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Molecular systematics of the emperor fishes (Teleostei: Lethrinidae) from the Persian Gulf and Gulf of Oman: New insights into cryptic diversity

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ABSTRACT

The emperor fishes, *Lethrinus* Cuvier, 1829, are generally considered to be ecologically and economically important fishes, occurring primarily in coral reef areas of the Indo-Pacific including the Persian Gulf and Gulf of Oman. The systematics and taxonomy of this genus are complicated due to subtle morphological differences among species. In addition, few molecular studies have investigated the genetic variability of *Lethrinus* species due to the limited number of taxa and restricted geographic distribution. To achieve this, we constructed a robust phylogenetic tree, various molecular species delimitations and phylogeographic analyses using mitochondrial COI sequences to determine phylogenetic relationships and reveal hidden species diversity in the Persian Gulf and Gulf of Oman. Our phylogenetic results revealed five major clades within *Lethrinus* with moderate to strong support at nodes. Our findings indicate the existence of at least four unconfirmed candidate species that are well supported by the haplotype network and multiple molecular species delimitations, a finding that contradicts previous taxonomic classification. These results suggest that *Lethrinus crocineus*, with two genetically distinct lineages, and *L. nebulosus*, with at least three evolutionarily distinct lineages, represent a cryptic species complex deserving recognition at the species level. In addition, *L. lentjan* was discovered as a third cryptic species with a robust genetic structure. Five distinct phylogenetic lineages in these complexes were observed in the ecoregions of the Persian Gulf and Gulf of Oman, which have been proven to be hotspots of endemic biodiversity.

1. Introduction

Accurate delineation of species is critical for understanding the distribution and evolution of biodiversity and for developing effective conservation strategies (Sheridan and Stuart, 2018). Lack of knowledge about hidden species diversity and their non-description has serious consequences, as these unrecognized taxa are not protected, resulting in a great loss of biodiversity. Cryptic species are distinct taxa with discrete evolutionary pathways. They have often been classified as a single species due to morphological similarities, which hinder proper identification and assignment of taxonomic status. However, recent advances in genetic analysis have revealed their widespread distribution (Adams et al., 2014; Delić et al., 2017). This revelation is significant because the discovery of cryptic species can drastically change the assumed distribution of diversity and endemism. Consequently, this can lead to a shift in our understanding of evolutionary processes and priorities for limited conservation resources (Elmer et al., 2007; Adams et al., 2014; Delić et al., 2017). In addition, cryptic species often have different ecological functions than their similar-looking relatives. Consequently, they play equally important but distinct roles in ecosystem function. If left undetected, these cryptic species can confound studies in all areas of biology, making their consideration essential in biological research and conservation approaches (De Meester et al., 2018; Rambaut and Schluter, 1996). The ongoing discovery of cryptic species raises questions about their abundance and distribution in specific biogeographic or management regions, as well as their proportion in different taxonomic groups.

The Persian Gulf and Gulf of Oman, situated in the northwestern Indian Ocean, are ecoregions with diverse marine environments, including a rich variety of fish species (Randall, 1995; Carpenter et al., 1997; Zajonz et al., 2022). The complex oceanographic features between these regions, characterized by reversed ocean currents, sea level fluctuations, seasonal variations in surface temperature and salinity, are thought to have contributed to this high species diversity (Randall, 1955; Carpenter et al., 1997; Feary et al., 2012; Ludt and Rocha, 2015;

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Ghanbarifardi et al., 2018; Maghsoudlou et al., 2019; Torquato et al., 2019; Damadi et al., 2021). Recent molecular studies on marine fishes have demonstrated the high genetic differentiation and existence of endemic species in the Persian Gulf and Gulf of Oman (Asgharian et al., 2011; DiBattista et al., 2017; Torquato et al., 2019; Rabaoui et al., 2019; Damadi et al., 2020; Kovačić et al., 2020; Esmaeili et al., 2022; Alavi-Yeganeh et al., 2021; Mehraban et al., 2021). However, despite the increasing amount of evolutionary and ecological research, the Persian Gulf and Gulf of Oman are still considered to be one of the least studied subtropical ecoregions (DiBattista et al., 2022; Zajonz et al., 2022).

The Lethrinidae family (Bonaparte, 1831) is composed of a diverse range of marine fishes. It includes 45 species that are classified into five genera and two subfamilies, namely Lethrininae and Monotaxinae. These Lethrinid species hold significant importance in both commercial and recreational fisheries, and they are found extensively in tropical and subtropical waters of the Indo-Pacific and Atlantic Oceans (Carpenter and Allen, 1989; Fricke et al., 2024). The phylogenetic relationships of lethrinids have long been studied based on both morphological (Akazaki, 1962; Johnson, 1980; Carpenter and Johnson, 2002) and molecular data (Lo Galbo et al., 2002; Mekkawy, 2017; Rabosky et al., 2018; Fabian et al., 2021), but with limited taxon. Based on morphological data, the Lethrinidae have typically been placed as a sister group to the Sparoidea (Nemipteridae and Sparidae) (Akazaki, 1962; Johnson, 1980; Carpenter and Johnson, 2002). More recently, large-scale molecular studies have strongly confirmed previous morphological data, and the lethrinids have been classified as a sister group to the Sparidae (Betancur-R et al., 2013; Near et al., 2013; Near et al., 2012). The monophyly of the Lethrinidae and both subfamilies Lethrininae and Monotaxinae has been supported by molecular phylogeny studies (Betancur-R et al., 2013; Rabosky et al., 2018; Chen and Borsa, 2020; Fabian et al., 2021). Systematics and taxonomy of the Lethrinidae have improved in the last decade, with six new species described or redescribed (Carpenter and Randall, 2003; Borsa et al., 2010, 2013; Allen et al., 2021; Holleman et al., 2022). Nevertheless, hidden diversity at the species level is controversial (Borsa et al., 2010, 2013; Healey et al., 2018; Chen and Borsa, 2020; Fabian et al., 2021). Lethrininae, which includes only one genus, *Lethrinus* Cuvier, 1829, is mainly distributed from the Indo-West Pacific to the eastern Atlantic (Fricke et al., 2024). *Lethrinus* represents a monophyletic clade (Lo Galbo et al., 2002) and is the most speciose genus among the lethrinids, with 30 recognized species (Fricke et al., 2024). Of these 30 species, five have been reported from the Persian Gulf and the Gulf of Oman (Damadi et al., 2024): *Lethrinus borbonicus* Valenciennes, 1830 occurs only in the western Indian Ocean; *L. crocineus* Smith, 1959, has been found in the Indian Ocean, *L. lentjan* (Lacepede, 1802); *L. microdon* Valenciennes, 1830, and *L. nebulosus* (Forsskal, 1775) are distributed in the Indo-West Pacific (Fricke et al., 2024). This genus has long been recognized by several diagnostic characters (Akazaki, 1962; Johnson, 1980) and more recently by osteological synapomorphies (Carpenter and Allen, 1989), although the delimitation of species within this genus has been somewhat problematic. Partially overlapping meristic counts and the relative stability of color patterns complicate the identification of species within the genus, especially among closely related species (Sato, 1971; Smith, 1959; Carpenter and Allen, 1989; Healey et al., 2018). Previous molecular phylogenetic studies have confirmed that *Lethrinus* is monophyletic (Lo Galbo et al., 2002), but the relationships within this clade remain unclear (Mekkawy, 2017; Healey et al., 2018). Mekkawy (2017) observed two evolutionarily distinct lineages of *L. nebulosus*, suggesting cryptic speciation in the southwestern Indian Ocean. Recently, these lineages were re-examined using morphological and molecular approaches, and one of the lineages (South African) was resurrected from synonymy with *L. nebulosus* and identified as *L. scoparius* (Holleman et al., 2022). In addition, two genetically distinct lineages of *L. nebulosus* have been discovered in the western Pacific and western Indian Oceans (Mekkawy, 2017).

Here, we used a single-locus species delimitation approach and to analyze the mitochondrial DNA sequence (COI) of *Lethrinus*. Our study aimed to achieve the following objectives: (i) reconstruct phylogenetic trees to infer their phylogenetic relationships, with extensive taxon sampling, (ii) test the initial validity of species diversity in the Persian Gulf and Gulf of Oman as reflected by traditional morphological classification, and (iii) identify the molecular operational taxonomic units (MOTUs) through extensive geographic sampling, while providing new evidence to evaluate hidden taxonomic diversity.

2. Materials and methods

2.1. Taxonomic sampling

Samples were collected from six commercial sites in the Gulf of Oman and Persian Gulf (Table S1). Of the five species collected, *L. borbonicus*, *L. nebulosus*, and *L. lentjan* exhibit a wider distribution across both the Persian Gulf and the Gulf of Oman, while the others are regionally endemic. *L. microdon* is restricted to the Persian Gulf, and *L. crocineus* is found only in the Gulf of Oman (Table S1).

Specimens collected were identified using the guidelines keys of Carpenter and Allen (1989) and Randall (1995). All specimens were photographed from the left side. Then, a small portion of muscle tissue was removed from each fresh specimen and preserved in absolute ethanol. The whole specimens were fixed at −20 °C. These new materials are stored in the Zoological Museum Ferdowsi University of Mashhad (ZMFUM), Iran.

2.2. DNA extraction, PCR amplification and sequencing

Genomic DNA was extracted from fish muscle using a salt method protocol (Bruford et al., 1992). Cytochrome c oxidase subunit I (COI) sequences were amplified by PCR using FishF1 and FishR1 primers (Ward et al., 2005). The amplifications were performed in a 25 µl reaction volume, which included 9.5 µl of ddH2O, 12.5 µl of a ready 2X Taq PCR Master Mix, 2 µl of DNA template, and 0.5 µl of each primer (10 pmol/µl). The PCR conditions were performed in a Biometra thermal cycler with an initial denaturation of 3 min at 95 °C, followed by 35 cycles of 45 s at 94 °C, 45 s at 52 °C, and 1 min at 72 °C, and a final extension at 72 °C for 5 min. The PCR products were purified and sequenced by Niagenenoor Laboratory, Iran. A total of 206 mitochondrial COI sequences of *Lethrinus* specimens from GenBank (www.ncbi.nlm.nih.gov/genbank) and 47 newly sequenced materials were used for comparative analyses (Table S1). Outgroups were selected based on previous phylogenetic hypotheses by Lo Galbo et al. (2002) and Fabian et al. (2021), including *Lutjanus fulviflamma* (Forsskål, 1775) and *L. russellii* (Bleeker, 1849).

2.3. Phylogenetic and phylogeographic analyses

The COI sequences (560 bp) were trimmed to minimize missing data and edited in MEGA 11 (Tamura et al., 2021). All newly generated sequences have been submitted to GenBank (Table S1). Genetic distance between and within species was calculated using the Kimura 2-parameter (K2P) model implemented in MEGA 11 (Tamura et al., 2021). A minimum threshold of 2 % genetic divergence for COI has been used (Ward, 2009), or divergence of 10-fold or more of the average intraspecific variability as an indicator of distinct species (Hebert et al., 2004). The best-fit nucleotide substitution model for the dataset was selected based on the Akaike information criterion (AIC) in jModelTest 2.1.3 (Posada, 2008), and a GTR+G model was accepted. Phylogenetic trees were constructed using Bayesian inference analysis (BI) in MrBayes v.3.2.7 (Ronquist et al., 2012) and maximum likelihood analysis (ML) using RAxMLv.7.2.6 (Stamatakis, 2014). The BI was run with four Markov Chains Monte Carlo (MCMC) chains in two independent runs of 30 million. To ensure adequate sampling of the posterior distribution in the Bayesian inference analyses, the Effective Sample Size (ESS) for all parameters was assessed in Tracer 1.5 software (Rambaut et al., 2014), with values above 200 indicating sufficient convergence of the MCMC chains.The first 25 % of samples were discarded as burn-in. A maximum likelihood procedure (ML) with 1000 bootstrap repetitions was implemented in RAxML 7.2.6 (Stamatakis, 2014). Phylogeographic patterns and evolutionary relationships among haplotypes were delineated using the median-joining (MJ) algorithm in PopART 1.7 (Leigh and Bryant, 2015).

2.4. Species delimitation

To identify potential species, the Assemble Species by Automatic Partitioning analysis (ASAP) was performed via a web interface (https://bioinfo.mnhn. fr/abi/public/asap/asapweb.html) using the Kimura-2 parameter (K2P) (Puillandre et al., 2021). The Automatic Barcode Gap Discovery (ABGD) (Puillandre et al., 2012), calculated all pairwise distances in the dataset to assess interspecific divergence, and sorted the terminals into candidate species based on the calculated P values. The ABGD tests were performed using the web server (https://bioinfo.mnhn.fr/abi/public/abgd/) using Pmin: 0.001, Pmax: 0.1, Steps: 10, X (relative gap width): 1.5 and Kimura 2-parameter (K2P) model, with the other parameters set to default values. The Bayesian Poisson Tree Processes (bPTP) (Zhang et al., 2013) was run on the web server (https://species.h-its.org/ptp/) with 300,000 Markov chain Monte Carlo (MCMC) generations, a thinning of 100, and a burn-in of 25 % initial samples. The Multi-Rate Poisson Tree Processes (mPTP) (Kapli et al., 2017) were implemented on the web server (http://mptp.h-its.org) using the Multi-Rate Poisson Tree Process model, following the default settings. Both bPTP and mPTP used the original BI as the input tree.

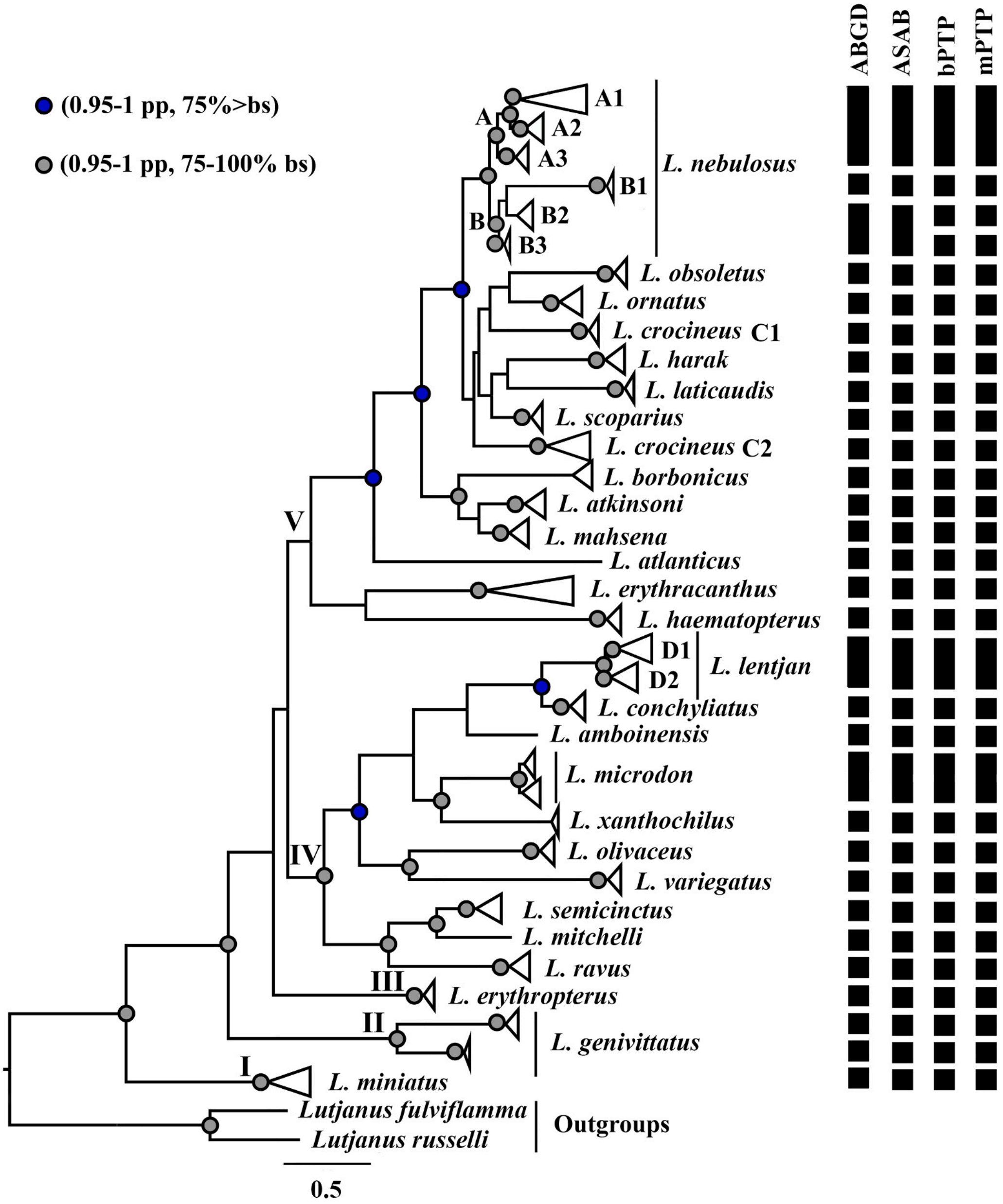

Fig. 1. Bayesian 50 % majority-rule consensus tree of *Lethrinus* species based on the COI sequences. The colored circles at the nodes indicate the BI posterior probability (PP) and ML bootstrap (BS) values. The black boxes of the tree denote the putative species identified by ASAP, ABGD, bPTP, and mPTP. Roman numerals (I-V) on branches denote major clades. The distribution of *L. nebulosus* spans several regions: A1 (northwestern Indian Ocean), A2 (Gulf of Oman), A3 (western Pacific), B1 (western Indian Ocean), B2 (Red Sea), and B3 (Gulf of Oman). *L. crocineus* is found in C1 (southwestern Indian Ocean) and C2 (Gulf of Oman and Bangladesh). *L. lentjan* is distributed in D1 (Persian Gulf and Gulf of Oman) and D2 (Indian-Pacific region, excluding samples from D1).

3. Results

3.1. Phylogeny reconstructions

The final data set consisted of 544 base pairs (bp) of COI, which had 218 variable positions. Both ML and BI analyses produced concordant trees with varying degrees of support (Fig. 1). The phylogenetic analyses are divided into five main clades, each with moderate to strong support at most nodes (Fig. 1). These clades are as follows: (I) *L. miniatus* as the sister species to all other clades; (II) *L. genivittatus*; (III) *L. erythropterus*; (IV) *L. ravus*, *L. mitchelli*, *L. semicinctus*, *L. variegatus*, *L. olivaceus*, *L. xanthochilus*, *L. microdon*, *L. amboinensis*, *L. rubrioperculatus*, *L. conchyliatus*, *L. lentjan*; (V) *L. haematopterus*, *L. erythracanthus*, *L. atlanticus*, *L. mahsena*, *L. atkinsoni*, *L. borbonicus*, *L. crocineus*, *L. scoparius*, *L. laticaudis*, *L. harak*, *L. crocineus*, *L. ornatus*, *L. obsoletus*, and *L. nebulosus*. The phylogenetic analyses also identified strongly supported new sequences, namely: *L. microdon*, *L. lentjan*, *L. borbonicus*, *L. crocineus*, and *L. nebulosus* from the Persian Gulf and Gulf of Oman. At the species level, K2P divergences ranged from 2.2 % (Lineages of *L. nebulosus*) and 6.92 % (*L. crocineus* and *L. nebulosus*) to 27.1 % (*L. microdon* and *L. nebulosus*) (Table S2).

3.2. Species delimitation

The molecular species delimitation methods (ABGD, ASAB, bPTP, and mPTP) yielded mostly congruent results (Fig. 1) with 30–31 genetically distinct MOTUs belonging to 27 nominal species. The ABGD and ASAB analyses delimited 30 putative species and the bPTP and mPTP analyses predicted 31 putative species. The only discrepancy involved a lineage of *L. nebulosus* from the Gulf of Oman (B3). Multiple species delimitation methods and COI-based trees revealed three highly divergent cryptic complexes in *L. nebulosus, L. crocineus*, and *L. lentjan* (Fig. 1). Six well-defined distinct monophyletic lineages have been identified in the *L. nebulosus* complex, which are divided into two main groups (A-B). Group A, which encompasses the majority of specimens, is further divided into three subclades with significant genetic divergence (> 2 %) (Table S3). These lineages include a lineage restricted to the Gulf of Oman (A2) and two widespread lineages with members from the northwestern Indian Ocean (A1) and the western Pacific (A3). Members of lineages B1 were identified as well-supported a monophyletic group corresponding to the western Indian Ocean, except for the Red Sea. Samples from lineages B2 and B3 are restricted to the Red Sea, including the type locality of *L. nebulosus* and Gulf of Oman, respectively. The average genetic distance between lineages within *L. nebulosus* ranged from 2.1 % (between lineages A2 and A3) to 15.9 % (between lineages A2 and B2) (Table S3). The haplotype network also confirmed the six lineages from the previous analyses (Fig. 1) and no shared haplotypes were found between them (Fig. 2 A, B). The *L. crocineus* included two distinct evolutionary lineages with high genetic divergence between them (10.5 %; the type locality is Mozambique in southeastern Africa) (Fig. 1) (Table S3). One lineage included specimens from Africa (southwestern Indian Ocean) (C1), while the other lineage included specimens from the Gulf of Oman and Bangladesh (C2). These lineages of *L. crocineus* are matched by divergences in the median-joining algorithm networks and are distinguished from each other by 24 fixed substitutions (Fig. 2C, D). The results of the phylogenetic (Fig. 1) and network analyses (Fig. 2E, F) are congruent and show the existence of two well-supported distinct lineages within *L. lentjan* with a genetic divergence of 2.4 % (Table S3). Lineage D1 was found in the Persian Gulf and Gulf of Oman, while lineage D2 was distributed in the rest of the Indian-Pacific Ocean distributions. However, these lineages were not confirmed by species delimitation methods (Fig. 1).

4. Discussion

This study is the first to investigate the diversity of emperor fishes in the Persian Gulf and Gulf of Oman. It presents a COI reference database for the region, which will serve as a foundation for future taxonomic studies, advanced evolutionary analyses, and conservation efforts.

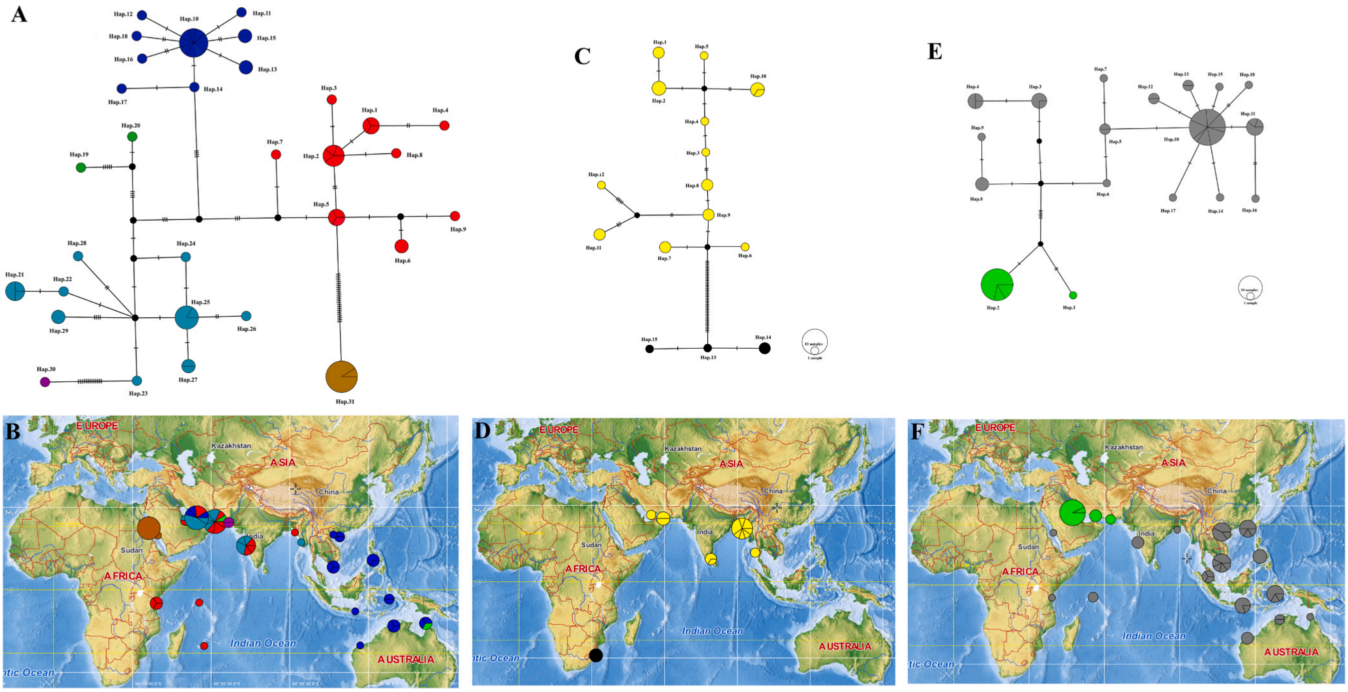

Fig. 2. the median joining haplotype network for the mitochondrial haplotypes observed in *L. nebulosus* (A) and *L. crocineus* (C) and in *L. lentjan* (E). The circle area is proportional to the frequency of the respective haplotype. Each color indicates the major lineages, each soft line connecting adjacent haplotypes represents a single mutational step. The small black circles correspond to the missing haplotypes. Biogeographic distributions for *L. nebulosus* (B) and *L. crocineus* (D) and *L. lentjan* (F).

4.1. Phylogenetic relationships

Although our research focuses on *Lethrinus* representatives in the northwestern Indian Ocean, including most lineages of this genus allowed for a more precise resolution of its phylogenetic framework. Previous molecular phylogenetic hypotheses among *Lethrinus* have been investigated with a limited number of taxa and exclusive geographic sampling (Lo Galbo et al., 2002, 18 spp; Mekkawy, 2017, 16 spp; Fabian et al., 2021, 6 spp). While our phylogenetic hypotheses are generally consistent with an earlier previous study (Lo Galbo et al., 2002), there are also new findings. In this study, we used twenty-seven out of the thirty valid *Lethrinus* species, and our phylogenetic hypothesis suggests the existence of five moderately to strongly supported clades. Using more species in phylogenetic studies improves tree accuracy, resolves relationships better, detects cryptic diversity, reduces bias, and clarifies evolutionary patterns and genetic divergence (Dellicour and Flot, 2018; Struck et al., 2018). The low resolution of phylogenetic relationships of some nodes may be due to the evolutionary rate of the COI gene in *Lethrinus* (Fig. 1), which is consistent with previous studies that used the Cyt *b* gene in *Lethrinus* (Lo Galbo et al., 2002). Despite this, COI is an established marker for species identification in the field of DNA barcoding (Hebert et al., 2003) and remains effective for analyzing interspecies relationships at the genus level. A total of five clades were identified (Fig. 1), with *L. miniatus* (Clade I) representing the earliest diverging lineage relative to all other clades. Previous molecular study based on the Cytb gene also confirm the high genetic divergence of this species from others congeners (Lo Galbo et al., 2002). It is evolutionarily older and has likely retained more ancestral characteristics, including an oval and compact body shape and conical, sharp teeth (Carpenter and Allen, 1989). Clades II and III include *L. genivittatus* and *L. erythropterus*, respectively. *Lethrinus genivittatus* and *L. erythropterus* mostly have deeper body shapes and tend to be uniformly dull coloured compared to *L. miniatus*, which generally inhabit coral reefs and have a distinct preference for waters with good visibility, such as lagoons and seaward reefs (Randall et al., 1998; Randall, 2005). Within clade IV, six out of ten species represent novel phylogenetic relationships (Fig. 1), which were not reported in previous studies (Lo Galbo et al., 2002; Fabian et al., 2021). In clade V, mainly species with molariform teeth and low bodies were found. The first three clades have the deepest body shapes with conical teeth compared to all other *Lethrinus* species (Carpenter, 1996). These results strongly support with the hypothesis proposed by Lo Galbo et al. (2002) that the mesocarnivore stalker is derived from a mesocarnivore generalist. The species of clades II and III, *L. genivittatus* and *L. erythropterus*, were included in clade V by Lo Galbo et al. (2002) based on of the Cyt *b* gene with weak support. However, additional markers are needed to clarify the phylogenetic relationships of these clades.

4.2. Cryptic diversity and distributions

The diversity in the genus *Lethrinus* is greater than previously thought (Healey et al., 2018; Rabosky et al., 2018; Holleman et al., 2022; Fabian et al., 2021). Our analyses confirm the presence of 30–31 distinct genetic groups within the genus, of which only 27 are currently recognized as named taxa. Despite the high morphological similarity, the average interspecific divergence between *Lethrinus* species in our study was 14.5 %, based on the COI gene. Similar levels of genetic divergence have been previously identified in related species of other genera (Chen et al., 2017), indicating that each MOTU may represent a distinct species and this could be a common pattern in marine fishes. However, the genetic variation within some *Lethrinus* species was higher than the 2 % threshold typically observed in marine fishes for the COI gene (Ward et al., 2009): 10.5 % within *L. crocineus*, 2.1–15.9 % within *L. nebulosus*, and 2.4 % within *L. lentjan*. This result suggests that the currently taxonomically recognized species do indeed exhibit a high degree of cryptic diversity. The presence of two putative dispersal barriers resulted in *L. crocineus* being divided into two well-supported lineages separated by 10.5 % divergence: upwelling systems and habitat discontinuity off the northern coast of Somalia and off the southern coast of Oman. One genetic lineage was associated with Madagascar and south Africa, and another lineage was associated with the Persian Gulf and Gulf of Oman to the Andaman Islands. Considering that the Madagascar/south Africa lineage contains sequences near the type locality of *L. crocineus* (Mozambique) (Smith, 1959; Fricke et al., 2024), it is possible that the other lineages represents a distinct species, depending on the results of further sampling and investigation based on integrative morphological and molecular data. Our data provide evidence of biogeographical breaks between these two lineages structured primarily by the activity of the southwest monsoon, which results in seasonal cold-water upwelling events that may impede the planktonic dispersal of species that cannot tolerate low temperatures (Hoeksema, 2007; Vic et al., 2017; DiBattista et al., 2022). In addition, such oceanographic events have also resulted in large areas of unsuitable larval habitat in upwelling areas, that can isolate populations by limiting stepping stone connections, increasing the likelihood of splitting into multiple species (Burt et al., 2016; Priest et al., 2016). Our findings support the hypothesis that the evolution of coral reef fishes in the Northwestern Indian Ocean was likely shaped by multiple vicariance events (DiBattista et al., 2017; Torquato et al., 2019). The spangled emperor, *Lethrinus nebulosus* also is a species complex consisting of several highly divergent lineages, as confirmed by phylogenetic analyses, molecular species delimitation and the haplotype network (Fig. 1-2A, B). These lineages were not detected in an earlier, limited study of *L. nebulosus* (Holleman et al., 2022), in which sampling in the western Indian Ocean was restricted to Madagascar and South Africa. This complex had by far the highest genetic diversity (2.1 %-15.9 %) (Table S2), suggesting that a number of *L. nebulosus* lineages were genetically represented at the species level. The Indo-West Pacific *L. nebulosus* lineage (A) was well represented with three main lineages (Northwest Indian Ocean (A1); Gulf of Oman (A2); West Pacific (A3)) (Fig. 1). Considering that the Red Sea lineages contains sequences from the type locality of *L. nebulosus* (Forsskål, 1775; Fricke et al., 2024), it is likely that the other lineages, which includes specimens from the Persian Gulf and Gulf of Oman, harbours a distinct species. The Western Pacific lineages appears to be allopatric in distribution and may be separated from two other Indian Ocean partitions by the Sunda Shelf barrier (Randall, 1998; Rocha et al., 2007; Ludt and Rocha, 2015). This barrier formed land bridges across the Indonesian archipelago that restricted exchange between the Pacific and Indian Oceans (Randall, 1998; Rocha et al., 2007; Waldrop et al., 2016), and this pattern has been documented in reef fishes (Waldrop et al., 2016; Ahti et al., 2016; Chen and Borsa, 2020). The mechanisms that distinguish two sympatric lineages in the Gulf of Oman and Arabian Sea (North Indian Ocean) are less well understood and may be related to the monsoon winds that cause seasonal reversals in the surface circulation (Shankar et al., 2002; Sivadas and Ingole, 2016). These two distinct lineages need further investigation. The WIO lineage of *L. nebulosus* (B1-B3) indicate a genetic and geographic division into three distinct lineages (Red Sea (B1); Western Indian Ocean (B2); Gulf of Oman (B3)). The Red Sea *L. nebulosus* was likely separated from the other two lineages by the closure of the Bab al Mandab Strait and sea-level fluctuations, leading to extreme changes in salinity and temperature (Siddall et al., 2004; Stevens et al., 2014; DiBattista et al., 2016), a conclusion supported by other marine fishes, such as wrasses (Froukh and Kochzius, 2007), butterflyfish and snappers (DiBattista et al., 2017), jacks (Bogorodsky et al., 2017). In the pink ear emperor, *L. lentjan*, the mtDNA partition distinguished samples from the Persian Gulf and Gulf of Oman by 2.4 % at the COI gene compared to the Indian-Pacific lineage. Despite being close to the conventional barcoding threshold, the 2.4 % divergence is interpreted here as evidence of cryptic diversity within *L. lentjan*. This conclusion is bolstered by a distinct haplotype network lacking shared (Fig. 2E) and by deep nodes in the phylogenetic trees that received strong statistical support in both ML and BI analyses (Fig. 1).

The type locality of *L. lentjan* is probably Java, Indonesia, in the western Pacific. The Persian Gulf/Gulf of Oman lineage detected here is the same as the West Pacific lineage reported by Biesack (2017). In the same study, Biesack reported a genetic heterogeneity of the population along the boundaries of the repeatedly isolated West Pacific. This symmetry of divergent lineages at the eastern (South China Sea and Philippines) and western (Persian Gulf/Gulf of Oman) ends of the range, and vast connectivity in between, adds to the accumulating evidence that peripheral habitats, especially those with unique environmental conditions, can serve as incubators of evolution (Hodge et al., 2014; Gaither et al., 2015; DiBattista et al., 2017). The isolation of the Persian Gulf/Gulf of Oman lineage is not surprising given the turbulent palaeoclimatic history of the region and the current heterogeneity of environmental conditions (Coles, 2003; Feary et al., 2010; Burt et al., 2011; Maghsoudlou et al., 2019). The Persian Gulf and Gulf of Oman border such a hotspot, where many endemic species occur that have split off from sister taxa (Iwatsuki, 2013; Damadi et al., 2020). This peripheral endemism was likely enhanced by modern glacial cycles of Pleistocene sea-level fluctuations and upwelling events off the southern coast of Oman, which may have isolated populations of widespread species (DiBattista et al., 2016), including *L. lentjan*. However, it remains no less important to critically examine the morphology of new specimens in the future to further test the taxonomy suggested by the DNA data. The best taxonomy is undoubtedly the result of a holistic approach in which morphological, ecological and genetic data are used together to delimit species.

Disclosure statement

The authors declare that they have no conflicts of interest. The authors obtained all necessary permits for sampling from the Iranian authorities (scientific permit NI2018/09).

CRediT authorship contribution statement

Ehsan Damadi: Writing – review & editing, Writing – original draft, Validation, Software, Methodology, Formal analysis, Data curation. **Faezeh Yazdani Moghaddam:** Visualization, Supervision, Project administration, Funding acquisition. **Mehdi Ghanbarifardi:** Validation, Software, Methodology, Formal analysis.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2025.104492.

Data availability

All of the relevant data is available in the main text or in the supplementary material.

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