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Molecular and Morphological Systematics of Caranx (Carangidae) Species in the Mediterranean Sea

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Abstract

The genetic and morphological structure and phylogenetic relationships of three Caranx species (*Caranx crysos*, *Caranx hippos*, and *Caranx rhoncus*) inhabiting Turkish marine waters were investigated for the first time using an integrative approach. Molecular phylogenetic analyses were performed based on nucleotide sequence variation of the mitochondrial DNA control region (D-loop) using the Tamura three-parameter substitution model. The nucleotide composition exhibited a clear AT bias, with GC content ranging from 35.7% to 38.1% (mean=37.2%) and AT content ranging from 62.0% to 63.8% (mean=62.8%). Genetic distance analysis revealed the highest nucleotide divergence between *C. crysos* and *C. hippos* (0.461), whereas *C. hippos* and *C. rhoncus* showed the closest genetic relationship (0.148). Maximum Likelihood phylogenetic reconstruction based on D-loop sequences resolved two main lineages: one comprising *C. rhoncus* and *C. hippos*, and the other consisting solely of *C. crysos*. The Minimum Spanning Tree haplotype network provided strong evidence for genetic differentiation among Caranx species and supports their recognition as distinct evolutionary lineages and suggests limited or no recent maternal gene flow between species, despite their potential geographic overlap. Morphological differentiation among species was assessed using 36 truss network morphometric characters and 12 meristic traits. Discriminant function analysis indicated that second dorsal fin length, interorbital distance, and the number of soft rays in the second dorsal fin were the most informative variables in the first discriminant function, whereas body depth measurements and lateral line scale counts contributed most strongly to species separation in the second discriminant function. Neighbor-Joining analysis of morphological data grouped *C. rhoncus* and *C. crysos* together, while *C. hippos* formed a distinct cluster. The contrasting clustering patterns obtained from molecular and morphological datasets reveal a notable discordance between genetic and phenotypic relationships among Mediterranean Caranx species. These results demonstrate that reliance on morphology alone may obscure true evolutionary relationships and highlight the importance of integrating molecular and morphological approaches for accurate systematics. This study provides the first molecular phylogenetic framework for Caranx species in Turkish marine waters and contributes to a better understanding of their evolutionary history and taxonomic relationships in the Mediterranean Sea.

Keywords
Caranx, Phylogeny, mtDNA, D-Loop, Morphology, Mediterranean Sea.

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Introduction

The genus Caranx (family Carangidae) represents a group of ecologically and economically important marine fishes widely distributed across tropical and subtropical regions of the Atlantic, Pacific, and Indian Oceans. Species of this genus typically inhabit coastal and offshore environments including bays, lagoons, coral reefs, and sandy or muddy substrates, and many exhibit both demersal and pelagic life-history traits accompanied by schooling behavior.

Globally, the genus Caranx comprises approximately eighteen recognized species. However, only three species have been documented from Turkish marine waters: *Caranx crysos* (Mitchill, 1815), *Caranx hippos* (Linnaeus, 1766), and *Caranx rhoncus* (Geoffroy Saint-Hilaire, 1817) (Mater & Meriç, 1996; Turan et al., 2007). Despite their commercial relevance and broad geographic distribution, the genetic diversity and phylogenetic relationships of Caranx species remain insufficiently resolved, particularly in the Mediterranean region.

Previous molecular studies on Caranx have primarily focused on populations from the Indo-Pacific and Atlantic regions. Murakami et al. (2007) investigated *C. ignobilis, C. sexfasciatus*, and *C. melampygus* using mitochondrial 16S rDNA and cytochrome oxidase I (COI) gene sequences from Hawaiian waters and reported evidence of interspecific hybridization, especially between *C. ignobilis* × *C. melampygus* and *C. melampygus* × *C. sexfasciatus*. Similarly, Santos et al. (2011) analyzed the genetic structure of *C. ignobilis* and *C. melampygus* based on ATPase6 and ATPase8 mitochondrial genes and identified multiple haplotypes without significant population-level genetic differentiation, while also detecting introgressive hybridization between these species.

In the Mediterranean, molecular investigations of Caranx species are scarce. Bektaş et al. (2009) examined the population genetics of *C. rhoncus* and the phylogenetic relationships of Trachurus species using mitochondrial cytochrome b and nuclear 5S rRNA genes, demonstrating that the 12S rRNA gene effectively discriminated between the closely related genera Caranx and Trachurus, although it lacked sufficient resolution at the species level within Trachurus. These findings underscore the need for more comprehensive molecular markers to clarify interspecific relationships within the genus Caranx.

Mitochondrial DNA (mtDNA) has been extensively applied in phylogenetic and population genetic studies of marine organisms due to its maternal inheritance, relatively rapid evolutionary rate, and lack of recombination (Turan et al., 2009; Turan et al. 2024; Yankova et al., 2025; Turan et al., 2025). Different mitochondrial genes evolve at variable rates, enabling the selection of appropriate markers for both interspecific and intraspecific analyses (Erguden et al., 2010; Turan et al., 2019). Among these, the mitochondrial control region (D-loop) has proven to be a particularly informative marker for resolving phylogenetic relationships in marine fishes and for detecting fine-scale genetic differentiation across taxonomic levels.

Integrative approaches combining molecular and morphological data have become increasingly important for resolving phylogenetic relationships in marine fishes, where phenotypic plasticity and convergent evolution often obscure species boundaries based solely on external characters (Erdoğan et al., 2009; Erguden et al., 2009; Turan & Basusta, 2001; Doğdu & Turan, 2021). Morphological traits remain fundamental for taxonomic identification and ecological interpretation; however, they can be strongly influenced by environmental conditions and may exhibit homoplasy across unrelated lineages. he joint use of genetic and morphological characters therefore enhances the robustness of phylogenetic inference, improves species delimitation, and facilitates a more comprehensive understanding of evolutionary processes in marine fish lineages.

Understanding the genetic divergence and phylogenetic structure of Caranx species occurring in the Mediterranean Sea is essential from both evolutionary and fisheries management perspectives. Accurate species identification and knowledge of evolutionary relationships are critical for the sustainable management of exploited stocks and for the assessment of biodiversity in the Mediterranean Sea (Carvalho et al., 1998). However, integrated studies combining molecular and morphological data on Caranx species from this region remain notably limited.

Therefore, the present study aims to elucidate the phylogenetic relationships of Caranx species distributed in the Mediterranean using an integrative approach based on molecular (mtDNA) and morphological markers. This study provides new insights into the systematics of the genus Caranx in the Mediterranean Sea and contributes to a more robust taxonomic framework for this economically important group.

Materials and Methods

Sample collection and biological data

A total of forty individuals from each Caranx species were collected from İskenderun Bay, northeastern Mediterranean Sea. All specimens were transported to the laboratory under refrigerated conditions and identified to species level based on standard taxonomic keys. Age determination was performed by counting annuli on sagittal otoliths. Sex was determined macroscopically through gonadal examination whenever possible.

DNA extraction and PCR amplification

Total genomic DNA was extracted from muscle tissue using the standard phenol–chloroform–isoamyl alcohol protocol (Sambrook et al., 1989). DNA quality and concentration were assessed by agarose gel electrophoresis and spectrophotometry. The mitochondrial DNA control region (D-loop) was amplified using the following universal primers:

Forward: 5′-TAC CCC AAA CTC CCA AAG CTA-3′
Reverse: 5′-GCG GAG GCT TGC ATG TGT A-3′

PCR amplification was performed in a total reaction volume of 25 µl containing 1.5 µl of 10× PCR buffer, 0.5 µl dNTPs (10 mM), 0.3 µl Taq DNA polymerase (3 U/µl), 0.10 µl of each primer, 1 µl of template DNA, and nuclease-free water. Thermal cycling conditions consisted of an initial denaturation at 94 °C for 4 min, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 52 °C for 20 s, and extension at 72 °C for 1 min 30 s, with a final extension step at 72 °C for 7 min.

Sequence alignment and phylogenetic analysis

Partial D-loop sequences were initially aligned using ClustalW (Thompson et al., 1994). Final alignments were manually refined in BioEdit (Hall, 1999). Sequence data were analyzed to determine nucleotide composition and pairwise genetic distances using MEGA software (Kumar et al., 2004). The best-fitting model of nucleotide substitution was selected using ModelTest (Posada & Crandall, 1998). Phylogenetic relationships were reconstructed using three complementary approaches: Neighbor-Joining (NJ) Maximum Parsimony (MP), and Maximum Likelihood (ML) (Saitou & Nei, 1985; Saitou & Ġmanishi, 1989). The robustness of the inferred phylogenetic trees was assessed by bootstrap resampling (Felsenstein, 1985) with 1000 replicates.

Meristic and morphometric analyses

Meristic characters commonly used in Caranx taxonomy were recorded for each specimen, including: first dorsal fin rays (DFR1), second dorsal fin rays (DFR2), ventral fin rays (VFR), anal fin rays (AFR), pectoral fin rays (PFR), gill rakers (GR), vertebrae number (VN), and lateral line scales (LS). Morphometric variation was analyzed using the truss network system described by Strauss and Bookstein (1982). Fourteen homologous anatomical landmarks were digitized, generating 36 inter-landmark distances (Figure 1). These landmarks corresponded to key anatomical points including the snout tip, neurocranium, dorsal and anal fin origins and terminations, caudal peduncle, and jaw extremities.

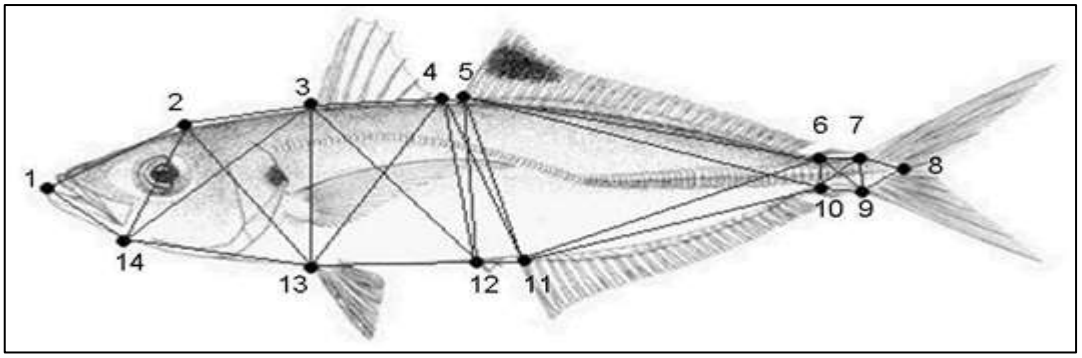

Figure 1. Truss network measurements and landmark configuration based on 14 anatomical points in.

Caranx species: 1) anterior tip of the snout; 2) posterior margin of the neurocranium (origin of nape measurement); 3) origin of the first dorsal fin; 4) termination of the first dorsal fin; 5) origin of the second dorsal fin; 6) termination of the second dorsal fin; 7) anterior dorsal margin of the caudal fin; 8) posterior end of the vertebral column; 9) anterior ventral margin of the caudal fin; 10) termination of the anal fin; 11) origin of the anal fin; 12) origin of the anterior hard spine of the anal fin; 13) origin of the ventral (pelvic) fin; 14) posterior end of the maxilla (jaw tip).

Size adjustment and statistical analyses

Because morphological variation is strongly influenced by body size (Junquera & Perez-Gandaras, 1993), shape variables were size-adjusted to remove allometric effects and avoid misinterpretation. The allometric transformation method described by Turan (1999) was applied to standardize morphometric measurements.

Principal Component Analysis (PCA) and Hierarchical Cluster Analysis (HCA) were performed to evaluate morphological differentiation and taxonomic relationships among species. All statistical analyses were conducted using SPSS and SYSTAT software packages.

Results

The ranges of the examined meristic characters of the Caranx species were consistent with the diagnostic descriptions reported by Fischer et al. (1987) and Turan et al. (2007) (Table 1). No overlapping anomalies or abnormal counts were observed among the specimens, confirming the accuracy of species identification. The modal values of meristic characters differed slightly among species, particularly for gill rakers (GR), lateral line scales (LS), and vertebra numbers (VN), providing additional morphological support for species discrimination.

Table 1. Range and mode of observed meristic characters of Caranx species. Roman numerals indicate spine rays. Abbreviations: DFR, dorsal fin rays; VFR, ventral fin rays; AFR, anal fin rays; PFR, pectoral fin rays; GR, gill rakers; LS, lateral line scales; VN, vertebra numbers.

Species	D1SIS	D2IS	AIS	PIS	VIS	SDS	OS	YPS1	YPS2
C. hippos	VII-VIII/VIII	I-20-24/20	III-17-19/17	I-18-20/19	I - 5	29-39/34	25	36-40/38	36-44/42
C. crysos	VII-VIII/VIII	I-23-26/24	III-20-24/20	I-18-22/22	I - 5	31-37/35	25	42-47-42	44-50/47
C. rhoncus	VII-VIII/VII	I-29-31/30	III-23-25/24	I-18-22/19	I - 5	38-50/41	25	40-47/44	34-44/38

Principal Component Analysis (PCA) revealed that the first two principal components accounted for 89% and 11% of the total morphological variation, respectively, explaining 100% of the observed variance. These two components were therefore used in subsequent Hierarchical Cluster Analysis (HCA). The Neighbor-Joining dendrogram based on squared Euclidean distances indicated that *C. rhoncus* and *C. crysos* clustered closely within the same node, whereas *C. hippos* formed a neighboring but distinct cluster (Figure 2). This pattern demonstrates a higher degree of morphological similarity between *C. rhoncus* and *C. crysos* compared to *C. hippos*.

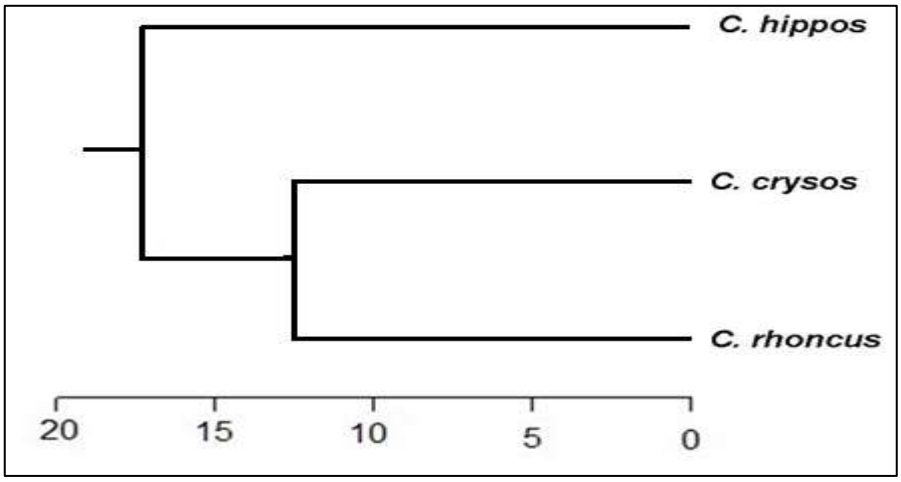

Figure 2. Neighbor-Joining dendrogram illustrating morphological relationships among Caranx species based on truss network measurements.

Following sequence alignment, partial mitochondrial D-loop sequences consisted of 610 base pairs. Nucleotide composition analysis revealed a high proportion of adenine (A=31.43%) and thymine (T=31.43%), indicating strong AT bias, which is typical of mitochondrial control regions in marine fishes. The dataset included 365 conserved sites, 245 variable sites, and 228 parsimony-informative sites, reflecting substantial genetic variation among the examined taxa.

Model selection using ModelTest identified the Tamura three-parameter (T92) model as the best-fitting nucleotide substitution model, and this model was applied in subsequent phylogenetic analyses.

Pairwise genetic distances among species are presented in Table 2. In interspecific comparisons, the highest genetic divergence was observed between *C. hippos* and *C. crysos*, whereas the lowest divergence occurred between *C. rhoncus* and *C. hi*ppos. For intraspecific comparisons, the lowest genetic divergence was detected within *C. hippos*, indicating relatively low genetic variability within this species compared to the others.

Table 2. Pairwise genetic divergence between species and within species (bold values).

	C. crysos	*C. rhoncus*	*C. hippos*
C. crysos	**0.011**		
C. rhoncus	0.450	**0.021**	
C. hippos	0.461	0.148	**0.009**

The Minimum Spanning Tree (MST) haplotype network based on mtDNA D-loop sequences revealed pronounced genetic structuring among the three examined Caranx species (*C. caranx, C. hippos*, and *C. rhoncus*) (Figure 3). Haplotypes of *C. caranx* formed a central star-like cluster characterized by short branch lengths (1-4 mutational steps), indicating low intraspecific divergence and suggesting recent diversification or ongoing gene flow within this species. Several low-frequency haplotypes radiated from a common central haplotype, consistent with the high variability of the D-loop region. In contrast, haplotypes of *C. hippos* and *C. rhoncus* were clearly separated from the *C. caranx* cluster by a large number of mutational steps (up to 198 and 75, respectively), reflecting deep interspecific divergence in the mitochondrial control region. *C. hippos* haplotypes formed a compact cluster with limited internal variation, whereas *C. rhoncus* haplotypes were grouped into a distinct cluster with moderate haplotype divergence. No haplotypes were shared among species, demonstrating complete haplotype segregation in the mtDNA D-loop dataset.

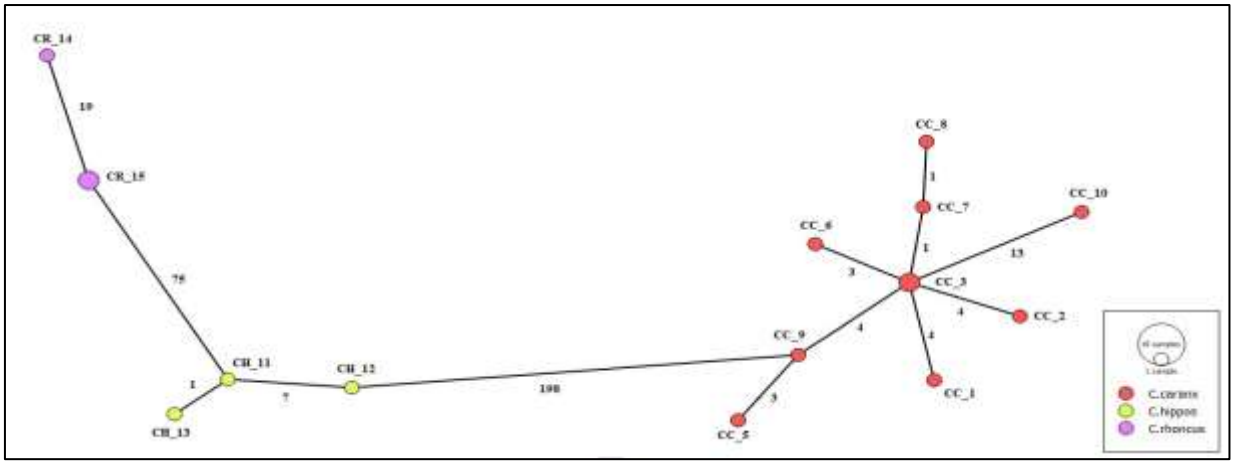

Figure 3. Minimum Spanning Tree haplotype network based on mitochondrial DNA (mtDNA) D-loop sequences of three Caranx species

(*C. caranx, C. hippos*, and *C. rhoncus*). Each circle represents a unique haplotype, with circle size proportional to haplotype frequency (number of individuals). Numbers on branches indicate the number of mutational steps between haplotypes.

Phylogenetic reconstructions using Neighbor-Joining, Maximum Likelihood, and Maximum Parsimony methods yielded congruent tree topologies with strong bootstrap support for major clades. In all three analyses (Figures 4–6), *C. rhoncus* clustered closely with *C. hippos*, forming a well-supported monophyletic group. In contrast, *C. crysos* formed a distinct and more divergent lineage, positioned outside this cluster. Running Neighbor-Joining with outgroup species *Sarda sarda* also resulted similar tree topology (Figure 7).

The consistency of tree topology across different phylogenetic methods indicates the robustness of the inferred relationships among the studied Caranx species. Bootstrap values further supported the separation of *C. crysos* from the *C. rhoncus* and *C. hippos* clade, highlighting its greater genetic divergence relative to the other two species.

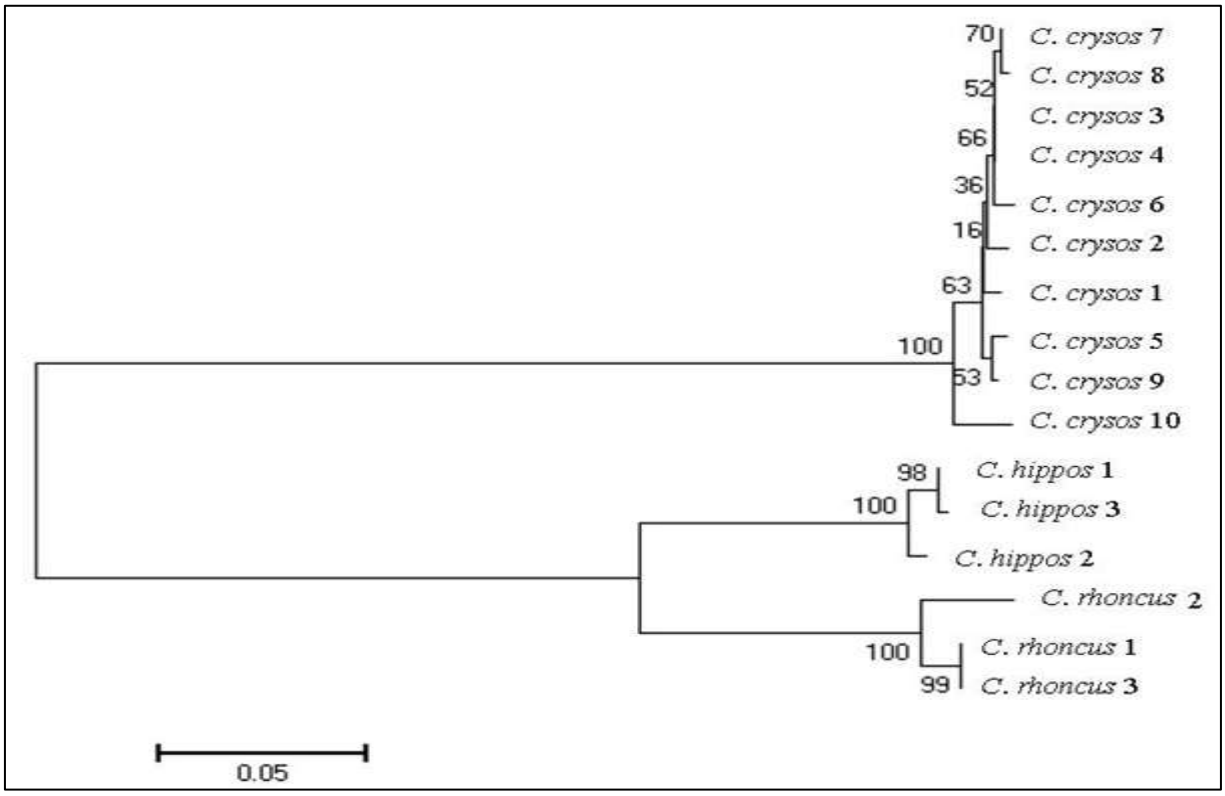

Figure 4. Phylogenetic tree constructed using the Neighbor-Joining method based on mitochondrial D-loop sequence data.

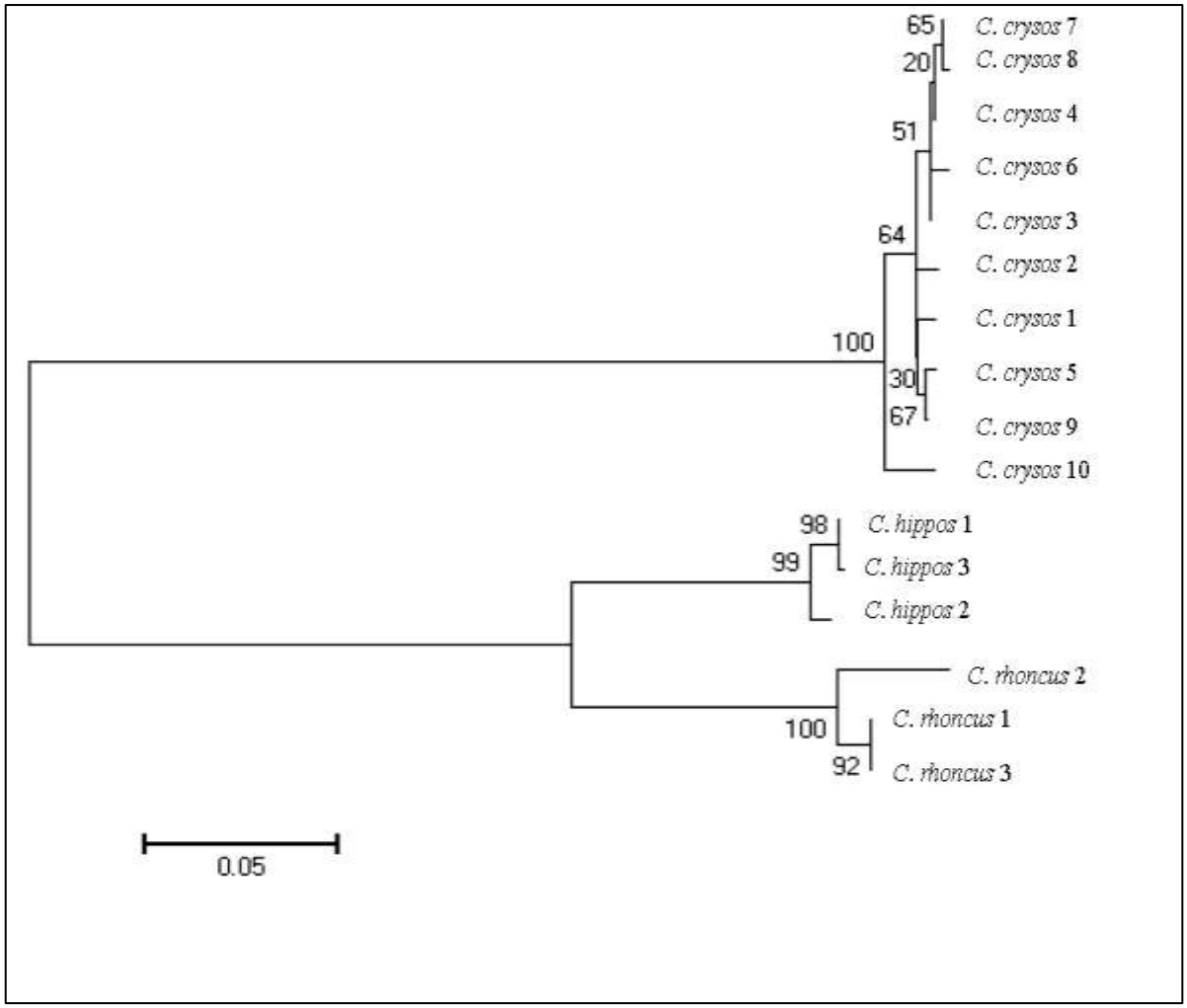

Figure 5. Phylogenetic tree inferred by the Maximum Likelihood method from mitochondrial D-loop sequence data.

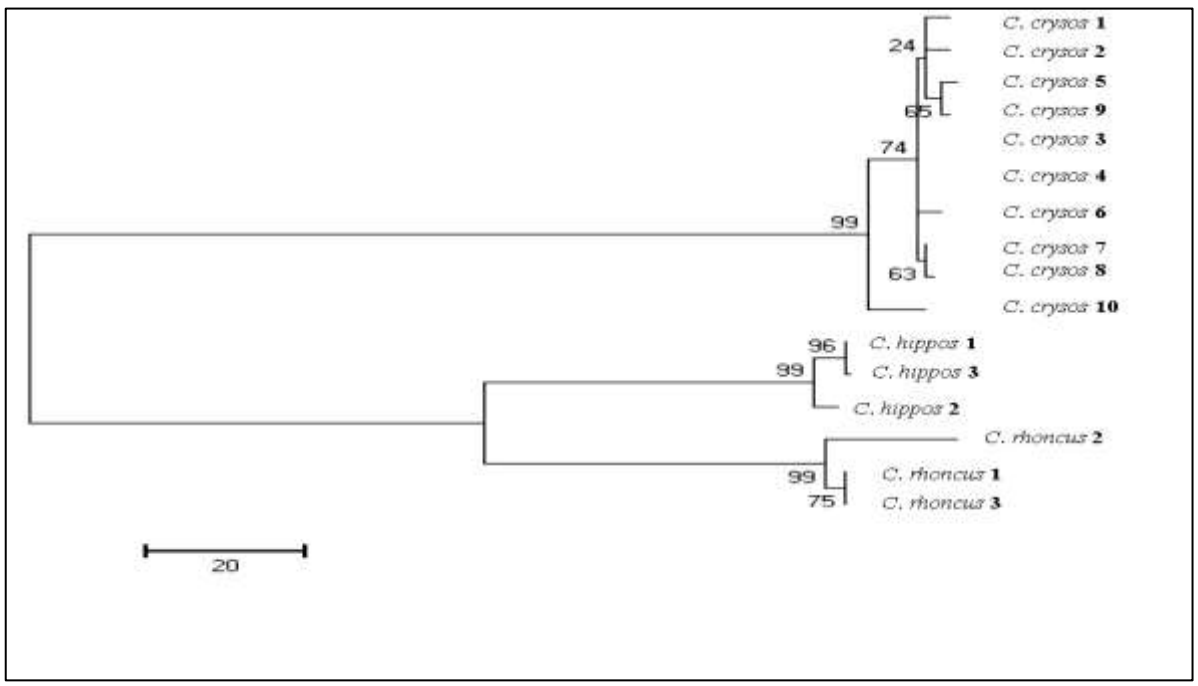

Figure 6. Phylogenetic tree generated using the Maximum Parsimony method based on mitochondrial D-loop sequence data.

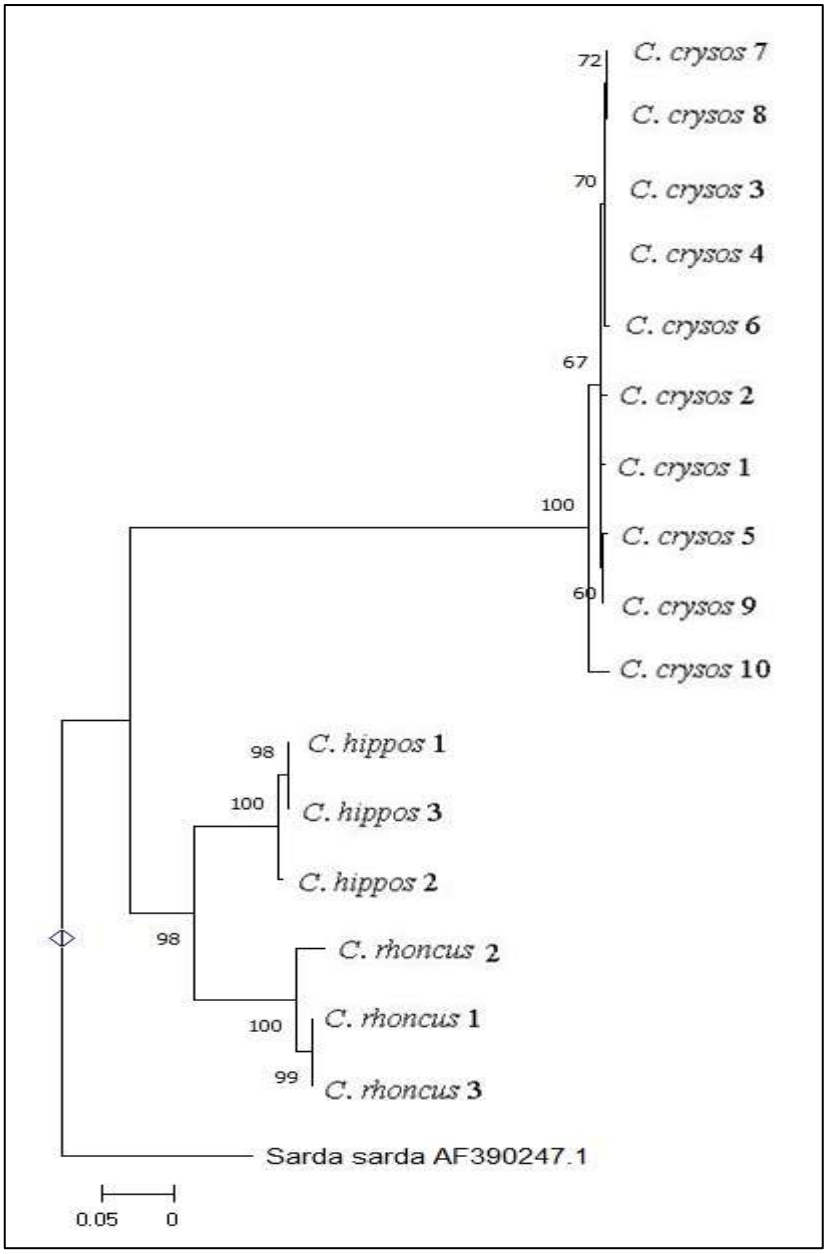

Figure 7. Phylogenetic tree constructed using the Neighbor-Joining method based on mitochondrial D-loop sequence data with outgroup *Sarda sarda* (from GenBank, accession mo: AF390247.1).

Discussion

This study represents the first successful molecular-based evaluation of the systematic and phylogenetic relationships of Caranx species inhabiting the Mediterranean Sea. By integrating mitochondrial D-loop sequences with morphometric and meristic analyses, our results provide new insights into the evolutionary relationships of Caranx species in the Mediterranean and allow direct comparison with previous molecular studies conducted in other geographic regions.

Morphological analyses indicated that *C. rhoncus* and *C. crysos* clustered closely based on truss network measurements and squared Euclidean distances, whereas *C. hippos* formed a neighboring but distinct group. Similar morphological proximity among Caranx species has been reported in earlier taxonomic studies relying on external characters and meristic counts (Fischer et al., 1987; Turan et al., 2007). These studies emphasized overlapping morphological traits among Caranx species, which can complicate reliable species discrimination based solely on phenotype.

The mtDNA D-loop haplotype network provides strong evidence for genetic differentiation among Caranx species and supports their recognition as distinct evolutionary lineages. The absence of shared

haplotypes among *C. caranx, C. hippos*, and *C. rhoncus* suggests limited or no recent maternal gene flow between species, despite their potential geographic overlap. The star-like topology observed in *C. caranx* is typical of populations that have experienced recent demographic expansion or rapid lineage diversification, a pattern commonly detected using the highly polymorphic D-loop region. Such a structure may reflect historical population growth following environmental or climatic changes affecting marine habitats (Avise, 2000; Grant & Bowen, 1998). The MST network highlights shallow variation within species and deep divergence among species, emphasizing the utility of haplotype network analyses in phylogeographic and population genetic studies of marine fishes.

In contrast, molecular phylogenetic analyses based on mitochondrial D-loop sequences consistently grouped *C. rhoncus* with *C. hippos*, forming a well-supported monophyletic clade, while *C. crysos* appeared as a distinct and more divergent lineage. This pattern is in partial agreement with previous genetic studies of the genus. Murakami et al. (2007) demonstrated close genetic relationships and hybridization among Indo-Pacific Caranx species (*C. ignobilis, C. melampygus*, and *C. sexfasciatus*), suggesting recent divergence within the genus. Similarly, Scott et al. (2011) reported limited genetic differentiation between *C. ignobilis* and *C. melampygus* based on ATPase6 and ATPase8 gene regions, supporting the idea of closely related lineages within Caranx.

Our findings extend these observations to Mediterranean Caranx species and reveal that *C. rhoncus* and *C. hippos* share a closer genetic affinity than either does with *C. crysos*. Bektaş et al. (2009), using mitochondrial Cyt b and nuclear 5S rRNA markers, showed that Caranx and Trachurus could be clearly separated at the genus level but did not resolve species-level relationships within Caranx. The present study improves upon this limitation by employing the highly variable mitochondrial D-loop region, which provided sufficient resolution to discriminate among Mediterranean Caranx species.

The discordance observed between morphological and molecular clustering patterns has also been reported in other fish taxa (Avise, 1994; Turan, 2006, 2008; Turan et al. 2009). Turan et al. (2009) highlighted that phenotypic similarity does not necessarily reflect genetic relatedness due to phenotypic plasticity, ecological convergence, and historical demographic processes. The morphological similarity between *C. rhoncus* and *C. crysos* observed in this study may therefore reflect adaptation to similar ecological conditions in the Mediterranean rather than close evolutionary ancestry.

Furthermore, Murakami et al. (2007) documented hybridization among several Caranx species in Hawaiian waters, indicating that incomplete lineage sorting and introgression may influence phylogenetic signals in this genus. Although hybridization was not directly tested in the present study, the genetic separation of *C. crysos* from the *C. rhoncus* to *C. hippos* clade suggests limited recent gene flow among Mediterranean species compared to Indo-Pacific populations.

From a biogeographic perspective, the distinct genetic position of *C. crysos* may reflect different colonization routes or historical isolation within the Mediterranean basin. Previous studies have shown that Pleistocene climatic oscillations strongly shaped the genetic structure of Mediterranean marine fishes (Turan et al., 2009). Our results are consistent with this framework and suggest that *C. crysos* may represent an earlier diverging lineage in this region.

From a fisheries management perspective, previous studies have emphasized the difficulty of species identification in Carangidae based solely on morphology (Fischer et al., 1987; Turan et al., 2007; Bektaş et al., 2009). The present molecular results provide a complementary and more reliable tool for distinguishing Caranx species in Turkish marine waters. This is particularly important because misidentification of morphologically similar species such as *C. rhoncus* and *C. crysos* could bias stock assessments and mask species-specific population trends.

In conclusion, our findings are broadly consistent with earlier molecular studies demonstrating close genetic relationships among certain Caranx species, while also revealing region-specific evolutionary patterns in the Mediterranean Sea. The close genetic affinity between *C. rhoncus* and *C. hippos*, contrasted with the divergent position of *C. crysos*, highlights the importance of molecular data in resolving systematic relationships that are not evident from morphology alone. By providing the first molecular phylogenetic framework for Mediterranean Caranx species, this study contributes to a more

robust understanding of the systematics, evolution, and management of this economically important genus.

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