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ARTICLE

DNA barcode, population genetic structure and a novel perspective on the global fishery management units of the dolphinfish *Coryphaena hippurus* (Perciformes: Coryphaenidae)

Código de barras de ADN, estructura genética poblacional y una nueva perspectiva sobre las unidades de gestión pesquería global del dorado *Coryphaena hippurus* (Perciformes: Coryphaenidae)

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Abstract: *Coryphaena hippurus* (dolphinfish) is an important epipelagic top predator and global fishery resource. Global fishing indices indicate a tenfold increase in catch, and intense fishing may reduce genetic diversity and increase vulnerability to extinction. Here, we assess population genetic patterns in dolphinfish using cytochrome c oxidase subunit I, a molecular marker not previously applied to this approach. We observed genetic diversity indices similar to those previously described for the mitochondrial NADH dehydrogenase subunit 1 gene in *C. hippurus*, with both markers showing moderate to high genetic diversity. However, these findings should be interpreted with caution, because cytochrome c oxidase subunit 1 has limitations that prevent direct inferences about the effects of fishing pressure on genetic variation. Our analyses revealed low genetic distinction among populations from the Pacific, Indian and Atlantic Oceans, except for the Mediterranean basin, which retained a mean Φ_{ST} difference of 59% from the other basins. This pattern is consistent with findings for NADH dehydrogenase subunit 1 and nuclear single-nucleotide polymorphisms, which indicated subgroups within the Mediterranean basin potentially associated with environmental variation. Despite this differentiation, no evidence supported a molecular operational taxonomic unit endemic to the Mediterranean basin. Future management plans must consider Mediterranean populations separately.

Keywords: mtDNA, COI, fishery management units, DNA barcoding, species delimitation, marine conservation, gene flow.

Resumen: *Coryphaena hippurus* (dorado) es una importante especie epipelágica, depredador superior y recurso pesquero mundial. Los índices mundiales indican un aumento de diez veces en sus capturas, y la pesca intensiva puede reducir su patrimonio genético, aumentando potencialmente la vulnerabilidad a la extinción. Evaluamos los patrones genético-poblacionales del dorado mediante la subunidad 1 de la citocromo c oxidasa (COI), un marcador aún no aplicado a este enfoque. Observamos índices de diversidad genética similares a los descritos para el gen mitocondrial ND1 en *C. hippurus*, con ambos marcadores mostrando diversidad moderada a alta. Sin embargo, el COI presenta limitaciones que impiden inferencias directas sobre los efectos de la presión pesquera en la variación genética. Los análisis revelaron baja diferenciación entre las poblaciones de los océanos Pacífico, Índico y Atlántico, excepto en la cuenca mediterránea, con una diferencia media de Phi-ST del 59% respecto a las demás cuencas. Este patrón concuerda con ND1 y marcadores nucleares, como SNP, que indicaron subgrupos mediterráneos potencialmente asociados con la variación ambiental. Pese a esta diferenciación, no hubo evidencia de una MOTU endémica del Mediterráneo. Los futuros planes de gestión y conservación deben considerar separadamente las poblaciones mediterráneas.

Palabras clave: ADNmt, COI, unidades de gestión pesquera, código de barras genético, delimitación de especies, conservación marina, flujo génico.

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Supplementary information ↓

1. INTRODUCTION

The paradigm that considered marine populations to be panmictic and genetically homogeneous, owing to the absence of visible barriers in the marine environment, is not always supported by current population genetic studies, which have revealed extensive genetic structuring across several taxa common to this ecosystem (Mattos *et al.* 2019, Bunholi *et al.* 2022), ranging from planktonic organisms (Melo *et al.* 2020) to species with high swimming activity (Andrade *et al.* 2021). Several factors can influence the genetic structuring of marine populations, including ocean circulation (Zhu *et al.* 2016), geographic distance (Momigliano *et al.* 2017) and climatic oscillations (Hsu and Gwo 2017, Lehnert *et al.* 2019, Queiroz-Brito *et al.* 2022), as well as the biological and historical characteristics of the species (White *et al.* 2010, Silva *et al.* 2018, Andrade *et al.* 2021).

Another factor capable of mediating variation in genetic structure in marine environments is fishing. The population decline caused by this activity has the potential to intensify problems such as inbreeding, genetic drift and loss of phenotypic plasticity as a consequence of reduced evolutionary potential (Frankham *et al.* 2002, Allendorf *et al.* 2014, Pinsky and Palumbi 2014). In addition, high selective pressure can promote changes of different magnitudes, with affected populations requiring decades to recover (Hutchings 2000, Briggs 2014).

Coryphaena hippurus (dolphinfish) is a species of fish belonging to the family Coryphaenidae, with an epipelagic and cosmopolitan distribution in tropical and subtropical waters above 20°C. The species is of considerable ecological importance because of its predatory characteristics and is also an important fishery resource worldwide (Lasso and Zapata 1999, Dallagnolo and Andrade 2008, Flores *et al*. 2008). Fishing exploitation of the species has increased substantially over recent decades, and in 2015 its global catch was estimated at approximately 255 thousand tonnes, of which 82550 t were attributed to Peru (Pauly *et al*. 2020). Over the past decade, some studies have sought to elucidate patterns of genetic diversity and structure in dolphinfish. Sequences from the mitochondrial NADH1 region (NADH dehydrogenase subunit 1) revealed significant interoceanic divergence among specimens from the Atlantic, Indian and Pacific Oceans and the Mediterranean Sea, indicating the formation of three phylogroups corresponding to populations from the Indo-Pacific, eastern Atlantic and Mediterranean Sea, with the latter being the most genetically distinct. These groupings support the hypotheses of recent dispersal of *C. hippurus* populations and partial genetic structuring among oceanic basins, despite the low genetic differentiation previously observed between populations separated by the Isthmus of Panama (Díaz-Jaimes *et al*. 2010).

Among populations of the species, those from the Mediterranean have consistently shown the greatest genetic divergence from those of other regions. Studies combining mitochondrial markers [cytochrome c oxidase subunit I (COI) and NADH1] reinforce this pattern, including the lack of differentiation among populations outside the Mediterranean Sea (Sacco *et al*. 2017). Merten *et al*. (2015) analysed dolphinfish populations on a smaller geographic scale, also using NADH1, and found no genetic heterogeneity among 183 specimens of *C. hippurus* from the northern and southern sectors of the Puerto Rican coast ($\Phi ST=-0.002$, $p=0.640$). In the most comprehensive assessment conducted across the central-western Atlantic, involving 324 dolphinfish specimens, the data indicated slight genetic structuring ($\Phi ST=0.009$, $p=0.023$), which was not supported by pairwise comparisons, reflecting low genetic differentiation among dolphinfish populations in the region.

Also based on the NADH1 gene, Maggio *et al*. (2019) analysed 203 specimens from the North Atlantic Ocean and the Mediterranean Sea, with substantial differentiation observed ($\Phi CT=0.331$). While mitochondrial data indicate a lack of genetic heterogeneity, nuclear data have recovered population structuring among geographically more distant locations (Ochoa-Zavala *et al*. 2022), with no differences when young-of-the-year individuals and adults were compared within the same location. Similarly, genomic analyses in the eastern Pacific recovered consistent patterns of genetic structure across different life stages, suggesting the presence of barriers to gene flow potentially associated with climatic variability along a latitudinal gradient (Mar-Silva *et al*. 2024).

Although some molecular studies have aimed to understand the structure of *C. hippurus* populations, most have focused almost exclusively on variation in the NADH1 gene, particularly at local scales. Therefore, no study has yet tested the limits of these populations or the implications for their conservation on a global scale, despite the large amount of COI data available that remain underexplored for this purpose. Thus, given the evidence of population structuring, the present study aimed to test the limits of *C. hippurus* populations at a global scale by assessing the genetic diversity and structure of the species based on COI variation, and by applying species delimitation methods. This approach allowed us to test whether deep genetic divisions may indicate candidate clades corresponding to previously unrecognized evolutionary lineages (species) currently classified under a single taxonomic designation. The results may contribute to a better understanding of the genetic stocks analysed, potentially improving the fishery management of this resource.

COI exhibits evolutionary characteristics distinct from those observed in NADH1 (Pesole *et al*. 1999). Therefore, this approach can also be used to test the population scenario indicated by NADH1 in *C. hippurus*. Although COI is not the first choice for detecting population genetic structure, it is a mitochondrial marker and is therefore linked to other mitochondrial regions. The present study also provides a previously unexplored global-scale perspective on the population genetic pattern of *C. hippurus* and allows its results to be compared with those obtained using other mitochondrial and nuclear markers. In addition, COI exhibits evolutionary characteristics distinct from those observed in other mitochondrial markers (Pesole *et al*. 1999) and may retain relevant information on genetic

diversity, demographic history and large-scale differentiation within a species (Avise *et al.* 1987). Furthermore, the widespread use of COI in taxonomic approaches (Hebert *et al.* 2003) and molecular species delimitation provides a precedent for assessing whether the magnitude of genetic variation observed in Mediterranean dolphinfish remains restricted to the population level or represents potential monophyletic evolutionary lineages. Evidence provided by the literature together with that obtained in the present study may constitute a broader basis for future conservation actions and for the management of global stocks of this important fishery resource.

2. MATERIAL AND METHODS

2.1. Composition of the database

The sequences used in the present study came from GenBank and the Barcode of Life Data System (www.boldsystems.org). Initially, 340 sequences referring to COI were downloaded and subjected to three selection criteria: 1) inclusion only of sequence data published in journals; 2) inclusion only of sequences associated with a geographic sampling location; and 3) identification and removal of duplicate COI sequences between the two databases. This was carried out using the "sequence identity" tool of the BioEdit v.7.0.5 software. In pairs of sequences whose identity was 100% and with identical geographic references, one was removed.

After applying these filters, the remaining sequences were aligned and edited using the BioEdit Sequence Alignment Editor 7.0.5 software (Hall 1999). The alignment algorithm used was ClustalW (Thompson *et al.* 1994), using the multiple-alignment strategy, with gap-opening and gap-extension values of 15 and 0.3, respectively (Hall 2001). The final database obtained consisted of 271 sequences, each containing 552 base pairs, distributed in the Atlantic, Pacific and Indian Oceans and the Mediterranean Sea (Fig. 1, Supplementary Table S1).

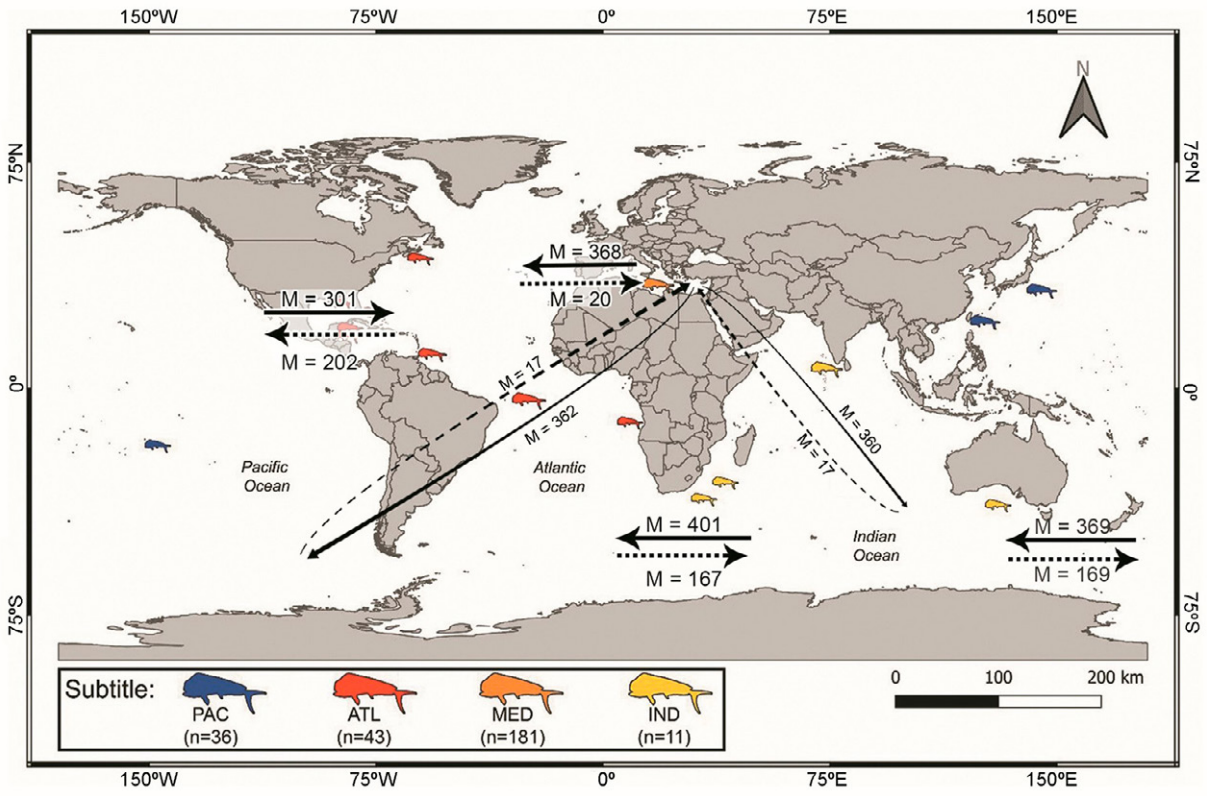

Figure 1. Distribution of sampled cytochrome c oxidase subunit I data and gene flow (M) estimates of *Coryphaena hippurus.* Solid arrows indicate greater gene flow, and dashed arrows indicate less gene flow between the sampled areas. PAC, Pacific Ocean; IND, Indian Ocean; ATL, Atlantic Ocean; MED, Mediterranean Sea.

2.2. Genetic diversity and demographic history

Nucleotide diversity (π) and haplotype diversity (Hd) were determined using the DnaSP v6 software (Rozas *et al.* 2017). The genealogical relationship of COI variation in *Coryphaena hippurus* was revealed by the haplotype network obtained using PopArt v1.7.2 software, based on the TCS Network algorithm (Clement *et al.* 2002). The demographic history of the species was assessed globally and for each basin using Fu's Fs (Fu 1997) and Tajima's D (Tajima 1989) neutrality tests implemented in DnaSP v6 (Rozas *et al.* 2017).

2.3. Genetic structure and migration

The global population structure for the database was also tested by degrees of genetic differentiation, obtained using ARLEQUIN v. 3.5.1.2 software (Excoffier and Lischer 2010), with global fixation index (ΦST) and pairwise fixation index (FST) calculated using 10000 and 1000 permutations, respectively ($p<0.05$). A Bonferroni correction for multiple comparisons was applied to the pairwise analysis.

To calculate the global Φ_{ST}, all samples were considered as belonging to a single population, under two structuring scenarios: (a) including the Mediterranean sampling and (b) excluding the Mediterranean sampling from the comparison. In the pairwise analysis of molecular variance (AMOVA), the samples were subdivided into four groups corresponding to the Atlantic Ocean, Indian Ocean, Mediterranean Sea and Pacific Ocean.

The population structure was also tested using Bayesian Analysis of Population Structure (BAPS) v6.0 (Corander and Marttinen 2006). Due to the haploid nature of the database, the initial analysis was "Mixture partition" with the "Clustering with linked loci" module (Corander and Tang 2007). For this analysis, possible K values of 2–4 were specified, corresponding to the number of sampled ocean basins and the potential population subdivisions in the dataset. Neutrality tests were also conducted for haplotypes restricted to the Mediterranean basin and for those originating outside it. This strategy was designed to detect possible differences in demographic patterns of the species, given previous evidence of population structure across the species distribution (Rozas *et al.* 2017).

To quantify the migration rates among the four basins, we used Migrate-n 4.3 (Beerli and Palczewski 2010) to recover the mutation-scaled values of effective population size (Θ) and migration rate (M) for each basin under a Bayesian approach. Using CIPRES Science Gateway (Miller *et al.* 2010), we ran two simulations in Migrate-n. The first simulation indicated the Mediterranean basin as a source of mitochondrial lineages for the remaining basins (Atlantic, Indian and Pacific), allowing bidirectional gene flow among basins only if they are connected to the Mediterranean basin, while gene flow was not allowed among the other basins. The second simulation considered a full migration matrix among all basins, except the Mediterranean. The Kimura two-parameter model (Kimura 1980) was set as the mutation model for both simulations, as selected in R (R Core Team 2019), using the 'phangorn' library (Schliep 2011) and assuming the lowest Bayesian information criterion values.

The transition/transversion ratio required to implement the Kimura two-parameter mutation model was estimated for both Migrate-n simulations using the 'strataG' R package (Archer *et al.* 2017). Finally, we set each Migrate-n simulation to run a single Markov chain Monte Carlo run of 200000 steps (sampling every 100). We applied a final burn-in of five million steps, and the swap intervals for the thermodynamic static heating were kept in default mode. Convergence of chain parameters was assessed using effective sample size values >200. Migration rates among basins were expressed as the number of immigrants per generation, calculated using the median values of Θ and M recovered for each simulation in Migrate-n as input. The formula used was $N_m = M_i \text{-j} \times \Theta \text{j}$, where *i* is the source population, and *j* is the recipient population (Gómez-Carballa *et al.* 2018, Machado *et al.* 2022).

2.4. Molecular phylogenetics and methods for species delimitation

To test whether the magnitude of the observed population divergence represented distinct molecular operational taxonomic units (Blaxter *et al.* 2005), we used a coalescent-based molecular species delimitation method, the Bayesian Poisson tree processes (bPTP) model. Here, we aimed to test

whether deep population genetic divisions would be recovered phylogenetically as monophyletic groups, indicating candidate lineages for unknown species. It is worth highlighting that distinguishing a population from a species has direct implications for management strategies aimed at conserving exploitable resources such as dolphinfish.

To this end, we implemented a phylogenetic analysis by Bayesian inference using MrBayes 3.0 software (Huelsenbeck and Ronquist 2000), with the model indicated by the jModelTest v2.1 software as the most appropriate evolutionary model (Guindon *et al*. 2010, Darriba *et al*. 2012) using the Bayesian information criterion (Schwarz 1978) which selected the Kimura model with invariant sites (K80+I; Kimura 1980). For this analysis, only effective sample size values >200 were considered (Bouckaert *et al*. 2019). The outgroup used was *Rachycentron canadum*, popularly known as cobia and taxonomically classified as a sister group of the family Coryphaenidae (GenBank accession KY372069.1).

A molecular species delimitation analysis based on coalescence was performed using the bPTP method. The analysis used the non-ultrametric tree obtained with MrBayes and was run on the online platform https://species.h-its.org/ (Zhang *et al*. 2013). The settings were: rooted tree, Markov chain Monte Carlo=100000, thinning=100 and burn-in=0.1. This analysis was executed on the bPTP webserver (http://species.h-its.org/ptp/). The outgroups were removed from the tree prior to species delimitation.

3. RESULTS

3.1. Genetic diversity and neutrality tests

Our analyses showed Hd ranging from 0.51 to 0.83. The Atlantic and Pacific Ocean populations had an Hd of 0.83, the Indian Ocean populations had an Hd of 0.60, and the Mediterranean populations had the lowest Hd, at 0.51. On average, the populations had an Hd of 0.76 and nucleotide diversity of 0.00351 (Table 1).

Tajima's D and Fu's Fs neutrality tests recovered negative, statistically non-significant values in the global and basin-by-basin estimations (Table 1). Significant deviations from neutrality were also observed for the genetic variation not exclusive to the Mediterranean (–1.78623, $p<0.05$ and 18.508, $p<0.01$). These tests still failed to detect statistically significant shifts toward non-neutral selection in genetic variation unique to the Mediterranean (–0.18511, $p>0.05$; –3.401, $p>0.05$).

Table 1. Genetic diversity parameters given the sampled cytochrome c oxidase subunit I data. ATL, Atlantic Ocean; PAC, Pacific Ocean; MED, Mediterranean Sea and IND, Indian Ocean; MED1, Haplotypes exclusively from outside the Mediterranean basin; MED2, Exclusively Mediterranean haplotypes.

Group	N	H	Hd	S	π	Tajima's D	Fu's Fs
ATL	43	16	0.83	15	0.00339	–1.53	–10.46
IND	11	4	0.60	4	0.00205	–0.63	–0.486
PAC	36	12	0.83	13	0.00377	–1.24	–4.55
MED	181	10	0.51	6	0.00172	–0.18	–3.40
MED1	–	–	–	–	–	–1.79	–18.51
MED2	–	–	–	–	–	–0.18	–3.40
Global	271	31	0.76	24	0.00351	–1.46	–21.86

N, total number of sequences analysed; H, total number of haplotypes; Hd, haplotype diversity; π, nucleotide diversity; S, segregating sites.

3.2. Genetic structure and migration

The haplotype network indicated a total of 31 haplotypes distributed across three main haplogroups (Fig. 2). Haplogroup 1 was composed almost exclusively of haplotypes restricted to the Mediterranean basin, with the exception of hap9, which, in addition to being more frequent, is also shared with

individuals from the Atlantic Ocean. Haplogroup 2 was the most diverse of the three groups, with hap4 being the most frequent haplotype and present in all sampled basins. Haplogroup 3 was also diverse, but to a lesser extent, with hap5 as the central haplotype shared between populations from the Atlantic and Indian Oceans (Fig. 2).

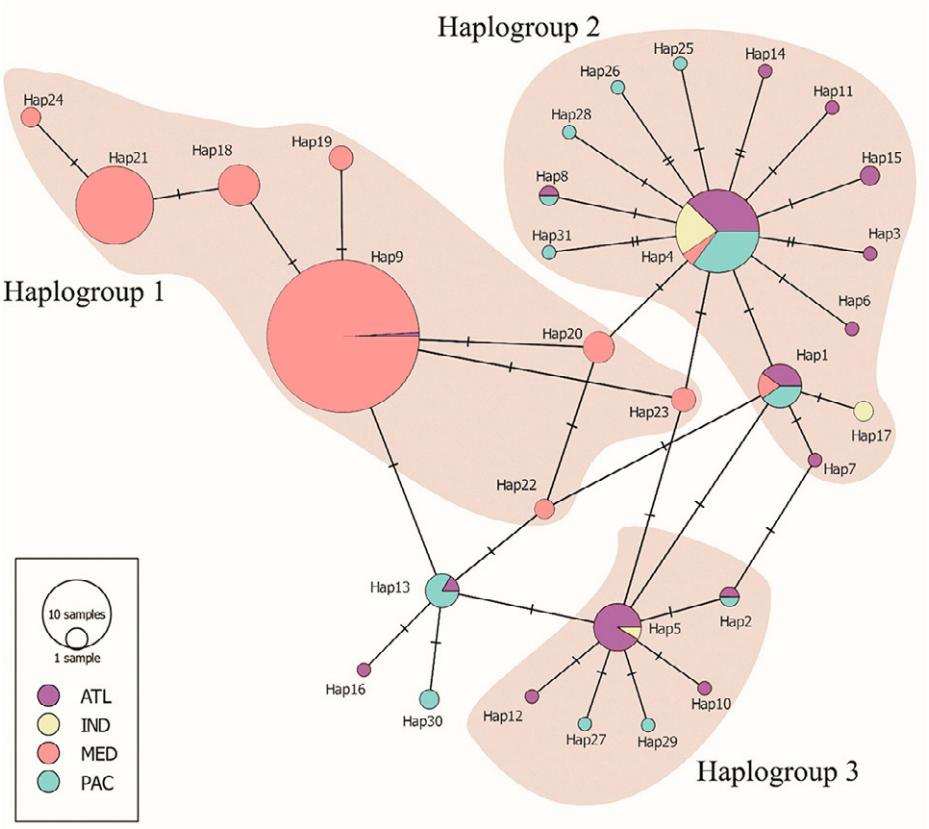

Figure 2. Haplotype network (TCS Network) against the sampled cytochrome c oxidase subunit I data. PAC, Pacific Ocean; IND, Indian Ocean; ATL, Atlantic Ocean; MED, Mediterranean Sea. The size of the circles is proportional to the haplotype frequency. The different colours indicate the geographic origin of the observed genetic variants. For details, see Figure 1.

The global AMOVA including the Mediterranean samples revealed that 53.74% of the variance occurred within populations and 46.26% among populations, with a genetic differentiation (ΦST) of 0.46. After removing the Mediterranean samples from the comparison, 96.98% of the variation occurred within populations and 3.02% among populations, with a Φ_{ST} of 0.03 (Table 2). The pairwise genetic differentiation (FST) ranged from −0.00159 to 0.73041, with the highest differentiation between *C. hippurus* from the Indian Ocean and the Mediterranean Sea (Table 3).

Table 2. Analysis of molecular variance (AMOVA) based on cytochrome c oxidase subunit I data sampled under two structuring scenarios; (a) considering the Mediterranean sample in the comparison and (b) excluding the Mediterranean sample from the comparison. In both tests, the samples were considered as belonging to a single population. Bold values indicate statistically significant fixation indices based on *p*-values lower than 0.05.

Source of the variation (%)	(a)	(b)
Between populations	46.26	3.02
Within populations	53.74	96.98
Fixation index ϕ_{ST}	**0.46261**	0.03022
p-value	<0.0001	0.06822

Table 3. Pairwise genetic-evolutionary differentiation (F_{ST}) values of *Coryphaena hippurus* based on the sampled cytochrome c oxidase subunit I data. ATL, Atlantic Ocean; PAC, Pacific Ocean; MED, Mediterranean Sea and IND, Indian Ocean. Bold values indicate statistically significant pairwise differentiation after Bonferroni correction (adjusted significance threshold: p<0.0083).

Location	ATL	IND	MED	PAC
ATL	–			
IND	0.08783	–		
MED	**0.51243**	**0.73041**	–	
PAC	–0.00159	0.08288	**0.52796**	–

The BAPS analysis recovered a total of four clusters (K=4) represented by the colours blue, green, red and yellow (Fig. 3). Mainly represented by the blue cluster, the Mediterranean population showed a conspicuous pattern with little contribution from the genetic profiles observed in the Atlantic, Indian and Pacific Oceans. In addition, the yellow cluster was almost exclusive to the Mediterranean. The populations from Atlantic, Pacific and Indian Oceans shared three of the four profiles recovered in the analysis in a similar way, with the red profile predominating, followed by smaller proportions of the blue and green profiles. The Pacific Ocean population showed the yellow profile in just one of its individuals, which was prominently displayed in the Mediterranean population of the species.

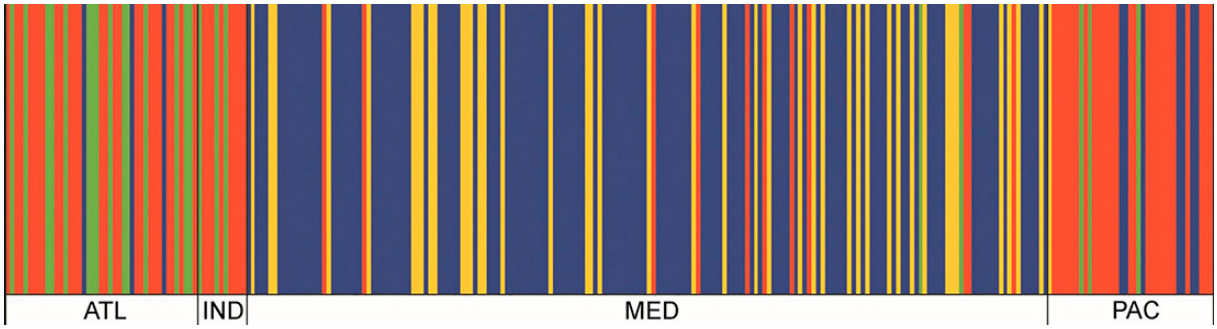

Figure 3. Analysis of genetic structure (BAPS) based on the sampled cytochrome c oxidase subunit I data. Note the presence of four genetic profiles (K=4, different colours) and the conspicuous genetic pattern of *C. hippurus* from the Mediterranean Sea (MED) in relation to the other regions sampled: Atlantic Ocean (ATL), Indian Ocean (IND) and Pacific Ocean (PAC). The colours of the recovered genetic profiles were defined arbitrarily by the programme. In this analysis, the colours themselves are not relevant for interpreting the result, but rather the variation among them.

In the Migrate-n analysis, for the simulation including all basins, the highest migration rates were detected between the Mediterranean and Atlantic basins, as well as between the Mediterranean and Pacific basins; the Atlantic and Pacific basins received a median of 5.76 and 4.58 immigrants per generation from the Mediterranean basin, respectively (Table 4). By contrast, in the simulation without the Mediterranean basin, the gene flow was more pronounced from the Indian to the Atlantic basin, with a median of 10.2 immigrants per generation. In the same simulation, low levels of gene flow were detected from the Atlantic to the Indian basin, and from the Pacific to the Indian basin (Table 4).

Table 4. Mutation-scaled values of the effective population size (Θ) and migration rate (M) recovered in Migrate-n for the simulations including the Atlantic (a), Indian (i), Mediterranean (m) and Pacific (p) basins, and also for the simulation without the Mediterranean basin. For the mutation-scaled migration rate, the number of immigrants per generation is given in parentheses.

Parameter	Raw value
First simulation (including all four basins)	
Θ a	0.01563
Θ i	0.00523
Θ m	0.01970
Θ p	0.01263
M m-a	368.3 (5.76)
M m-i	360.3 (1.88)
M a-m	20.3 (0.40)
M i-m	17.0 (0.33)
M p-m	17.0 (0.33)
M m-p	362.3 (4.58)
Second simulation (without the Mediterranean basin)	
Θ a	0.02543
Θ i	0.00223
Θ p	0.00943
M i-a	401.7 (10.2)
M p-a	301.0 (7.65)
M a-i	167.0 (0.37)
M p-i	169.7 (0.38)
M a-p	202.3 (1.91)
M i-p	369.0 (3.48)

3.3. Molecular phylogenetics and methods for species delimitation

Bayesian phylogenetic analysis did not indicate monophyletic groupings related to the population structure detected here using other methods. Posterior probabilities were very low even for clades that appeared to show signs of monophyly, and branch support was low (between 0.17 and 0.18). The bPTP analysis also failed to detect monophyletic groupings that would indicate candidate lineages for unknown species housed under the designation *Coryphaena hippurus*.

4. DISCUSSION

4.1. Genetic diversity and conservation

From a conservation-genetics perspective, the main elements to be preserved are genetic diversity and the historical processes that shaped its magnitude and distribution (Moritz 2002). The available genetic diversity data for the mitochondrial NADH1 gene of *C. hippurus* showed 0.87 and 0.1 for haplotype and nucleotide diversity, respectively (Díaz-Jaimes *et al.* 2010, Sacco *et al.* 2017, Maggio *et al.* 2019). These values are close to those found in the present study in COI. It is worth noting that COI accumulates mutations approximately three times more slowly than NADH1 (Pesole *et al.* 1999, Hebert *et al.* 2003). Therefore, a slower-evolving gene harbouring genetic variation at the same levels as another gene that accumulates more mutations in the same time is evidence of a favourable global conservation status of *C. hippurus*, due to the importance of genetic diversity as raw material for long-term adaptation in marine fish species. These data therefore suggest that *C. hippurus* may be resilient in the face of increasing exploitation. This ecological attribute had already been pointed out

in previous studies considering the rapid growth and reproductive precocity of the species (Moltó *et al.* 2020). Early sexual maturity is positively related to greater genetic variation, favouring effective population size (Ne, genetic variability) (Martinez *et al.* 2018). Therefore, the global data obtained here on *C. hippurus* support genetic diversity as a fundamental component in regulating the adaptive performance of fish populations, including in species under intense exploitation.

Despite the evidence reported here suggesting that global genetic diversity indices are of little concern in *C. hippurus*, the Mediterranean population of the species showed lower variation than populations from the other sampled regions. While the global Hd of *C. hippurus* is at the level of 0.76, in the Mediterranean sample it did not exceed 0.51. Thus, the Mediterranean *C. hippurus* shows a genetic variation that is more than 25% lower than that detected globally. This means that the Mediterranean *C. hippurus* has at least one quarter of the global genetic variation. Although this circumstance could be associated with different anthropogenic or demographic processes, data on fishing exploitation of *C. hippurus* from 2018 show that exploitation is lowest in the Mediterranean (www.seaaroundus.org).

Therefore, a more recent Mediterranean colonization by the species would currently be a reasonable hypothesis to explain the lower genetic variation in this stock, although this interpretation does not constitute a formal demographic inference. This does not mean that managing the exploitation of *C. hippurus* in that region should be any less of a priority. On the contrary, this remains important because lower genetic variation may indicate greater vulnerability of this stock. Thus, future fishery management plans for this species should consider Mediterranean populations a conservation priority, considering the genetic diversity observed in these populations and the need for continued monitoring under current and future exploitation scenarios.

Currently, *C. hippurus* has a conservation status of "least concern" according to the IUCN (International Union for Conservation of Nature) (Collette *et al.* 2011). However, exploitation of the species has increased by at least seven orders of magnitude in the last 60 years (Pauly *et al.* 2020), which may indicate increasing pressure on the species. Furthermore, studies have shown that fish species exploited by fishing have lower evolutionary potential (Allendorf *et al.* 2014, Pinsky and Palumbi 2014) than less-exploited populations. However, the degree of genetic diversity observed here suggests that global genetic diversity remains relatively high based on COI data, despite the increase in exploitation. Thus, this interpretation should be treated with caution, considering the limitations of the marker used.

4.2. Genetic structure, management units and species delimitation test

The high mobility of many marine species was long interpreted as a limiting factor for the formation of population structure. However, accumulated evidence from genetic approaches in marine fishes has revealed that this pattern is not universal (Hauser and Carvalho 2008). Thus, a high dispersal potential does not necessarily imply an absence of genetic structure, with examples already reported in highly mobile large pelagic species, such as bigeye tuna, *Thunnus obesus* (González *et al.* 2008) and Atlantic swordfish, *Xiphias gladius* L. (Alvarado Bremer *et al.* 2005, Smith *et al.* 2015), the latter being an especially relevant analogue for *C. hippurus* at the Atlantic–Mediterranean interface. The haplotype network obtained here for the COI data (Fig. 2) revealed three main haplogroups of dolphinfish, one of them clearly distinct from the others and mainly composed of Mediterranean haplotypes (haplogroup 1), whereas haplogroups 2 and 3 showed greater geographic sharing.

Haplogroup 2 was the most diverse and displayed a star-like configuration, a pattern compatible with episodes of recent demographic expansion. In swordfish, a highly migratory pelagic species, patterns partially similar to those observed in dolphinfish have been recovered, including star-like haplogroups, reduced genetic diversity in Mediterranean populations, and limited contact with the Atlantic, with a mixing zone mainly restricted to the northeast Atlantic waters adjacent to the Strait of Gibraltar (Alvarado Bremer *et al.* 2005, Smith *et al.* 2015). This comparison reinforces the idea that the high migratory capacity of a species may not be sufficient to produce connectivity between certain regions, where biogeographic factors, historical processes and oceanographic features may override the dispersal potential of these taxa.

These patterns suggest that Haplogroup 2 experienced a recent and more pronounced expansion episode in the Atlantic and Pacific ocean basins, given their greater haplotype richness. Furthermore, this haplogroup, by presenting greater haplotypic diversity, may indicate that it includes areas near the centre of origin, since accumulating more variation implies a longer period of existence (Wilkins and Wakeley 2002, Maggio *et al.* 2019). The greater distribution amplitude of genetic variation observed in Haplogroups 2 and 3 is also supported by the vagility of the species (Oxenford 1999) and has already been observed in other studies on *C. hippurus* with other genetic information (NADH1, Díaz-Jaimes *et al.* 2010, Sacco *et al.* 2017, Maggio *et al.* 2019). The additional evidence observed by Bayesian structuring (BAPS) is consistent with the above hypotheses about the high connectivity between *C. hippurus* occurring in the Atlantic and Pacific basins. More recently, high gene flow and potential barriers to gene flow have been reported in *C. hippurus* in the Tropical Eastern Pacific Ocean. According to the authors, these patterns appear to be related to different seascape features along a latitudinal gradient and also to the age of fishes, i.e. juveniles showing site fidelity (Mar-Silva *et al.* 2024). Therefore, this combined understanding about patterns of cohesiveness in dolphinfish highlights a great ecological heterogeneity of the species, including the genetic particularity of the Mediterranean Sea population.

The isolation of Mediterranean COI haplotypes that characterized Haplogroup 1 confirmed this phenomenon detected in different studies by other mitochondrial markers (Díaz-Jaimes *et al.* 2010, Sacco *et al.* 2017, Maggio *et al.* 2019). Therefore, the data obtained here reinforce strong isolation of *C. hippurus* in the Mediterranean basin. In addition, this evidence allows us to suggest a period of isolation that might be older than that suggested to date, since the mutation rate of COI is around one-third that of NADH1 (Pesole *et al.* 1999).

The fixation index (ΦST) retrieved by global AMOVA, together with the significant pairwise F_{ST} results involving the Mediterranean basin, supports the genetic differentiation of Mediterranean *C. hippurus*. Overall, the population in this basin differs genetically from the others by around 59% based on the data obtained here. Similar values of genetic differentiation (~54%) between *C. hippurus* from the Mediterranean and other oceanic basins were observed using NADH1 data (Díaz-Jaimes *et al.* 2010, Maggio *et al.* 2019). Therefore, the combined evidence of these two distinct mitochondrial regions supports the existence of a distinct population of the species in the Mediterranean Sea. The BAPS analysis also was also consistent with this pattern, considering that the Mediterranean genetic profile was not widely present in other locations.

Some population genetic approaches have also demonstrated phenomena of genetic isolation in other species from the Mediterranean, such as the Mediterranean grenadier (*Coryphaenoides mediterraneus*) (Catarino *et al.* 2017), the allis shad (*Alosa alosa*) and the twaite shad (*Alosa fallax*) (Sabatino *et al.* 2022) and the European pilchard (*Sardina pilchardus*) (Caballero-Huertas *et al.* 2022). Thus, the results obtained here together with those reported in the literature suggest a biogeographic particularity of the Mediterranean basin that may favour population-level differentiation. The evidence potentially associated with this genetic isolation of the *C. hippurus* population from the Mediterranean is the desiccation of the Mediterranean during the Messinian salinity crisis and its refilling during the Zanclean flood (Roveri *et al.* 2014). In general, the Mediterranean has undergone extreme desiccation, corresponding to one of the most dramatic ocean modification events of the last 20 million years (Hsü *et al.* 1973). This process of sea-level decline leading to its complete isolation from the Atlantic Ocean began around 7 million years ago (Hilgen *et al.* 1995) and reached its maximum degree 5.33 million years ago (Lourens *et al.* 1996, Krijgsman *et al.* 1999). This event differs from Plio-Pleistocene glacial sea-level reductions and is better explained by extreme local geological and palaeoclimatic processes in the Mediterranean Sea region.

Therefore, the combination of genetic data obtained here with the history of geological and climatic isolation of the Mediterranean may help explain the magnitude of differentiation observed here for the local population of *C. hippurus* there. Furthermore, it is possible to suggest a molecular calibration for Coryphaenidae in the order of one mutation event every 5.33 million years. This conclusion is based on the occurrence of one mutational step of Haplogroup 1 relative to the others (Fig. 2).

According to Flores *et al*. (2008), *C. hippurus* is a species that is generally limited to waters warmer than 20°C. However, despite its vagility, an asymmetry was observed in the gene flow of *C. hippurus* between the Mediterranean and the Atlantic, with more gene flow estimated from the Mediterranean to the Atlantic than in the reverse direction (Table 4). Patarnello *et al*. (2007) and Maggio *et al*. (2019) indicated the presence of a biogeographic filter at the interface between the Mediterranean Sea and the North Atlantic Ocean that could, to some degree, limit mixing of *C. hippurus* between these basins. Recently, Mendoza-Portillo *et al*. (2026) assessed the genomic structure of *C. hippurus* from the western Atlantic Ocean and the Mediterranean Sea using nuclear single-nucleotide polymorphism data, revealing clear genetic structuring between populations from these basins. Less pronounced, but still detectable, differences were observed between western and eastern Mediterranean subgroups based on neutral loci.

In contrast, outlier loci putatively associated with local adaptation, particularly those related to temperature and salinity, recovered a more refined signal of differentiation among Mediterranean populations of *C. hippurus*, resulting in three genetically distinct groups within this region despite its reduced geographic extent. Complementary genotype–environment association analyses indicated the potential influence of environmental factors such as salinity, temperature and nitrate on the genetic variation observed in the species within the Mediterranean basin. These results reinforce the importance of considering seascape features when interpreting the genetic structure of *C. hippurus*, particularly at the interface between the Atlantic Ocean and the Mediterranean Sea.

The COI results also contrast with some of the nuclear data reported by Mendoza-Portillo *et al*. (2026) regarding the genetic variation recovered in Mediterranean and Atlantic populations of dolphinfish. While the mitochondrial marker revealed a marked difference in Hd between populations from these basins (ATL=0.83; MED=0.51), the neutral single-nucleotide polymorphisms analysed by those authors showed similar levels of Ho (ATL=0.159–0.168; MED=0.143–0.162) and He (ATL=0.144–0.150; MED=0.130–0.150). The mtDNA is haploid and generally inherited uniparentally and has an effective population size approximately one-quarter that of nuDNA. Thus, mitochondrial markers may be more susceptible to the effects of genetic drift (Toews and Brelsford 2012), especially under demographic scenarios such as population bottlenecks and founder events, in which mitochondrial genetic diversity may be reduced more strongly than nuclear diversity (Canino *et al*. 2010). In addition, ancestral polymorphisms tend to be lost more rapidly in mtDNA, since the rate of this process is inversely proportional to effective population size (Funk and Omland 2003). Thus, the COI haplotypic diversity recovered in Mediterranean dolphinfish may result from the greater sensitivity of this marker to historical demographic processes in the region.

Additional evidence for this hypothesis was provided by the neutrality tests that indicated deviations from neutrality in COI genetic variation in the North Atlantic group of *C. hippurus* (Table 1). It is well accepted that different environmental circumstances can favour genetic structuring between biological populations (Slatkin 2017). Thus, the period of confinement of *C. hippurus* in the Mediterranean basin during its dissection, associated with the accumulated differences in the adaptive seascapes of the North Atlantic and Mediterranean Sea over time, may have contributed to the formation of two distinct genetic units of *C. hippurus*. It is important to remember that different adaptive seascapes limiting gene flow and favouring ecological specialization have been shown in dolphinfish (Mar-Silva *et al*. 2024).

The molecular species delimitation analysis did not recover groupings supporting the hypothesis that the marked genetic differentiation of Mediterranean populations represents a distinct evolutionary lineage within *Coryphaena*. The bPTP analysis grouped all *Coryphaena hippurus* sequences into a single clade, with 94% node support. This evidence does not support the idea that the genus *Coryphaena* requires a taxonomic-systematic review based on combined evidence on morphology-genetic data (Ayşe 2025). This could be important for other Coryphaenidae species but excluding *C. hippurus* given the evolutionary stability of this lineage observed herein. The results also indicated the absence of a distinct molecular operational taxonomic unit that could represent an endemic Mediterranean species and also suggest that the genetic variation in Mediterranean populations occurs at the population level. The identification of possible molecular operational taxonomic units, in practical terms, is important due to the need to know what entity is being evaluated in fisheries studies, a species or a population. The effectiveness of a good management plan depends directly on an increasingly accurate

information base to provide a more appropriate resource management strategy. To strengthen this information base, recognizing the significant genetic attributes present in a population in a geographic area is always fundamental, as has recently been argued (Holderegger *et al*. 2019, Hoban *et al*. 2020).

When significant genetic differences are detected, populations must be considered as demographically independent, and it is ultimately necessary to consider these differentiations when establishing management plans and ensuring the persistence of fishery stocks (Shaklee and Bentzen 1998, Mat Jaafar *et al*. 2020, Queiroz-Brito *et al*. 2024). Therefore, the combination of population genetic evidence and molecular species delimitation tests indicates that the main evidence of genetic differentiation is concentrated in the Mediterranean populations, which should be considered separately in future management proposals. In contrast, comparisons between Atlantic, Pacific and Indian populations do not support a clear separation between these basins based on COI data.

The global genetic analysis of *Coryphaena hippurus* based on the COI marker revealed overall low levels of population structure among the Atlantic, Pacific and Indian Oceans, with no statistically significant pairwise differentiation among these basins. The Mediterranean was the most clearly differentiated region, showing reduced genetic diversity compared with all other regions. However, this pattern should be interpreted with caution, since the lower variation recovered with COI may reflect intrinsic features of the mitochondrial marker, including its greater sensitivity to historical demographic processes. Nevertheless, the reduction observed in the Mediterranean population may be particularly relevant considering the increase in fishing pressure over recent decades. Molecular species delimitation tests indicated that the observed differences do not represent monophyletic evolutionary lineages, but rather population-level variation. Accordingly, the evidence supports the recognition of the Mediterranean as a distinct management unit, whereas comparisons among the remaining basins do not support a clear separation based on COI data.

Supplementary information ↑

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Supplementary material

The supplementary material contains a list of sequences used in this study, including sequence name, country, ocean, GenBank accession number and DOI link for each corresponding publication.

Data availability

Not applicable.

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Authorship contribution statement

Cláudio Pereira: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Validation; Writing – original draft; Writing – review & editing. Carolina Machado: Data curation; Formal analysis; Writing – review & editing. Stênio Foerster: Formal analysis. Píndaro Díaz-Jaimes: Writing – review & editing. Rodrigo Torres: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Writing – original draft; Writing – review & editing.

Competing interests

The authors of this article declare that they have no financial, professional or personal conflicts of interest that could have inappropriately influenced this work.

Statement on the use of Artificial Intelligence

Not applicable.

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