, 3,616 for *Selene vomer* and 3611 for *Selene setapinnis*. In all three *Selene* species the RSCU values are larger in Leucine and Serine as compared with other amino acids due to the combination of six types of coding nucleotides (Fig. 7). The computation of the nonsynonymous (Ka) and synonymous (Ks) substitution ratio validated that each PCG present in the mitogenome of *Selene dorsalis*

and its related species within the Carangidae family are under the influence of comparable selective pressure. Average values recorded for pairwise Ka/Ks values ranged from a low of '0' (*ND3* and *ND4L*) to a high of 0.0324 ± 0.00049 (*ND2*). This is represented by the order *ND3* < *ND4L* < *COX1* < *COX3* < *ND6* < *ATP6* < *ND4* < *COX2* < *ND5* < *ND1* < *CYTB* < *ATP8* < *ND2*. The Ka/Ks value is broadly accepted as a strong indicator used to measure the degree of selective pressure under the framework of Darwinian theory, thus simulating the evolutionary influences recognized at a molecular scale is crucial across both homogeneous and heterogeneous selection of species (Yang et al., 2000). According to Elmer et al (2010), Ka/Ks ratio are very essential for evaluating selective pressure, values exceeding '1' validates purifying selection, a value of '1' indicates neutral selection, and values below '1' suggests negative selection. Results from this study revealed that all Ka/Ks values were below '1' suggesting strong negative selection among three *Selene* species (*Selene dorsalis*, *Selene vomer* and *Selene setapinnis*) (Table S4). This phenomenon mirrors the effects of natural selection in reducing destructive mutations with adverse selective factors consistent with trends observed in various vertebrate species, such as teleost's (Kundu et al., 2024). In addition, the investigation of Ka/Ks ratios derived from the mitogenomes of *Selene* provides a platform for obtaining new perceptions into the shades of natural selection which comprises the evolutionary path and dispersion within these species, aiding in elucidating the complex interaction between mutations and selective pressures, and clarifying their combined impact on guiding protein evolution.

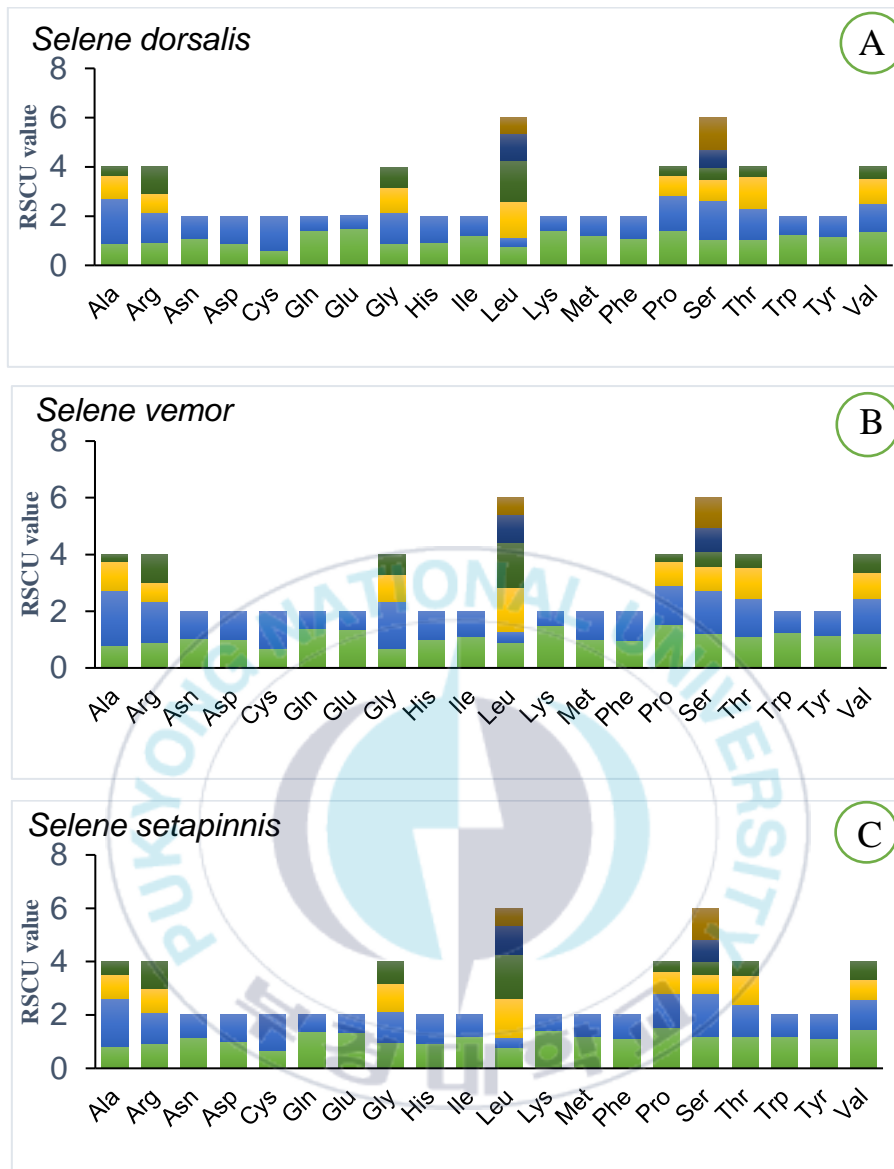


Fig. 9. Relative synonymous codon usage (RSCU) of three *Selene* species (*Selene dorsalis* (A), *Selene vomer* (B) and *Selene setapinnis* (C)).

Table 7. Amino acid composition and RSCU values of the complete PCGs in three *Selene* species

<i>Selene dorsalis</i>											
Codon	Count	RSCU	Codon	Count	RSCU	Codon	Count	RSCU	Codon	Count	RSCU
UUU(F)	91	1.11	UCU(S)	72	1.06	UAU(Y)	102	1.16	UGU(C)	24	0.62
UUC(F)	73	0.89	UCC(S)	108	1.59	UAC(Y)	74	0.84	UGC(C)	54	1.38
UUA(L)	76	0.77	UCA(S)	58	0.85	UAA(*)	85	1.55	UGA(W)	66	1.26
UUG(L)	36	0.37	UCG(S)	32	0.47	UAG(*)	26	0.47	UGG(W)	39	0.74
CUU(L)	142	1.44	CCU(P)	159	1.42	CAU(H)	78	0.93	CGU(R)	41	0.94
CUC(L)	164	1.66	CCC(P)	157	1.4	CAC(H)	90	1.07	CGC(R)	53	1.21
CUA(L)	110	1.12	CCA(P)	94	0.84	CAA(Q)	90	1.4	CGA(R)	34	0.78
CUG(L)	63	0.64	CCG(P)	39	0.35	CAG(Q)	39	0.6	CGG(R)	47	1.07
AUU(I)	98	1.22	ACU(T)	77	1.05	AAU(N)	110	1.1	AGU(S)	50	0.74
AUC(I)	63	0.78	ACC(T)	93	1.27	AAC(N)	90	0.9	AGC(S)	88	1.29
AUA(M)	67	1.21	ACA(T)	94	1.28	AAA(K)	84	1.4	AGA(*)	61	1.11
AUG(M)	44	0.79	ACG(T)	29	0.4	AAG(K)	36	0.6	AGG(*)	47	0.86
GUU(V)	36	1.37	GCU(A)	44	0.9	GAU(D)	23	0.87	GGU(G)	33	0.87
GUC(V)	30	1.14	GCC(A)	88	1.81	GAC(D)	30	1.13	GGC(G)	48	1.27
GUA(V)	27	1.03	GCA(A)	45	0.92	GAA(E)	59	1.48	GGA(G)	39	1.03
GUG(V)	12	0.46	GCG(A)	18	0.37	GAG(E)	21	0.53	GGG(G)	31	0.82
<i>Selene vomer</i>											
Codon	Count	RSCU	Codon	Count	RSCU	Codon	Count	RSCU	Codon	Count	RSCU
UUU(F)	74	0.98	UCU(S)	80	1.23	UAU(Y)	86	1.14	UGU(C)	25	0.67
UUC(F)	77	1.02	UCC(S)	98	1.51	UAC(Y)	65	0.86	UGC(C)	50	1.33
UUA(L)	85	0.9	UCA(S)	54	0.83	UAA(*)	57	1.23	UGA(W)	72	1.24
UUG(L)	37	0.39	UCG(S)	34	0.52	UAG(*)	30	0.65	UGG(W)	44	0.76
CUU(L)	148	1.56	CCU(P)	157	1.54	CAU(H)	75	0.99	CGU(R)	38	0.9
CUC(L)	149	1.57	CCC(P)	141	1.38	CAC(H)	77	1.01	CGC(R)	61	1.45
CUA(L)	93	0.98	CCA(P)	85	0.83	CAA(Q)	80	1.4	CGA(R)	28	0.67
CUG(L)	57	0.6	CCG(P)	26	0.25	CAG(Q)	34	0.6	CGG(R)	41	0.98

AUU(I)	86	1.11	ACU(T)	70	1.12	AAU(N)	91	1.03	AGU(S)	56	0.86
AUC(I)	69	0.89	ACC(T)	82	1.32	AAC(N)	86	0.97	AGC(S)	68	1.05
AUA(M)	49	1.01	ACA(T)	69	1.11	AAA(K)	77	1.48	AGA(*)	52	1.12
AUG(M)	48	0.99	ACG(T)	28	0.45	AAG(K)	27	0.52	AGG(*)	46	0.99
GUU(V)	28	1.22	GCU(A)	36	0.8	GAU(D)	31	1	GGU(G)	24	0.69
GUC(V)	28	1.22	GCC(A)	87	1.92	GAC(D)	31	1	GGC(G)	57	1.64
GUA(V)	21	0.91	GCA(A)	47	1.04	GAA(E)	44	1.35	GGA(G)	34	0.98
GUG(V)	15	0.65	GCG(A)	11	0.24	GAG(E)	21	0.65	GGG(G)	24	0.69

Selene setapinnis

Codon	Count	RSCU	Codon	Count	RSCU	Codon	Count	RSCU	Codon	Count	RSCU
UUU(F)	87	1.12	UCU(S)	77	1.21	UAU(Y)	83	1.12	UGU(C)	29	0.67
UUC(F)	69	0.88	UCC(S)	101	1.59	UAC(Y)	65	0.88	UGC(C)	58	1.33
UUA(L)	74	0.77	UCA(S)	45	0.71	UAA(*)	64	1.35	UGA(W)	62	1.18
UUG(L)	36	0.38	UCG(S)	31	0.49	UAG(*)	31	0.65	UGG(W)	43	0.82
CUU(L)	138	1.45	CCU(P)	155	1.52	CAU(H)	74	0.94	CGU(R)	39	0.92
CUC(L)	159	1.66	CCC(P)	131	1.29	CAC(H)	84	1.06	CGC(R)	50	1.18
CUA(L)	106	1.11	CCA(P)	84	0.83	CAA(Q)	76	1.39	CGA(R)	37	0.88
CUG(L)	60	0.63	CCG(P)	37	0.36	CAG(Q)	33	0.61	CGG(R)	43	1.02
AUU(I)	87	1.18	ACU(T)	76	1.18	AAU(N)	95	1.14	AGU(S)	52	0.82
AUC(I)	61	0.82	ACC(T)	78	1.21	AAC(N)	72	0.86	AGC(S)	76	1.19
AUA(M)	57	1.21	ACA(T)	71	1.1	AAA(K)	68	1.43	AGA(*)	48	1.01
AUG(M)	37	0.79	ACG(T)	33	0.51	AAG(K)	27	0.57	AGG(*)	47	0.99
GUU(V)	35	1.46	GCU(A)	36	0.8	GAU(D)	29	1	GGU(G)	36	0.95
GUC(V)	27	1.13	GCC(A)	83	1.83	GAC(D)	29	1	GGC(G)	45	1.18
GUA(V)	18	0.75	GCA(A)	40	0.88	GAA(E)	46	1.35	GGA(G)	40	1.05
GUG(V)	16	0.67	GCG(A)	22	0.49	GAG(E)	22	0.65	GGG(G)	31	0.82

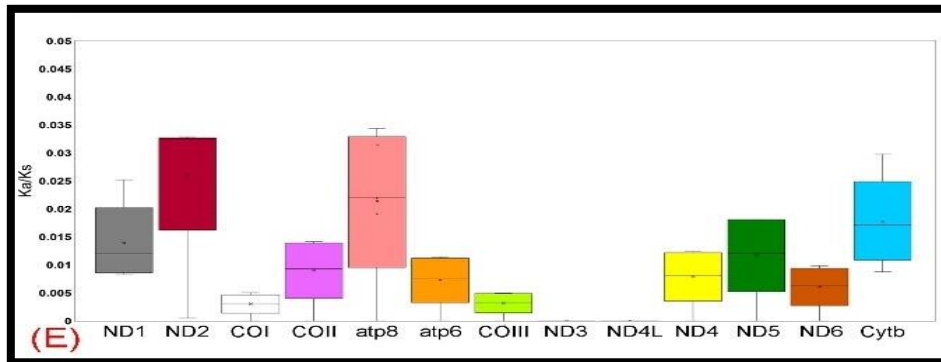


Fig 10. A box plot depicting the pairwise divergence of Ka/Ks ratios for each mitochondrial PCG of three *Selene* species (*Selene dorsalis*, *Selene setapinnis* and *Selene vomer*).

Table 8. Ka/Ks values of each PCG for three *Selene* species

Species	<i>nad1</i>	<i>nad2</i>	<i>cox1</i>	<i>cox2</i>	<i>atp8</i>	<i>atp6</i>	<i>cox3</i>	<i>nad3</i>	<i>nad4l</i>	<i>nad4</i>	<i>nad5</i>	<i>nad6</i>	<i>Cytb</i>
<i>S. vomer</i> vs <i>S. setapinnis</i>	0.0083	0.0319	0.0043	0.0141	0.0314	0.0114	0.0050	0.0000	0.0000	0.0124	0.0000	0.0089	0.0171
<i>S. vomer</i> vs <i>S. dorsalis</i>	0.0121	0.0325	0.0050	0.0137	0.0344	0.0110	0.0048	0.0000	0.0000	0.0120	0.0181	0.0098	0.0130
<i>S. setapinnis</i> vs <i>S. dorsalis</i>	0.0252	0.0329	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0181	0.0000	0.0297
Average	0.0152	0.0324	0.0031	0.0093	0.0219	0.0075	0.0033	0.0000	0.0000	0.0081	0.0121	0.0062	0.0199
STDEV	0.0088	0.0005	0.0027	0.0080	0.0191	0.0065	0.0028	0.0000	0.0000	0.0070	0.0104	0.0054	0.0087

1.3 Substitution patterns in PCG's matrices

An analysis of the mutation saturation present within the DNA sequences demonstrated that the variance (quantitative indicator of variation) in transitions and transversions consistently heightened as the genetic distance (measured using the Kimura 2-parameter model) between the sequences increased. This finding suggests that the sequences have yet

to attain mutation saturation, implying that the genetic disparities between them can still be precisely quantified without the confounding effects of overlapping mutations.

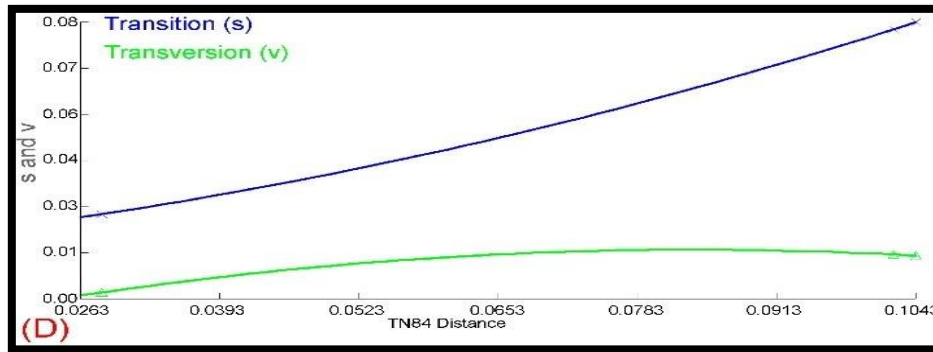


Fig 11. Patterns of Substitution in PCG matrices: variance of transitions and transversions relative to Kimura 2-Parameter genetic distance.

1.4 Ribosomal RNA and Transfer RNA

The mitogenome of *Selene dorsalis* comprised two ribosomal RNA subunits namely, 12S rRNA (955bp) and 16S rRNA, (1715 bp) spanning a total length of 2670 bp which constitutes 16.14 % of the entire mitogenome. Extensive analysis uncovered diverse lengths of ribosomal RNAs ranging from 2670 bp (*Selene dorsalis*) to 2669 bp (*Selene vomer*). Comparative comparisons of rRNAs of *Selene setapinnis* could not be assessed as the necessary data was not available for the species in GenBank. The rRNA genes showed an AT bias, ranging from 52.28% in *Selene dorsalis* to 52.34% in *Selene setapinnis*.

Additionally, AT-skew ranged from 0.192% in *Selene dorsalis* to 0.195% in *Selene vomer*, and GC skewed from -0.107 (*Selene dorsalis*) to -0.116 (*Selene vomer*) (Table 5). Ribosomes play an essential role in the establishment of the proteome of eukaryotic organisms, the assemblage of ribosomal proteins with rRNA is completed transcription. Additionally, the conserved loops (rRNA) and circular RNAs (circRNAs) are essential for catalytic mechanisms involved in protein synthesis, fish immunity and growth regulation respectively (Rbbani et al., 2021). Therefore, the magnitude of nucleotide discrepancies within the rRNA genes of the comparative mitogenomes have prospective to use as a genetic marker application for population genetics studies (Quraishia et al., 2015). The collective length of the tRNAs of *Selene dorsalis* was 1576 bp constituting 9.5% of its entire mitogenome. Further analyses with other *Selene* species revealed varying tRNAs lengths ranging from 1556 bp (*Selene vomer*) to 1415 bp in *Selene setapinnis*. Additionally, AT bias ranged from 55.01% in (*Selene dorsalis*) to 55.19% (*Selene setapinnis*) and AT-skew of 0.114 in (*Selene dorsalis*) to 0.001 (*Selene setapinnis*). Most of the tRNA exhibited the classical cloverleaf secondary structure except *tRNA Serine* (S1) (absence of DHU-arm) as reported in other studies (Satoh et al., 2016). Transfer RNAs (tRNAs) play an important role in protein biosynthesis and post-transcriptional regulation in all living organisms (Thornlow et al., 2018).

The anticodons for most of 22 transfer RNAs expressed similarity with other *Selene* species, exception was made for *tRNA-Ile* (I) in *Selene vomer* which exhibited anticodon TAA instead GAT. Similarly, *Selene setapinnis* displayed anticodon GTA contrasting with

TGA exhibited by *Selene dorsalis* and *Selene vomer* (Table S3). The tRNA gene as catalytic adaptors play vital roles in the process of translating transcribed DNA sequences into essential proteins. Moreover, the redistribution of tRNA genes and the existence of significant levels of length heteroplasmy within the WANCY region which is a common occurrence in mitogenomes are influential factors in shedding light on the evolutionary patterns of mitochondrial genes (Cantatore et al., 1987; Ponce et al., 2008).



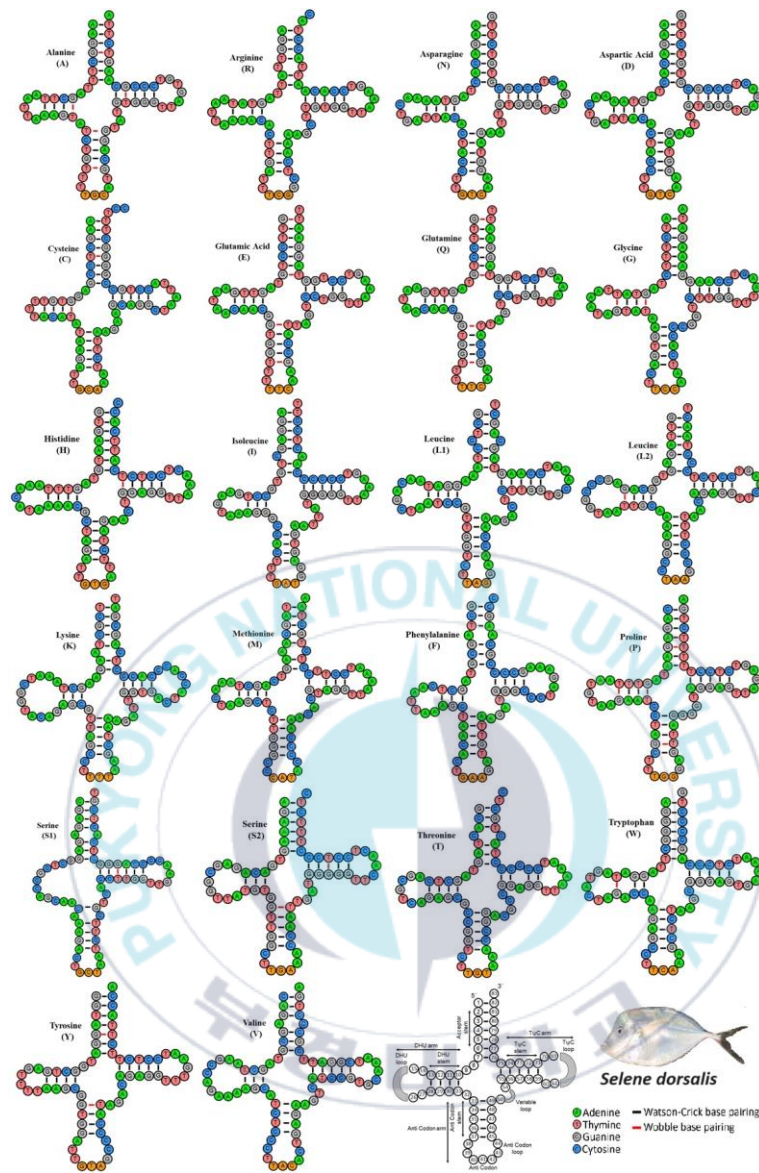
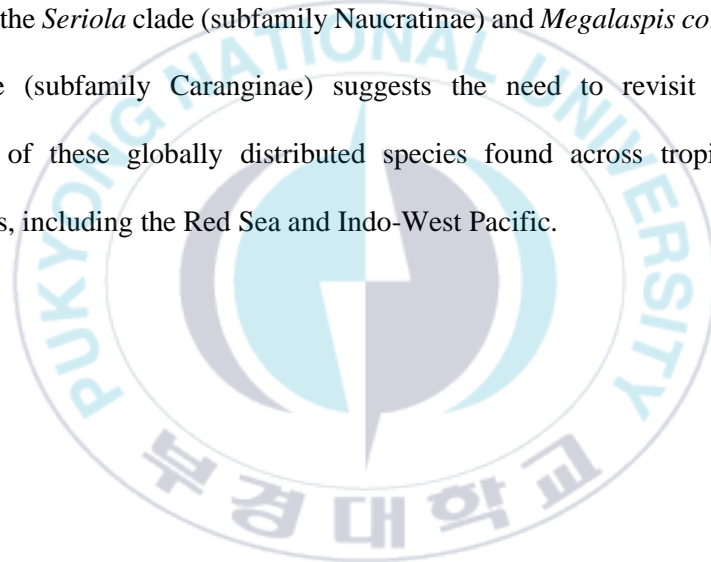


Fig. 12. Secondary structures of 22 transfer RNAs (tRNAs) of *Selene dorsalis* and structural variations in base pairing.

1.6 Control Regions

The total length of the CR of *Selene dorsalis* was determined to be 847 bp representing 5.12% of the total mitogenome and exhibited an AT richness of 62.81%. The specific location of the CR was observed between *tRNA-Pro* (TGG) and *tRNA-Phe* (GAA) genes (Table 4). Comprehensive analysis of the mitogenome of species within the *Selene* genus revealed varying lengths within the CRs which ranged from 862 bp (*Selene vomer*) to 718 bp (*Selene setapinnis*). The spectrum of AT skew ranged from 0.038 (*Selene dorsalis*), 0.064 (*Selene setapinnis*) to 0.009 (*Selene vomer*) while GC skew varied from -0.213 (*Selene dorsalis*), -0.176 (*Selene setapinnis*) and -0.266 (*Selene vomer*). The CR of *Selene* species encompasses four conserved domains comprising CSB-D, CSB-1, CSB-2, and CSB-3, this unique configuration is observed in the mitogenome of other teleost species (Kundu et al., 2022). Furthermore, the conserved domains of the control region of *Selene dorsalis* revealed CSB-1 showed the longest base pair (22bp) followed by CSB-3 (19bp), CSB-D (18bp) with CSB-2 exhibiting the shortest (17bp) (Fig. 9). This region rich in AT content holds the potential for appraising the population structure of any given species, the presence of diverse nucleotides in this region allows for the discrimination between populations and individuals of *Selene* species. Additionally, CR plays a critical role in modulating transcription and replication processes within the mitochondrial genome (Taanman, 1999).

clusters emerged. Cluster 1 includes species from *Selar*, *Decapterus*, *Trachurus*, and the monotypic genus *Kaiwarinus*. Cluster 2 comprises *Uraspis*, *Scyris*, *Selene*, *Platycaranx*, *Atropus*, and six monotypic genera (*Parastromateus*, *Ferdauia*, *Alectis*, *Craterognathus*, *Turrum*, and *Flavocaranx*). Cluster 3 contains species from *Chloroscombrus*, *Alepes*, *Caranx*, and five other monotypic genera (*Selaroides*, *Gnathanodon*, *Alepes*, *Atule*, and *Megalaspis*). This phylogeny aligns with recent evolutionary findings based on 1,314 ultraconserved elements (UCEs) (Glass et al., 2023) and supports current genus-level classification within Carangidae. However, the close grouping of the monotypic *Naucrates ductor* within the *Seriola* clade (subfamily Naucratinae) and *Megalaspis cordyla* within the *Caranx* clade (subfamily Caranginae) suggests the need to revisit the taxonomic classification of these globally distributed species found across tropical and warm temperate seas, including the Red Sea and Indo-West Pacific.



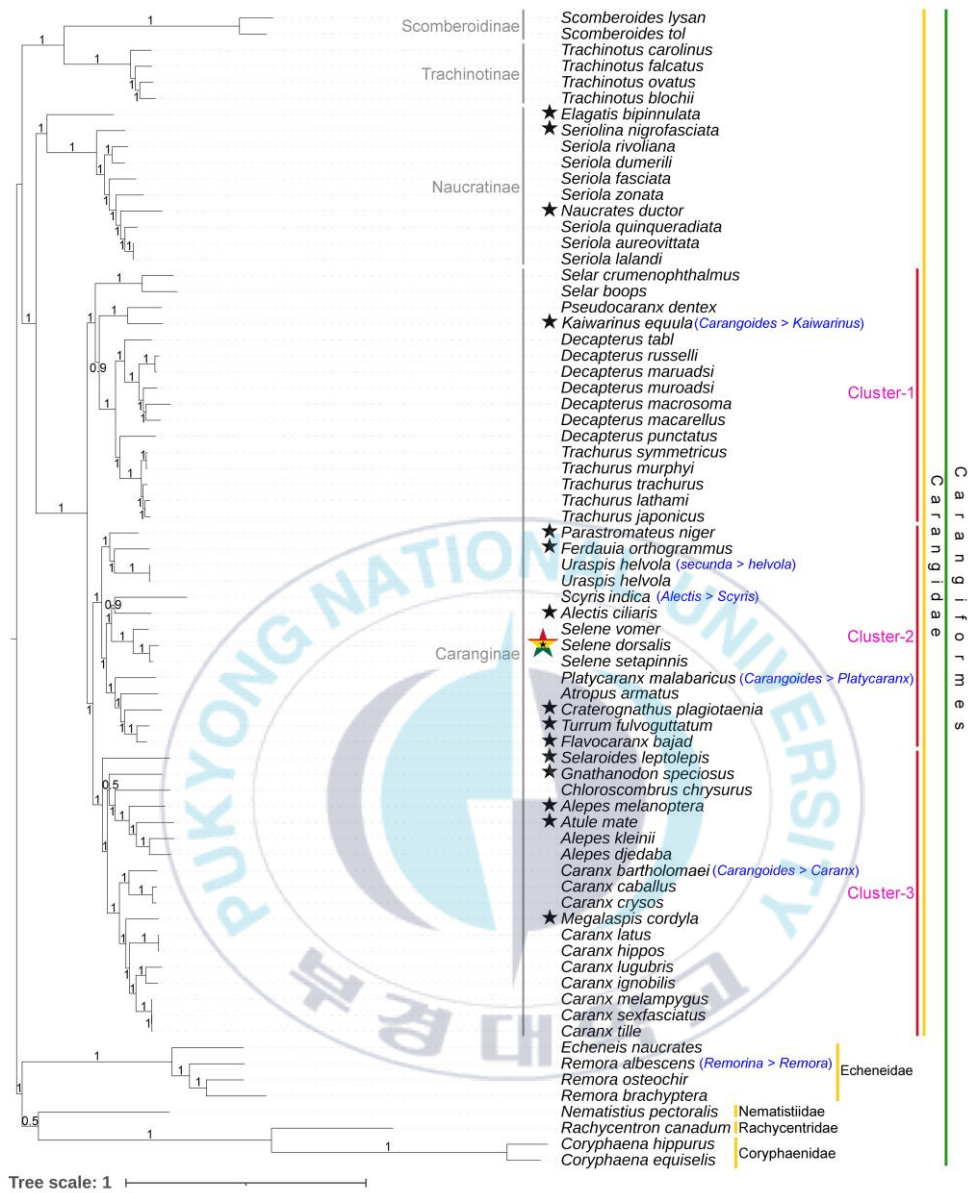


Fig. 14. Bayesian phylogeny based on 13 concatenated PCGs distinguishes *Selene dorsalis* (marked by a star-shaped Ghana map) from other *Selene* species.

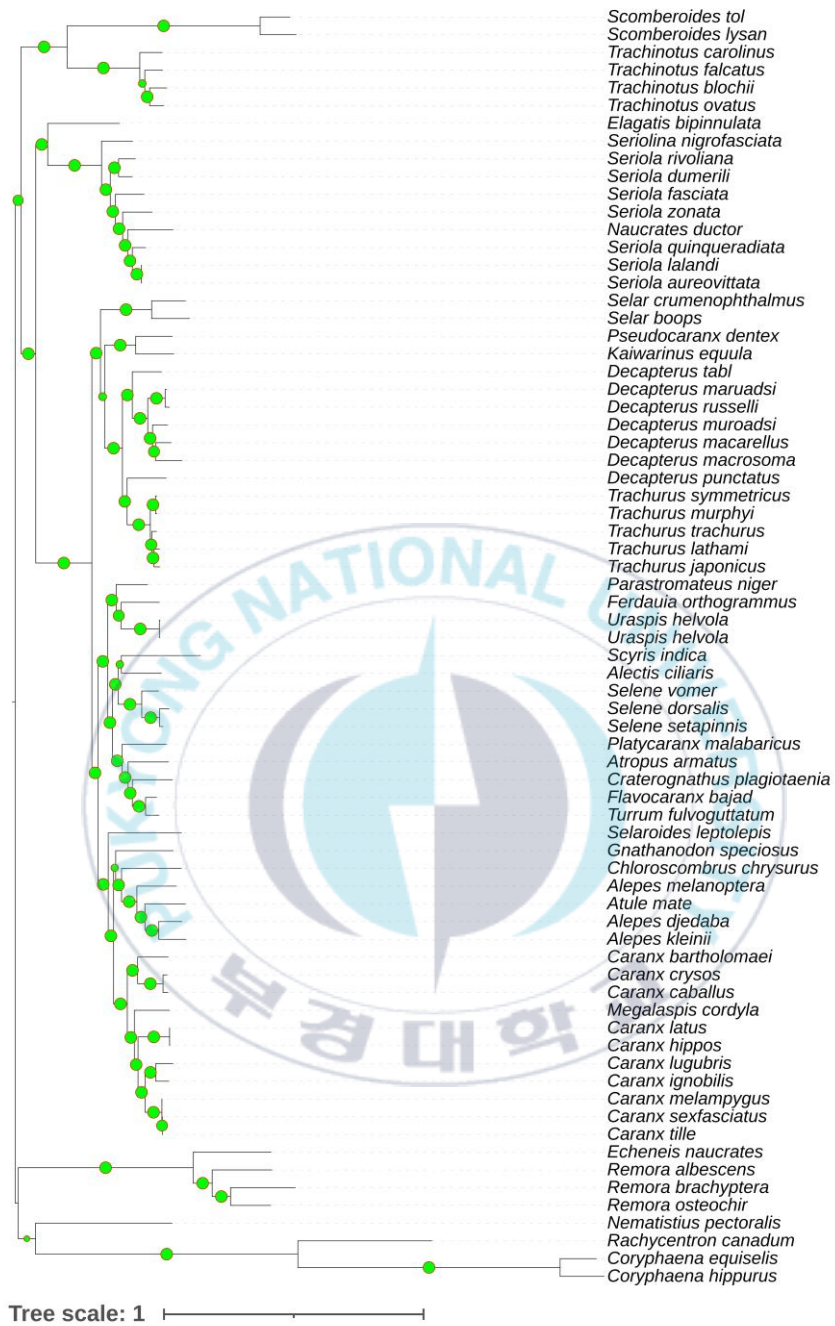


Fig 15. Maximum likelihood phylogeny tree for carangid species.

2.1 Lineage diversification of *Selene* species

The suborder Carangoidei, belonging to the order Carangiformes, comprises a varied range of species including *Selene* species inhabiting diverse marine habitats stretching from coral reefs to open pelagic zones (Glass et al., 2023). Probing into the diversification and biogeographical spread of Carangoidei generates crucial perceptions on marine speciation mechanisms, evolutionary past, and ecological alterations. The diversification of Carangoidei emphasizes the intricate interplay among historical, ecological, and biogeographical factors in the process of their excellent examples of marine speciation. The Eocene, described by significant climate, plate tectonic shift, and oceanographic alterations, appears as a central era for the early diversification of this particular lineage (Leprieur et al., 2016; Lepprieur et al., 2021; Glass et al., 2023). The predominant sympatry witnessed in Carangoidei stands in contrast to conventional allopatric speciation models, indicating that ecological variation observed in coral reefs and habitat separation play crucial roles in driving speciation within marine ecosystems (Glass et al., 2023).

Nevertheless, the spatial distribution of marine organisms is not even or random but instead follows profound biotic factors such as recruitment, competition, and predation, abiotic factors like water quality, and salinity, as well as historical factors comprising hurricanes and tsunamis (Caley et al., 1996; Bax, 1998; Adjeroud et al., 1998; Harrison and Whitfield, 2006). This phenomenon occurs because different species demonstrate diverse reactions to changes in environmental conditions, this varied distribution can result in

allopatric or sympatric speciation. Such speciation mechanism exhibits high importance in evolutionary inferences on the hereditary diversity of species, particularly in marine environments (Glass et al., 2023). Data on the known biogeographic extent of *Selene* members and their cladistics pattern indicates, *Selene vomer* and *Selene setapinnis* demonstrate comparable geographical distribution inhabiting the Western Atlantic Ocean and could possibly undergo sympatric speciation with other know species *Selene brownii*. However, due to the lack of mitogenome sequences the study could not elaborate on the biogeographic patterns of *Selene peruviana* and *Selene brevoortii* which could be separated by the physical barrier of Isthmus of Panama through allopatric speciation. However, the present mitogenomic phylogeny revealed the close association of Eastern Atlantic *Selene dorsalis* with Western Atlantic *Selene setapinnis* compared with other Western Atlantic species *Selene vomer* aligned with the recent studies (Glass et al. 2023). The separation by the presence of an open ocean between the Eastern and Western Atlantic Oceans functions as a vicariance facilitating isolation by distance between these species and restricted to the respective range distribution, which needs further investigation through in-depth molecular data of other extant species to perceive their accurate lineage diversification scenario. Further, looking at the overall carangid's phylogeny, the *Selene* lineage is close to the widespread *Alectis ciliaris* and *Scyris indica*, distributed circumglobal in tropical, subtropical and temperate seas as well as in Red Sea and Indo-West Pacific respectively. These closely related carangids' may be separated by the cold-water barrier formed by the Benguela and Agulhas currents off the southern coast of South Africa separating the

Atlantic. Further, the unique oceanic currents in both north and south Atlantic gyres as well as in north and south Pacific gyres may act as a significant barrier for the unique diversification and adaptation of *Selene* species in both Atlantic and Pacific Ocean.

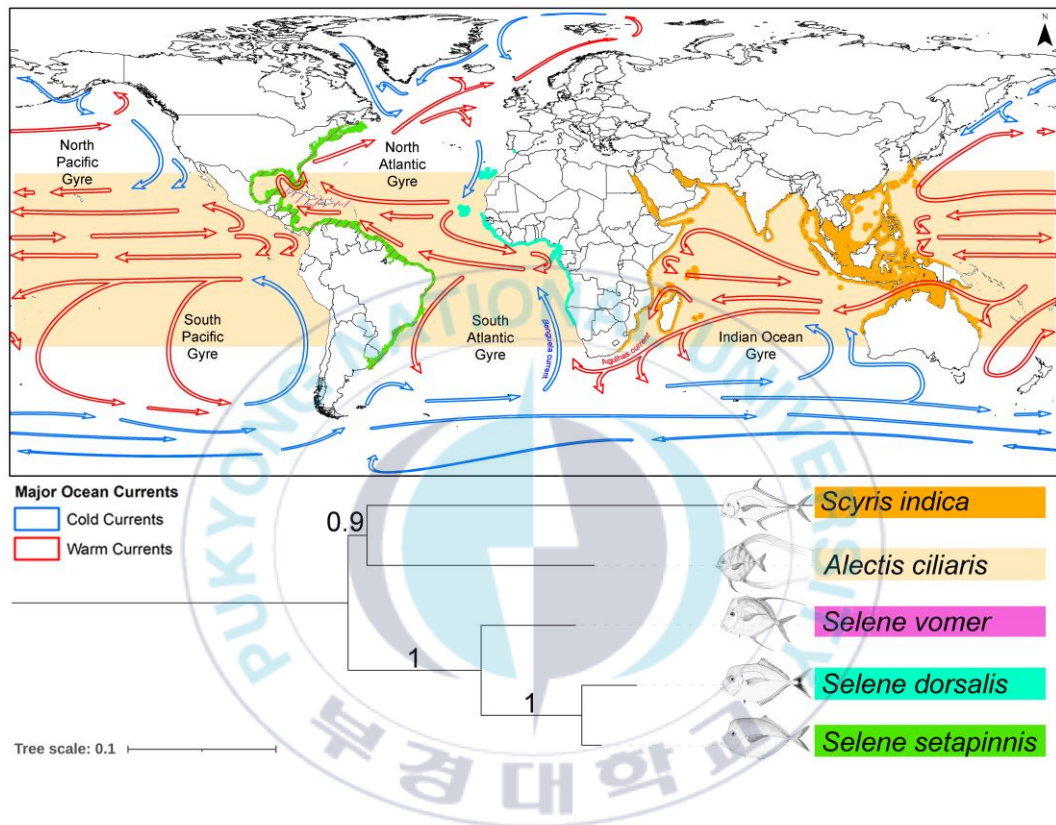
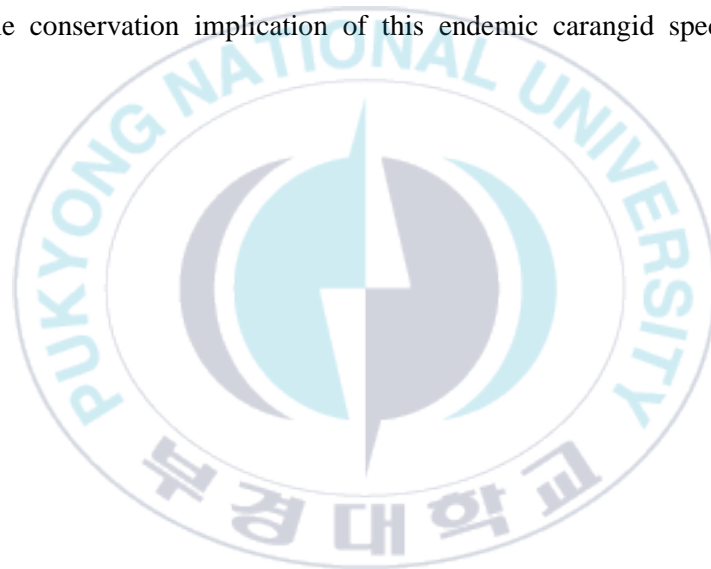


Fig 16. A composite figure of the pruned Bayesian tree and global range distribution illustrating the potential impact of major ocean currents on the diversification of *Selene* species in both the Eastern and Western Atlantic Oceans.

2.2 Conservation implication of *Selene* species in East Atlantic Ocean

It is well known that global climate change is impacting the ecology and geographical distribution of marine fish populations, especially for the reef-associated species (Munday et al., 2008; Arvedlund, 2009; Rijnsdorp et al., 2009; Dahms and Killen, 2023). This is foreseen to bring about significant impacts on marine ecosystems, including modifications in ocean acidity, temperature alteration, altered food web, shifting species distribution, rise in sea level, and decreased ocean productivity (Brierley and Kingsford, 2009; Hoegh-Guldberg and Bruno, 2010). In the case of the carangids, these alterations may result in the destruction and deterioration of habitats, particularly in coastal, estuarine areas and coral habitats where these species commonly inhabit particularly in the western Africa (Smith and Parrish, 2002, Mat et al., 2020). Ocean warming has brought changes in the geographical distribution of many carangids such as *Seriola fasciata*, *Selene dorsalis*, *Caranx crysos* and other species causing migration towards the north as these species search for suitable thermal environments (Andaloro et al., 2005; Juárez et al., 2008; Vella and Deidun, 2009; Di Blasi et al., 2024). This movement has the capacity to reduce productivity and disturb local ecosystems and fishing communities that are dependent on carangids and other reef-associated fishes for economic activities, especially in west African countries (Ateweberhan et al., 2012; Polidoro et al., 2017). Thus, the implementation of operative fisheries management policies is needed to ensure sustainable harvesting practices and reduce the risks of overexploitation leading to declining Catch Per

Unit Effort (CPUE) particularly in Ghana where the study has been conducted (Nunoo and Asiedu, 2013). Furthermore, it is important to employ adaptive management strategies, such as incorporating molecular methods to accurately identify species and their genetic diversity to address the impacts of climate change, ensuring the long-term sustainability of the carangid fisheries (Teletchea, 2009). Although the present analysis of *Selene dorsalis* mitogenome sequence derived from Ghana, researchers can generate the molecular data of this Atlantic moonfish from other West African countries to achieve a valuable perspective on its genetic variability, population structure, and gene flow between different populations for sustainable conservation implication of this endemic carangid species in Eastern Atlantic.



Conclusion

The increasing impacts of global warming and extreme temperature events pose significant threats to marine biodiversity, leading to substantial declines in fisheries worldwide. Carangids, economically and recreationally important reef-associated fish, face uncertain futures under these environmental pressures. While species identification has advanced, a comprehensive understanding of carangid evolutionary patterns, particularly through mitogenomic analysis, remains limited globally. This study provides an in-depth examination of *Selene dorsalis*, a species endemic to the Eastern Atlantic Ocean, focusing on its complete mitogenome and its structural variations in comparison to its allopatric relatives, *Selene setapinnis* and *Selene vomer*. Findings reveal critical structural differences that shed light on evolutionary dynamics within *Selene* species, contributing to the understanding of phylogenetic relationships across the Carangidae family. Additionally, this research explores the role of historical and environmental factors in shaping the restricted distribution of *Selene* species across the Atlantic and Pacific Oceans. These results hold substantial value for advancing carangid identification, conservation genetics, and studies on speciation which are essential for the development of effective conservation strategies.

Acknowledgement

I am deeply grateful to everyone who has supported me throughout my Master's thesis journey. First and foremost, I would like to express my sincere gratitude to my advisors Professor Kim Hyun-Woo and Professor Shantanu Kundu, for their continuous guidance, insightful feedback, and encouragement throughout my research. Your mentorship has been invaluable in shaping this thesis. I would also like to thank the faculty and staff at Pukyong National University, particularly the Department of Fisheries and Marine Biology, for providing the resources and environment necessary for my studies.

A special thank you to my colleagues and fellow researchers, Sarifah Aini, Arief Wudji and Essa Kathleen de la Cruz, for their collaboration, support, and the many enlightening discussions that contributed to the progress of this research. I am also thankful to KOICA-PNKU International Graduate Program of Fisheries Science, for providing financial support, without which this project would not have been possible. To my family and friends, your unwavering support, love, and patience have been my greatest source of strength. I am especially thankful to my parents for their sacrifices and belief in me. Finally, I extend my gratitude to all staff of the Fisheries Scientific Survey Division of the Fisheries commission whose cooperation was instrumental in gathering essential data for this research. Thank you all for making this journey possible.

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Appendix

Table S1. Details of the mitogenomes of other *Selene* species acquired from the GenBank database

Sl. No.	Family	GenBank Name	Valid Name	Accession No.	References
1	Carangidae	<i>Carangoides bartholomaei</i>	<i>Caranx bartholomaei</i>	PP032955	Alvarenga et al., 2024
2	Carangidae	<i>Carangoides malabaricus</i>	<i>Platycaranx malabaricus</i>	KJ174514	Li et al., 2016
3	Carangidae	<i>Carangoides equula</i>	<i>Kaiwarinus equula</i>	KM201334	Zou and Li, 2016
4	Carangidae	<i>Uraspis helvola</i>	<i>Uraspis helvola</i>	KM978993	-
5	Carangidae	<i>Uraspis secunda</i>	<i>Uraspis helvola</i>	KT819204	Ma et al., 2017
6	Carangidae	<i>Parastromateus niger</i>	<i>Parastromateus niger</i>	KJ192332	Chen et al., 2016
7	Carangidae	<i>Alectis ciliaris</i>	<i>Alectis ciliaris</i>	KM522837	Li et al., 2016
8	Carangidae	<i>Selene vomer</i>	<i>Selene vomer</i>	PP033011	Alvarenga et al., 2024
9	Carangidae	<i>Selene setapinnis</i>	<i>Selene setapinnis</i>	OR575618	-
10	Carangidae	<i>Selene dorsalis</i>	<i>Selene dorsalis</i>	PP857611	This Study
11	Carangidae	<i>Atropus armatus</i>	<i>Atropus armatus</i>	AP004444	Miya et al., 2003
12	Carangidae	<i>Atule mate</i>	<i>Atule mate</i>	KM522838	Cheng et al., 2015
13	Carangidae	<i>Alepes melanoptera</i>	<i>Alepes melanoptera</i>	PP231954	-
14	Carangidae	<i>Alepes djedaba</i>	<i>Alepes djedaba</i>	KP408222	Li et al., 2020
15	Carangidae	<i>Alepes kleinii</i>	<i>Alepes kleinii</i>	KF728081	Li and Zou, 2016
16	Carangidae	<i>Gnathanodon speciosus</i>	<i>Gnathanodon speciosus</i>	MT922005	Jiang et al., 2022
17	Carangidae	<i>Selaroides leptolepis</i>	<i>Selaroides leptolepis</i>	KM522839	Li et al., 2020
18	Carangidae	<i>Chloroscombrus chrysurus</i>	<i>Chloroscombrus chrysurus</i>	PP032962	Alvarenga et al., 2024
19	Carangidae	<i>Caranx crysos</i>	<i>Caranx crysos</i>	MW435597	Jeol et al., 2021
20	Carangidae	<i>Caranx tille</i>	<i>Caranx tille</i>	KT805946	Ma et al., 2016
21	Carangidae	<i>Caranx ignobilis</i>	<i>Caranx ignobilis</i>	KF649842	Santos et al., 2011
22	Carangidae	<i>Caranx melampygus</i>	<i>Caranx melampygus</i>	AP004445	Santos et al., 2011
23	Carangidae	<i>Caranx hippos</i>	<i>Caranx hippos</i>	OP035266	-

24	Carangidae	<i>Caranx latus</i>	<i>Caranx latus</i>	OR482464	Alvarenga et al., 2024
25	Carangidae	<i>Caranx caballus</i>	<i>Caranx caballus</i>	OP057043	-
26	Carangidae	<i>Caranx lugubris</i>	<i>Caranx lugubris</i>	OP035166	-
27	Carangidae	<i>Caranx sexfasciatus</i>	<i>Caranx sexfasciatus</i>	OP035090	Kainama et al., 2023
28	Carangidae	<i>Craterognathus plagiotaenia</i>	<i>Craterognathus plagiotaenia</i>	MT677872	Kaure et al., 2021
29	Carangidae	<i>Megalaspis cordyla</i>	<i>Megalaspis cordyla</i>	KM522836	Li et al., 2016
30	Carangidae	<i>Trachurus trachurus</i>	<i>Trachurus trachurus</i>	AB108498	Takashima et al., 2006
31	Carangidae	<i>Trachurus murphyi</i>	<i>Trachurus murphyi</i>	PP533446	Asorey et al., 2024
32	Carangidae	<i>Trachurus japonicus</i>	<i>Trachurus japonicus</i>	AP003092	-
33	Carangidae	<i>Trachurus lathami</i>	<i>Trachurus lathami</i>	OP057107	-
34	Carangidae	<i>Trachurus symmetricus</i>	<i>Trachurus symmetricus</i>	OR482443	-
35	Carangidae	<i>Decapterus muroadsi</i>	<i>Decapterus muroadsi</i>	OP057048	-
36	Carangidae	<i>Decapterus maruadsi</i>	<i>Decapterus maruadsi</i>	KJ004518	Li et al., 2016
37	Carangidae	<i>Decapterus russelli</i>	<i>Decapterus russelli</i>	MN711693	Josh et al., 2022
38	Carangidae	<i>Decapterus tabl</i>	<i>Decapterus tabl</i>	MN102718	Li et al., 2020
39	Carangidae	<i>Decapterus macarellus</i>	<i>Decapterus macarellus</i>	KM986880	Zou et al., 2016
40	Carangidae	<i>Decapterus macrosoma</i>	<i>Decapterus macrosoma</i>	KF841444	Li et al., 2016
41	Carangidae	<i>Decapterus punctatus</i>	<i>Decapterus punctatus</i>	OP035108	-
42	Carangidae	<i>Selar boops</i>	<i>Selar boops</i>	MW581014	-
43	Carangidae	<i>Selar crumenophthalmus</i>	<i>Selar crumenophthalmus</i>	KJ148633	Li et al., 2016
44	Carangidae	<i>Pseudocaranx dentex</i>	<i>Pseudocaranx dentex</i>	MZ359280	Li et al., 2021
45	Carangidae	<i>Naucrates ductor</i>	<i>Naucrates ductor</i>	OR546204	Shi et al., 2019
46	Carangidae	<i>Seriola dumerili</i>	<i>Seriola dumerili</i>	MZ398238	Iguchi et al., 2012
47	Carangidae	<i>Seriola lalandi</i>	<i>Seriola lalandi</i>	OR482442	Iguchi et al., 2012
48	Carangidae	<i>Seriola quinqueradiata</i>	<i>Seriola quinqueradiata</i>	AB517556	Iguchi et al., 2012
49	Carangidae	<i>Seriola rivoliana</i>	<i>Seriola rivoliana</i>	AB517559	Iguchi et al., 2012
50	Carangidae	<i>Seriola zonata</i>	<i>Seriola zonata</i>	OP035199	Swart et al., 2015
51	Carangidae	<i>Seriola fasciata</i>	<i>Seriola fasciata</i>	OR482462	Swart et al., 2015
52	Carangidae	<i>Seriola aureovittata</i>	<i>Seriola aureovittata</i>	MH211123	Shi et al., 2019
53	Carangidae	<i>Seriolina nigrofasciata</i>	<i>Seriolina nigrofasciata</i>	KT591876	Liu et al., 2016

54	Carangidae	<i>Elagatis bipinnulata</i>	<i>Elagatis bipinnulata</i>	KT824759	Ma et al., 2017
55	Carangidae	<i>Trachinotus carolinus</i>	<i>Trachinotus carolinus</i>	KJ556976	Zhang et al., 2016
56	Carangidae	<i>Trachinotus blochii</i>	<i>Trachinotus blochii</i>	KJ184305	Zhang et al., 2016
57	Carangidae	<i>Trachinotus ovatus</i>	<i>Trachinotus ovatus</i>	KF356397	Xie et al., 2015
58	Carangidae	<i>Trachinotus falcatus</i>	<i>Trachinotus falcatus</i>	OP056886	Seyoum et al., 2017
59	Carangidae	<i>Alectis indica</i>	<i>Scyris indica</i>	KP710215	Li et al., 2020
60	Carangidae	<i>Scomberoides tol</i>	<i>Scomberoides tol</i>	OR668917	-
61	Carangidae	<i>Scomberoides lysan</i>	<i>Scomberoides lysan</i>	MZ329991	Hoban et al., 2022
62	Carangidae	<i>Flavocaranx bajad</i>	<i>Flavocaranx bajad</i>	LC557137	Song et al., 2020
63	Carangidae	<i>Ferdauia orthogrammus</i>	<i>Ferdauia orthogrammus</i>	OP035068	-
64	Carangidae	<i>Turrum fulvoguttatum</i>	<i>Turrum fulvoguttatum</i>	OR499749	-
65	Echeneidae	<i>Remora brachyptera</i>	<i>Remora brachyptera</i>	OR546234	-
66	Echeneidae	<i>Remora osteochir</i>	<i>Remora osteochir</i>	OR575559	Kurtis et al., 2009
67	Echeneidae	<i>Echeneis naucrates</i>	<i>Echeneis naucrates</i>	AB355905	Miya et al., 2013
68	Echeneidae	<i>Remorina albescens</i>	<i>Remora albescens</i>	OP057074	-
69	Coryphaenidae	<i>Coryphaena equiselis</i>	<i>Coryphaena equiselis</i>	PP032965	Alvarenga et al., 2024
70	Coryphaenidae	<i>Coryphaena hippurus</i>	<i>Coryphaena hippurus</i>	OR582674	Pindaro et al., 2006
71	Rachycentridae	<i>Rachycentron canadum</i>	<i>Rachycentron canadum</i>	FJ154956	Musika et al., 2014
72	Nematistiidae	<i>Nematistius pectoralis</i>	<i>Nematistius pectoralis</i>	ON838225	Molina-Quiros et al., 2022

List of Publications

1. Ewusi, E. O. M., Lee, S. R., Kim, A. R., Go, Y., Htoo, H., Chung, S., ... & Kundu, S. (2024). Endemic Radiation of African Moonfish, *Selene dorsalis* (Gill 1863), in the Eastern Atlantic: Mitogenomic Characterization and Phylogenetic Implications of Carangids (Teleostei: Carangiformes). *Biomolecules*, *14*(10), 1208.



Article

Endemic Radiation of African Moonfish, *Selene dorsalis* (Gill 1863), in the Eastern Atlantic: Mitogenomic Characterization and Phylogenetic Implications of Carangids (Teleostei: Carangiformes)

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Citation: Ewusi, E.O.M.; Lee, S.R.; Kim, A.R.; Go, Y.; Htoo, H.; Chung, S.; Amin, M.H.F.; Andriyono, S.; Kim, H.-W.; Kundu, S. Endemic Radiation of African Moonfish, *Selene dorsalis* (Gill 1863), in the Eastern Atlantic: Mitogenomic Characterization and Phylogenetic Implications of Carangids (Teleostei: Carangiformes). *Biomolecules* **2024**, *14*, 1208. <https://doi.org/10.3390/biom14101208>

Academic Editor: Carl A. Pinkert

Received: 22 August 2024

Revised: 19 September 2024

Accepted: 24 September 2024

Published: 25 September 2024



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Abstract: This study offers an in-depth analysis of the mitochondrial genome of *Selene dorsalis* (Gill 1863), a species native to the Eastern Atlantic Ocean. The circular mitochondrial DNA molecule measures 16,541 base pairs and comprises 13 protein-coding genes (PCGs), 22 transfer RNA (tRNA) genes, two ribosomal RNA genes, and a control region (CR). The nucleotide composition exhibits a notable adenine-thymine (AT) bias, accounting for 53.13%, which aligns with other species in the Carangidae family. Most PCGs initiate with the ATG codon, with the exception of Cytochrome C oxidase subunit I, which starts with GTG. Analysis of relative synonymous codon usage reveals that leucine and serine are the most prevalent amino acids in the mitochondrial genome of *S. dorsalis* and its congeners (*S. vomer* and *S. setapinnis*). All tRNAs display the typical cloverleaf structure, though *tRNA Serine* (S1) lacks a dihydrouracil arm. Pairwise comparisons of synonymous and non-synonymous substitutions for all PCGs yielded values below '1', indicating strong purifying selection. The CR spans 847 bp, representing 5.12% of the mitochondrial genome, and is characterized by high AT content (62.81%). It is situated between *tRNA-Pro* (TGG) and *tRNA-Phe* (GAA). The CR contains conserved sequence blocks, with CSB-1 being the longest at 22 bp and CSB-D the shortest at 18 bp. Phylogenetic analysis, using Bayesian and Maximum-likelihood trees constructed from concatenated PCGs across 72 species, successfully differentiates *S. dorsalis* from other carangids. This study also explores how ocean currents and gyres might influence lineage diversification and parapatric speciation of *Selene* species between the Atlantic and Pacific Oceans. These results highlight the importance of the mitochondrial genome in elucidating the structural organization and evolutionary dynamics of *S. dorsalis* and its relatives within marine ecosystems.