Rev Fish Biol Fisheries (2025) 35:929–942
https://doi.org/10.1007/s11160-025-09941-y

RESEARCH

Mitonuclear genetics reveals a novel perspective on the stock structure and fishery management of skipjack tuna (*Katsuwonus pelamis*) in the Atlantic Ocean

Maria Clara G. Queiroz-Brito · Fernando F. Mendonça · Joana I. Robalo · Freddy Arocha · N'Guessan Constance Diaha · Monin Justin Amandé · Fambaye Ngom Sow · Davy Angueko · Paulo Travassos · Rodrigo A. Torres

Received: 5 June 2024 / Accepted: 20 March 2025 / Published online: 11 April 2025

Abstract The skipjack tuna, *Katsuwonus pelamis* is the worldwide most fished and economically significant tuna species. In the Atlantic Ocean, the management strategy of the International Commission for the Conservation of Atlantic Tunas (ICCAT) includes two stocks: (a) eastern (SKJ-E) and (b) western (SKJ-W) stocks. However, the genetic cohesiveness between these stocks remains poorly understood. Here, we provide this information through mitochondrial [control region (CR)] and nuclear (intron S7) data. In both markers, high genetic diversity and no contraction signals in effective population sizes were found, supporting the species conservation status as 'Least Concern' by the IUCN and the results of the latest ICCAT assessment of the two stocks. In general, no well-defined genetic-geographic structure was detected, which may be explained by the

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11160-025-09941-y.

M. C. G. Queiroz-Brito (✉) · R. A. Torres
Programa de Pós-Graduação Em Biologia Animal, Centro de Biociências, Universidade Federal de Pernambuco, Recife, Brazil
e-mail: claraqueirozbrito@gmail.com

M. C. G. Queiroz-Brito · R. A. Torres
Laboratório de Genômica Ambiental, Universidade Tecnológica Federal Do Paraná, Campus Londrina, Curitiba, Brazil
e-mail: rodrigotorres@utfpr.edu.br

F. F. Mendonça
Instituto Do Mar, Universidade Federal de São Paulo, Campus da Baixada Santista, Santos, Brazil
e-mail: fernandoffm@yahoo.com.br

J. I. Robalo
ARNET–Aquatic Research Network, MARE–Marine and Enviromental Sciences Centre, ISPA Instituto Universitário, Lisbon, Portugal
e-mail: jrobalo@ispa.pt

F. Arocha
Instituto Oceanográfico de Venezuela, Universidade de Oriente, Cumana, Venezuela
e-mail: farocha@gmail.com

N. C. Diaha · M. J. Amandé
Centre de Recherches Océanologiques (CRO), Abidjan 01, Côte d'Ivoire
e-mail: diahaconstance@yahoo.fr

M. J. Amandé
e-mail: m.amande@africanmarineexpertises.com

F. N. Sow
Centre de Recherches Océanographiques de Dakar Thiaroye (CRODT), Dakar, Senegal
e-mail: famngom@yahoo.com

D. Angueko
Direction Génerale Des Pêche Et de L'Aquaculture, Libreville, Estuaire, Gabon
e-mail: davyangueko83@gmail.com

specie life history strategies, such as large population effective sizes and migratory behavior, with a broad geographical distribution, that reduce the isolation, inbreeding, and genetic drift effects. However, pairwise F_{ST} values within and between the Eastern and Western Atlantic suggest some weak to moderate genetic differentiation. These results involved mainly the Eastern Temperate Zone, represented herein by the Azores archipelago. It is important to highlight that higher differentiation levels were found between sites from different stocks. In addition, the CR data revealed a weak but significant genetic differentiation between the eastern and western stocks ($F_{ST} = 0.0006$). These results can be used to improve and support the ICCAT management strategies of skipjack tuna stocks, highlighting the need for a reevaluation and possible alignment between Eastern and Western Atlantic management actions.

Keywords Conservation · Fishery stocks · Genetic cohesiveness · Population structure · Skipjack tuna

Introduction

The skipjack tuna, *Katsuwonus pelamis* (Scombridae), is the third most caught species among the world's marine resources and the most important tuna species, accounting for around 37% of all tuna and tuna-like species fished, being commercialized as frozen, fresh, and canned meat (ISSF 2024; FAO 2024; WCPFC 2024). The fishing pressure started around the 1950s in the Pacific Ocean and expanded to the other oceans between 1950 and 1970 (Sea Around Us 2020). In 2022, 3.1 million tons of skipjack tuna were caught globally (FAO 2024).

In the Atlantic Ocean, the management strategies adopted by the International Commission for the Conservation of Atlantic Tunas (ICCAT) assume the presence of two stocks: (1) Eastern skipjack stock (SKJ-E) and (2) Western skipjack stock (SKJ-W). In 2023, fisheries targeting the species generated a total catch of 219,874 tons for the SKJ-E stock, and 29,555 tons for the SKJ-W stock (ICCAT 2025). Considering ICCAT's latest stock assessments (ICCAT 2025), both stocks presented a high probability (78% for SKJ-E and 91% for SKJ-W) to be in a sustainable condition (Kobe plot green quadrant), indicating that these stocks are not overfished and are not undergoing overfishing. According to the Kobe II Strategy Matrix (K2SM) projections for both stocks, with catches remaining at the Maximum Sustainable Yield (MSY) median of 216,617 tons, SKJ-E will have around a 55% probability of remaining in the green quadrant of the Kobe plot until 2028, while SKJ-W will have around a 70% probability, with future catches remaining at the MSY median of 35,277 tons until 2028 (ICCAT 2025). These results agree with the IUCN (International Union for Conservation of Nature—Red List of Threatened Species) assessment, where the species is globally listed as 'Least Concern' (Collette et al. 2021).

Katsuwonus pelamis is a widely distributed pelagic species, occurring in tropical and subtropical waters, and only limited by the 15 °C isotherm (Collete and Nauen 1983; FAO 2004). Migration behavior is mainly influenced by environmental conditions such as temperature, salinity, and food availability, and aggregations are associated with convergence zones and other oceanographic phenomena (Collette and Nauen 1983). The species is also sensitive to low dissolved oxygen levels (Collette et al. 2021), being able to swim more than 60 km per day to facilitate respiration (Sharp and Dizon 1978; ICCAT 2025). In addition, skipjack tuna has a short life cycle (median age of 4.5 years, living for 6–8 years; Collette et al. 2021), which makes them the fastest-growing tuna species. In the Atlantic, there is a distinction between two growth patterns: slow growth in the equatorial waters, where the energy is mainly used for reproduction, and faster growth in temperate waters (Gaertner et al. 2008; Fonteneau 2015a).

Skipjack tuna has distinctly high reproductive potential. The species has an estimated 50% probability of reaching sexual maturity at around 1.5 years of age or approximately 40 cm (Ashida et al. 2008; Murua et al. 2017; Soares et al. 2019), and fecundity ranging from 80 thousand to 2 million eggs per spawning event (FAO 2004). Spawning seems to occur continuously throughout the year in favorable conditions, at sea temperatures of 25–30 °C (ICCAT 2025; Collette et al. 2021). This translates to diverse reproductive peaks in different parts of the Atlantic, such as during the second and third quarters of the year at the northern portion of the Guinea Gulf,

---

P. Travassos
Departamento de Pesca E Aquicultura, Universidade Federal Rural de Pernambuco, Recife, Brazil
e-mail: paulo.travassos@ufrpe.br

and during the first and fourth quarters of the year at the southern portion of the Guinea Gulf, and between December and March along the Brazilian coast, with peaks in January and February (ICCAT 2006–2016; Soares et al. 2019). In the Mediterranean Sea (MS), there are very few data about the reproduction season of the skipjack tuna, and the spawning season was unknown for many years (Di Natale et al. 2009). Only Tortonese (1975) mentioned that the reproductive season for *K. pelamis* in MS occurs generally during the summer, and Puerto et al. (2022) reported that skipjack tuna has a reproductive period between May and August in the Balearic Sea.

The life history features described above, plus the absence of large gene flow barriers in marine environments, can reduce population differentiation, and it leads to possible scenarios of panmixia (Cowen et al. 2006; Cowen and Sponaugle 2009; Funk et al. 2012). However, the available data have revealed a complex scenario for the population structure of *K. pelamis*, which differs according to the study area and design, identifying both significant and non-significant genetic differentiation. These studies are mainly focused on the Indian (Dammannagoda et al. 2011; Menezes et al. 2012; Jatmiko et al. 2019), Pacific (Anderson et al. 2020), or both Oceans (Grewe et al. 2019; Menezes et al. 2006). Regarding the Atlantic Ocean, the available data suggests strong gene flow within the West region (Carvalho et al. 2020) and a close relationship with the Pacific Ocean (Ely et al. 2005). It is important to highlight that there is still no consensus in the literature about the skipjack tuna population structure, especially in the Atlantic, where the available information is quite limited.

The current study aimed to investigate the genetic structure and connectivity of the skipjack tuna, at various scales within the Atlantic Ocean, encompassing both eastern and western stocks. In particular, we addressed the question of whether *K. pelamis* from the East and West Atlantic comprise two different stocks, since other studies in small and large spatial scales have found both structuring and panmixia along the species distribution (Carvalho et al. 2020; Dammannagoda et al. 2011; Ely et al. 2005; Grewe et al. 2019; Jatmiko et al. 2019; Menezes et al. 2006, 2012). We endeavor to access the genetic and connectivity patterns of the skipjack tuna throughout its Atlantic range to help fill a serious data gap for this social-economically important species.

Material and methods

Sample collection and molecular procedures

Tissue (muscle) and fin (first dorsal) samples of *K. pelamis* were collected between 2019 and 2021 from both Atlantic stocks currently considered by the ICCAT (International Commission for the Conservation of Atlantic Tunas) [Western Atlantic—SKJ-W, represented by the Western tropical zone (WTZ; Venezuela), Western equatorial zone (WEZ; Northeastern of Brazil), and Western Subtropical Zone (WSZ; South of Brazil); Eastern Atlantic—SKJ-E, represented by the Eastern temperate zone (ETZ; Azores), Eastern-central equatorial zone (ECEZ; St. Peter and St. Paul Archipelago), and Eastern equatorial zone (EEZ; African coast of Senegal, Ivory Coast, and Gabon)], through bait boat and purse seine fisheries based in Venezuela, Brazil, Portugal (Azores), Senegal, Ivory Coast, and Gabon (Fig. 1; Table 1; Supplementary Table S1), along the Economic Exclusive Zone. The samples were stored in 96% ethanol and kept at -20 °C. The total genomic DNA was extracted using the *Invitrogen Extraction Kit* (Thermo Fisher Scientific®), following the manufacturer's protocol, stained with Gelred™, visualized in 1% electrophoresis gel, and quantified using a nano spectrophotometer 2000 (Thermo Scientific).

Two loci were amplified through PCR using the primer sets: CRA 5' TTCCACCTCTAACTCCCA AAGCTAG 3' and CRE 5' CCTGAAGTAGGA ACCAGATG 3' (Lee et al. 1995), and S7RPEX1F 5' TGGCCTCTTCCTTGGCCGTC 3' and S7RPEX2R 5' AACTCGTCTGGCTTTTCGCC 3' (Chow and Hazama 1998), for the control region (CR; mtDNA) and the first intron of the S7 ribosomal protein (S7; nuDNA), respectively. The reactions were carried out in 25 µL using: (a) CR: 12.5 µL of 2X Taq Pol Master Mix (Cellco®), 1 µL of each primer (10 mM), 0.5 µL of magnesium chloride (50 mM), 2 µL of DNA (40 ng/µL), and 7.5 µL of ultrapure water, following the cycle described by Domingues et al. (2006); (b) S7: 12.5 µL of 2X Taq Pol Master Mix (Cellco®), 0.75 µL of each primer (10 mM), 0.5 µL of magnesium chloride (50 mM), 2 µL of DNA

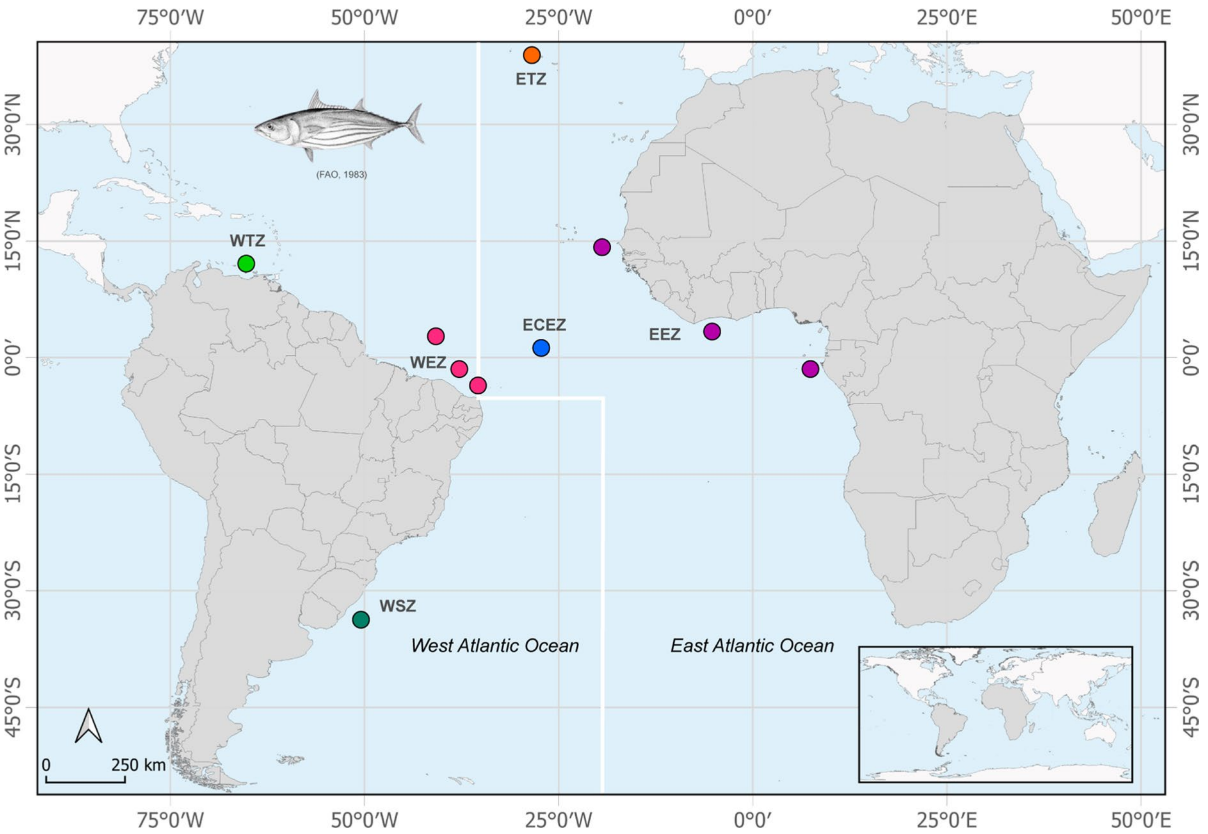

Fig. 1 Map showing the sample sites of *K. pelamis*. The white line represents the ICCAT geographical division between eastern and western Atlantic stocks. (WTZ: Western tropical zone; WEZ: Western equatorial zone; WSZ: Western subtropical zone; ETZ: Eastern temperate zone; ECEZ: Eastern-central equatorial zone; EEZ: Eastern equatorial zone)

(40 ng/μL), and 8.5 μL of ultrapure water, following the cycle described by Chow and Hazama (1998).

The PCR products were stained with Gelred™ and visualized in 1.8% electrophoresis gel. The positive amplifications were purified using the NucleoSAP kit (Cellco®), following the recommended protocol provided by the manufacturer. The purified amplicons were quantified using a nano spectrophotometer Nanodrop 2000 (Thermo Scientific), diluted to a final concentration of 20 ng/μL and Sanger sequenced in the forward direction using the Bigdye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems), on an automatic sequencer ABI 3500 (Applied Biosystems).

Data analysis

The electropherograms were visualized and edited using the BioEdit Sequence Alignment Editor v.7.0 (Hall 1999). After applying this quality filter, sequences that presented a large number of non-identified bases (referred as ‘N’) were excluded.

The sequences obtained from each marker were aligned using the ClustalW algorithm (Thompson et al. 1994) implemented on BioEdit Sequence Alignment Editor v.7.0 (Hall 1999). Due to the presence of polymorphisms of a recombinant nature in the nuclear genome, the S7 alleles were reconstructed using the PHASE v.2.1 tool (Stephens et al. 2004) implemented on DnaSP v.6.0 (Librado and Rozas 2009), considering only allelic states with probabilities higher than 70% (Stephens et al. 2004). The analysis described below was performed separately for each marker.

Table 1 Genetic diversity indices and neutrality tests obtained from the *K. pelamis* control region (CR; mtDNA) and intron S7 (nuDNA) data

Marker	Site	N	H	S	h	Π	Fu's Fs	Tajima's D
CR	WTZ	40	38	103	0.99	0.059	−16.35*	−0.24*
	WEZ	40	40	109	1	0.059	−21.09*	−0.48
	WSZ	39	39	108	1	0.058	−23.63*	−0.44
	SKJ-W	119	115	133	0.99	0.056	−23.88*	−0.478
	ETZ	48	43	111	0.99	0.056	−23.83*	−0.52
	ECEZ	23	23	88	1	0.058	−8.18*	−0.15
	EEZ	87	56	133	1	0.056	−23.9*	−0.50
	SKJ-E	158	151	142	0.99	0.055	−23.77*	−0.48
	Total	277	263	159	0.99	0.054	−23.56*	−0.63
S7[a]	WTZ	84	62	103	0.99	0.039	−24.11*	−0.78
	WEZ	52	39	93	0.98	0.023	−20.17*	−1.87*
	WSZ	50	39	97	0.99	0.039	−10.36*	−0.96
	SKJ-W	186	112	111	0.99	0.033	−23.88*	−0.91
	ETZ	88	59	105	0.98	0.031	−21.27*	−1.28
	ECEZ	26	22	23	0.98	0.012	−9.61*	−0.63
	EEZ	166	110	119	0.99	0.032	−23.98*	−1.25
	SKJ-E	280	165	125	0.98	0.03	−23.84*	−1.29
	Total	466	230	129	0.98	0.03	−23.62*	−1.11

The '*' values represent significant values ($p < 0.05$). (N = sample size; H = number of haplotypes; S = number of polymorphic sites; h = haplotype diversity; π = nucleotide diversity)

WTZ: Western tropical zone; WEZ: Western equatorial zone; WSZ: Western subtropical zone; ETZ: Eastern temperate zone; ECEZ: Eastern-central equatorial zone; EEZ: Eastern equatorial zone

[a] The value in parentheses in the 'N' column refers to the number of recovered alleles

Genetic diversity indices [number of haplotypes (H), polymorphic sites (S), haplotype (h), and nucleotide diversities (π)] were obtained through DNAsp v.6.0 (Librado and Rozas 2009). To investigate the relationships among the haplotypes and their geographic distributions, a haplotype network was built in the software PopART using the TCS method (Clement et al. 2002; Leigh and Bryant 2015). The *K. pelamis* population structure was also tested through a Bayesian approach in the software BAPS v.6.0 (Bayesian Analysis of Population Structure grouping analysis; Corander and Marttinen 2006; Corander et al. 2008).

Genetic differentiation was tested through the pairwise F_{ST} for both sample sites and the SKJ-E *vs* SKJ-W ICCAT stocks in ARLEQUIN v.3.5.2.2 (Excoffier and Lischer 2010) using 1000 permutations ($p < 0.05$). Significant values were corrected through the False Discovery Rate (FDR) (Benjamini and Hochberg 1995) and Bonferroni (Rice 1989) test using the 'tidyverse' package in 'R' (R Core Team 2017; https://www.R-project.org/). The Analysis of Molecular Variance (standard AMOVA), using 1000 permutations ($p < 0.05$), was also performed in ARLEQUIN v.3.5.2.2, and considered four hierarchical models: (a) Panmixia or null hypothesis (all samples in the same group), (b) Two ICCAT stocks (SKJ-E and SKJ-W), (c) Three groups: SKJ-E (removing ETZ samples), SKJ-W and ETZ, and (d) Two groups: SKJ-E (removing ETZ samples) + SKJ-W and ETZ.

Demographic oscillations over time were investigated through three approaches. The first one consisted of the traditional neutrality tests, Fu's Fs (Fu 1997) and Tajima's D (Tajima 1989), obtained in ARLEQUIN v.3.5.2.2 ($p < 0.05$). Secondly, the Mismatch distribution analysis was performed on DnaSP v.6.0 (Librado and Rozas 2009; Rogers and Harpending 1992), considering: (a) both Atlantic stocks, (b) SKJ-W and (c) SKJ-E. For mitochondrial data, using a historical approach, the Bayesian Skyline Plot (BSP—Drummond et al. 2005) was performed on BEAST v.2.4.7 (Bouckaert et al. 2014), using a mutational rate of $3.6\% \times 10^{-8}$ per site per million years (Donaldson and Wilson 1999), considering the same groups used in the Mismatch analysis. The best evolutionary model of each dataset was determined in jModelTest v.2.1.7 (Darriba et al. 2012) using the Akaike Information Criterion (HKY + I + G for 'a' and 'b', and K80 + I + G for 'c'). Three independent runs of 30 million MCMC interactions for 'a' and 20 million MCMC interactions for 'b' and 'c', were performed, assuming a burn-in of 25%. Each dataset run (log and tree files) was combined using LogCombiner in BEAST v.2.4.7, and the effective sampling size (> 200) was checked in Tracer v.1.7.1 (Rambaut et al. 2018), and the BSP was reconstructed.

Results

The final alignment of the 277 CR fragments obtained had 404 bp, defining 263 haplotypes, of which only 12 were shared, and 159 polymorphic sites. In the S7 dataset, 233 fragments were sequenced with 410 bp, recovering 466 alleles and 129 polymorphic sites. In general, the haplotype (h) and nucleotide (π) diversity were high for both markers (CR: h = 0.99, π = 0.054; S7: h = 0.98, π = 0.03). The genetic diversity indices observed by CR data ranged from 0.99 to 1 for haplotype diversity, and from 0.055 to 0.059 for nucleotide diversity. In S7 data, the genetic diversity indices ranged from 0.98 to 0.99 for haplotype diversity, and from 0.012 to 0.039 for nucleotide diversity (Table 1). Both ICCAT Atlantic stocks presented similar haplotype diversity for both markers. Nucleotide diversities were slightly different, being 0.055 (CR) and 0.03 (S7) for SKJ-E, and 0.056 (CR) and 0.033 (S7) for SKJ-W.

Both haplotype networks revealed a low and homogeneous frequency among the recovered haplotypes (Fig. 2a) and alleles (Fig. 2b). BAPS analysis recovered 4 genetic profiles (K = 4; $P = 1$) for both CR and S7 data, distributed, in general, throughout all sample sites in different frequencies (Fig. 3).

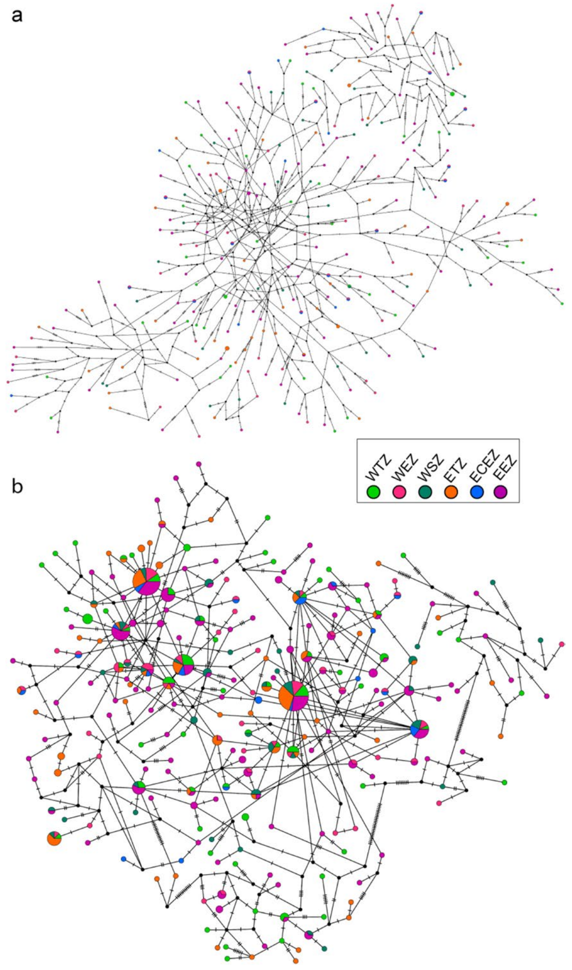

Fig. 2 Haplotype networks of *K. pelamis* based on the TCS method generated, on PopART for **a** control region and **b** intron S7 data. The circles represent the haplotypes, and their sizes represent the frequencies in each sample site (different colors). Lines between the haplotypes represent the mutational steps and the black circles represent missing or not sampled haplotypes. (WTZ: Western tropical zone; WEZ: Western equatorial zone; WSZ: Western subtropical zone; ETZ: Eastern temperate zone; ECEZ: Eastern-central equatorial zone; EEZ: Eastern equatorial zone)

The pairwise F_{ST} values differ between the two markers and can be observed in Fig. 4. The F_{ST} values for mitochondrial data were low but statistically significant ($p < 0.05$) in comparisons which encompass, especially, samples from ETZ, ranging from ~ 0.003 (when ETZ was compared to the WEZ, WSZ, EEZ) to 0.0057 (compared to the WTZ). In addition, the comparison between WTZ and EEZ presented a low and significant value (0.003). Concerning S7 data, pairwise F_{ST} values were statistically significant only when the ETZ and EEZ were compared ($F_{ST} = 0.004$). All these values remain statistically significant after the FDR correction, and two

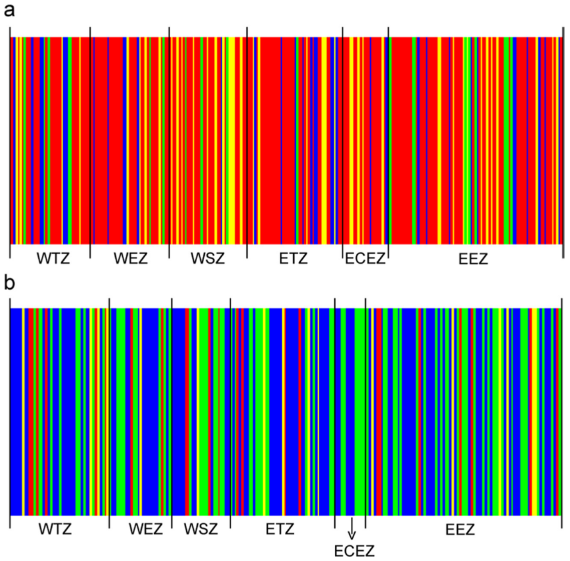

Fig. 3 BAPS analysis of *K. pelamis* for **a** control region and **b** intron S7 data. Different colors represent the recovered genetic profiles in each geographical sampled zone. (WTZ: Western tropical zone; WEZ: Western equatorial zone; WSZ: Western subtropical zone; ETZ: Eastern temperate zone; ECEZ: Eastern-central equatorial zone; EEZ: Eastern equatorial zone)

comparisons (ETZ compared to WEZ and to WSZ) presented a p-value increase after the Bonferroni correction (more details about the corrected p-values can be found in Table S2). Between SKJ-E and SKJ-W ICCAT stocks, the pairwise F_{ST} presented a low but significant value ($F_{ST} = 0.0006$; $p < 0.05$) in CR data, and a negative value ($F_{ST} = -0.0002$) in S7 data.

In all hierarchical models tested, AMOVA results indicate that more than 99% of the genetic variation resides within the sampled zones. The null model of panmixia presented low and significant F_{ST} values both in CR and S7 data (0.0024 and 0.004, respectively) (Table 2). When the two ICCAT stocks (SKJ-E and SKJ-W) were considered, no genetic differentiation between groups (F_{CT}) was found (CR: −0.0001; S7: −0.0012; Table 2). The third model, which separated SKJ-E (removing ETZ samples), SKJ-W, and ETZ samples, presented a low and non-significant genetic differentiation between groups by both markers (CR: $F_{CT} = 0.001$; S7: $F_{CT} = 0.0005$). When only the ETZ was separated as a different group (the other sample sites were treated as one single group) the F_{CT} value remained low and non-significant (Table 2).

The neutrality tests showed no statistical significance when analyzing the data for both markers (Table 1). However, the mismatch distribution analyses revealed a unimodal pattern in all simulated scenarios [Atlantic (SKJ-E + SKJ-W), SKJ-E, and SKJ-W] (Supplementary Fig. S1). The BSP data showed a long period of population expansion of *K. pelamis* in the Atlantic Ocean, between 850 and 350 thousand years ago (Fig. 5). A similar pattern was shared between SKJ-E and SKJ-W, which seems to have gone through two expansion events: one approximately 1 million years ago, and one about 500 thousand years ago (Supplementary Fig. S2).

Discussion

Eastern and Western Atlantic stock structure and demographic history

The mitonuclear data suggests a homogeneous distribution of the genetic diversity of *K. pelamis* in the Atlantic Ocean and did not confirm the geographic structure in two stocks (East and West) as currently considered by ICCAT for management purposes. This lack of a geographic genetic structure is consistent with the biological features of the skipjack, as we will argue below.

K. pelamis is a migratory and widely distributed species, being able to swim more than 60 km per day (Sharp and Dizon 1978) and sustains a large effective population size (Vincent et al. 2019). These life history features, associated with the marine environment physical structure (e.g., absence of large gene flow barriers), can reduce the genetic drift effects (Cowen et al. 2006; Cowen and Sponaugle 2009; Funk et al. 2012) and may support a lack of a genetic structure of the skipjack tuna, at least in the Atlantic Ocean. Results obtained by the AOTTP (Atlantic Ocean Tropical Tuna Tagging Program) show an interchange, even if minimal, between the East and West stocks (ICCAT 2025). This admixture was also suggested by Hermida et al. (2019), who

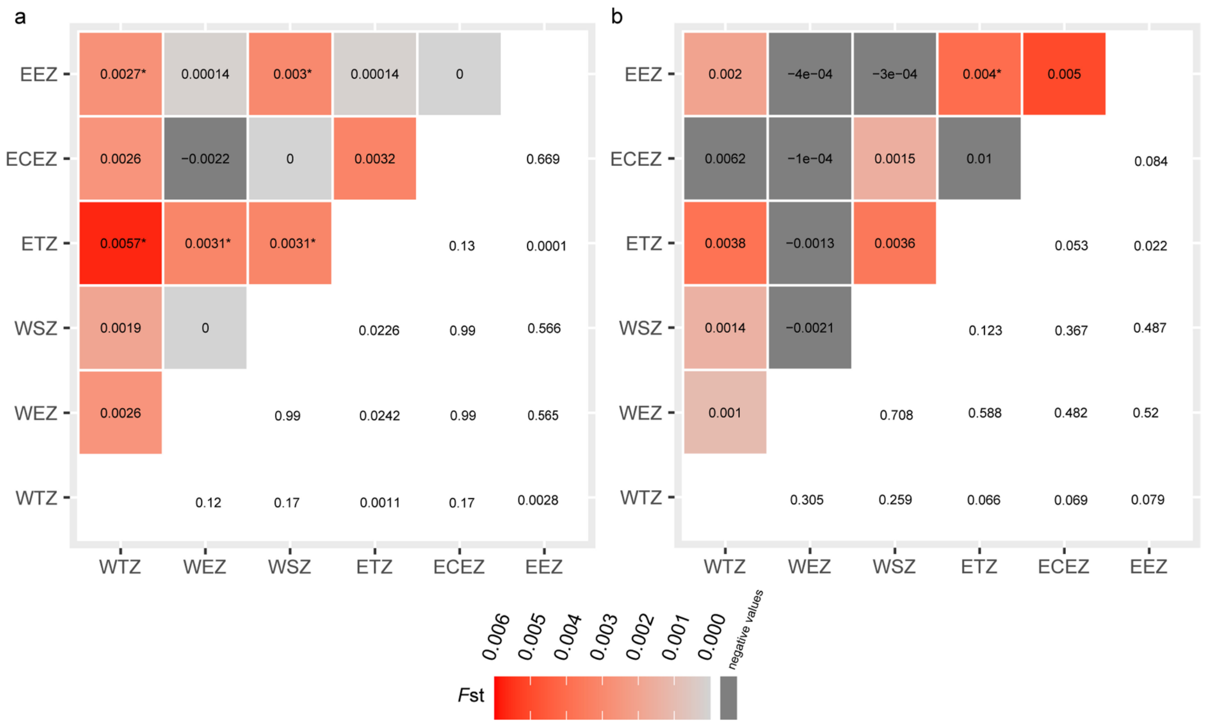

Fig. 4 Heat map of pairwise differences among each sample site represented on both the x and y axes for **a** control region and **b** intron S7 data. F_{ST} values can be found above diagonal, and *p*-values below diagonal. Significant pairwise F_{ST} values are indicated by '*' ($p < 0.05$). (Corrected *p*-values can be found in Table S2. WTZ: Western tropical zone; WEZ: Western equatorial zone; WSZ: Western subtropical zone; ETZ: Eastern temperate zone; ECEZ: Eastern-central equatorial zone; EEZ: Eastern equatorial zone)

Table 2 AMOVA for control region (mtDNA) and intron S7 (nuDNA) of *K. pelamis*, testing four hierarchical models: (a) Panmixia (SKJ-E + SKJ-W ICCAT stocks), (b) Two ICCAT stocks (SKJ-E and SKJ-W), (c) Three groups: SKJ-E, SKJ-W, ETZ, and (d) Two groups: SKJ-E + SKJ-W, ETZ

Hierarchical models		*SKJ-E + SKJ-W*		*1)SKJ-E* *2)SKJ-W*		*1)SKJ-E* *2)SKJ-W* *3)ETZ*		*1)SKJE + SKJ-W* *2)ETZ*	
		CR	S7	CR	S7	CR	S7	CR	S7
Variation source (%)	*Among groups*	–	–	−0.01	−0.12	0.10	0.05	0.25	0.22
	Among populations	0.18	0.22	0.18	0.29	0.11	0.18	0.09	0.13
	Within populations	99.82	99.78	99.82	99.83	99.80	99.77	99.65	99.65
Fixation indices	F_{SC}	–	–	0.002*	0.003*	0.0011*	0.0018	0.001*	0.0013
	F_{ST}	0.002*	0.002*	0.002*	0.002*	0.002*	0.002*	0.003*	0.0035*
	F_{CT}	–	–	−0.0001	−0.0012	0.001	0.0005	0.002	0.002

*Significant values ($p < 0.05$)

found 'exclusive' parasites of the western skipjacks in individuals sampled in eastern regions. Furthermore, the skipjack tunas from these areas seem to share similar population dynamics regarding growth parameters, at least in equatorial zones (e.g. Hallier and Gaertner 2006; Vilela and Castello 1991). It is also important to acknowledge that the expansion of the use of Fishing Aggregating Devices (FADs) by

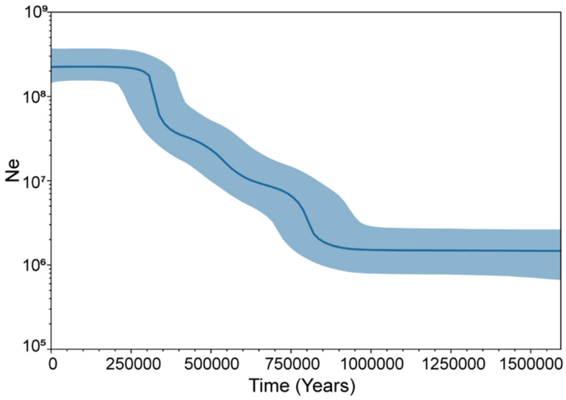

Fig. 5 Bayesian Skyline Plot of *K. pelamis*. The 'y' axis represents population size, and the 'x' axis the time in years. The blue line is the mean population size × generation time, and the blue bar corresponds to the 95% confidence intervals

the purse seine fleet in the eastern Atlantic changed the fishery dynamic in the Atlantic Ocean, affecting the spatial distribution of the tuna species (Sempo et al. 2013). The drift of these devices, driven by the South Equatorial Current, promoted an expansion of the skipjack tuna's fishery area in the western direction (Hallier and Gaertner 2008; ICCAT 2025). Thus, these devices may have changed the original movement patterns of the skipjack tuna, contributing to the connectivity between SKJ-E and SKJ-W, as already hypothesized by Fonteneau (2015b) and observed by Wang et al. (2014) in the Pacific Ocean. However, more studies are needed to better elucidate this issue, including determining whether the boundary between stocks in the Western Equatorial Zone needs to be adjusted.

Furthermore, Grewe et al. (2019) discussed that *K. pelamis*, compared to *Thunnus obesus* (bigeye tuna) and *T. albacares* (yellowfin tuna), seem to be the least genetically differentiated tuna species in the Pacific Ocean, which was also found by Anderson et al. (2020) through genomic data. In general, the genetic differentiation of these scombrids is associated with specific behaviors, such as defined periods of reproductive migrations and philopatry, not observed so far for *K. pelamis* (Richardson et al. 2016; Schaefer et al. 2007). Moreover, Ely et al. (2005) found a genetic structure between the Pacific and Atlantic Oceans for yellowfin tuna but not for skipjack tuna. The mitonuclear data presented here follow, in general, a long tradition of similar conclusions on *K. pelamis* in different oceans, including the Atlantic. However, an exception seems to be the Indian Ocean, where some data reveal signals of genetic structure (e.g., Dammannagoda et al. 2011; Menezes et al. 2006, 2012).

On the other hand, the CR data presented a low but significant differentiation between western and eastern Atlantic, unlike the nuclear data. It is important to highlight that those incongruences between mitochondrial and nuclear data are natural, since the nuclear DNA coalesces up to four times slower than mtDNA, being more susceptible to incomplete lineage sorting (Després, 2019; Towes and Brelsford 2012). In addition, low differentiation values are expected in migratory species since one migrant per generation can homogenize the populations (Waples 1998). Furthermore, the pairwise F_{ST} was slightly higher between zones from ICCAT different stocks than between those from the same stock and involved, especially samples from the Eastern temperate zone (ETZ) represented by the Azores archipelago.

The distinctiveness of the Azores samples can be explained by oceanographic features. These Islands are located in the SJ01 ICCAT area, "isolated" from the other sample sites, and ICCAT proposed a separation of this region for future stock assessments (ICCAT 2014). Similar evidence of genetic differentiation by limited gene flow and possibly mediated by factors such as ocean currents, historical processes, and differences between insular and continental environments were found by other studies, especially for nektonic species (e.g., Almada et al. 2017; Robalo et al. 2021). Additionally, the population dynamics of the skipjack tuna seem to differ between temperate and equatorial zones (Collete et al. 2021; Fonteneau 2015a; Hallier and Gartner 2006). In warmer equatorial areas, the skipjack tuna seems to be focused on directing their energy to reproduction more than growing, since they spawn opportunistically at sea temperatures between 25 and 30 °C. On the contrary, individuals from temperate areas present faster growth rates, focusing on feeding and growing.

However, since the differences observed were subtle, it is reasonable to suggest that individuals of skipjack tuna from the North retain plasticity to overcome ecological and physical barriers between these provinces to complete their biological cycle in the Southern hemisphere, as confirmed by Arregui et al. (2020) through AOTTP tagging results, showing significant southward movements (1500 nm) in fish tagged in the Azores. These North–South movements are probably seasonal (Fonteneau 2015b) and are contrary to the data obtained by Gaertner et al. (2008) that showed low north–south admixture in the SKJ-E. Nevertheless, despite the limitation of the data analyzed (low tagged number, data obtained before FADs uses), the revision conducted by Fonteneau (2015b) highlighted that the East–West movements seem to be limited at the temperate latitudes due to the presence of the ocean gyres, which can contribute to the genetic differentiation observed.

Otolith and genetic data showed no differentiation between South (Rio Grande do Sul) and Southeast (Rio de Janeiro) of Brazil, and from South, Southeast and Northeast of Brazil, respectively (Carvalho et al. 2020; de Souza Corrêa et al. 2022). The results presented herein agree with these previous data, confirming the lack of differentiation within the SKJ-W ICCAT stock. Regarding the SKJ-E, subtle levels of genetic differentiation were found mainly between the temperate and equatorial zones, as argued above. This pattern should be further investigated through a holistic approach, by using whole genomic sequencing, which can improve the investigation of weakly hypothetical differentiated population by searching for local adaptation signals (outliers loci), tagging and otolith chemistry, focusing on adults to investigates potential spawning movements and area fidelity, since they can be sensitive to different biological process and spatial-time scales (Moore et al. 2020; Papa et al. 2021). However, until now, the data presented herein are the first to explore the population structure within this region.

The demographic analyses indicated recent expansion events in the western and eastern Atlantic. This shared demographic history reinforces the absence of the skipjack genetic structure in the Atlantic Ocean as mentioned above. In addition, such evidence suggests that the ICCAT stocks worked historically as a cohesive group by sharing the same demographic phenomenon.

The periods of population expansions in BSP date from the Pleistocene. Sharp expansion peaks date from the glacial [~800 thousand years ago (Atlantic), ~950 thousand years ago (SKJ-W) and ~900 thousand years ago (SKJ-E)] and interglacial periods [~350 thousand years ago (Atlantic), ~550 thousand years ago (both SKJ-E and SKJ-W)]. The Pleistocene was a period characterized by oscillations in the sea level and temperature (Chappell and Shackleton 1986), playing a key role in shaping the history of many marine populations by providing, sometimes, new areas to be colonized and allowing adaptative radiation (Chen et al. 2020; Neves et al. 2020), including demographic aspects of skipjack tuna in the Atlantic Ocean. In a global warming scenario, projections indicate that the habitat suitability of skipjack tuna will increase as the sea temperature warmed, especially in higher latitudes (Dueri et al. 2014; Erauskin-Extramiana et al. 2019; Muhling et al. 2015).

Fisheries management comments

ICCAT manages the skipjack tuna in the Atlantic Ocean considering two stocks: SKJ-E and SKJ-W. Although we detected some subtle degrees of genetic differentiation between skipjack tuna from different Atlantic Ocean sample sites, especially involving the Eastern Temperate Zone, other analyses failed to detect genetic-geographic structure. In addition, as the differentiation levels were subtle, there is insufficient evidence to suggest that these groups represent different populations. However, it is important to recognize the possible limitation regarding the resolution power of the two fragments used herein. Thus, as observed by other studies throughout its distribution, the stock structure of the Atlantic skipjack tuna remains controversial.

High genetic diversity in all sites and groups (SKJ-E and SKJ-W), by both mitochondrial and nuclear data, and the absence of signals of contraction and bottleneck by demographic analysis agreed with the Least Concern status assessment provided by IUCN (Colette et al. 2021). These data reinforce the large effective population sizes reported by Vincent et al. (2019), indicating the resilience of skipjack tuna, despite the fishing pressure, and the absence of evidence for overexploitation throughout the Atlantic Ocean. This can be confirmed by the results of the latest ICCAT assessment of the two stocks (ICCAT 2025), which indicate that these stocks are not overfished and are not undergoing overfishing. In this case, we recommend that the ICCAT conservation strategies be maintained. However, since the SKJ-E stock is much more productive than the western stock, which can lead to a higher risk of overexploitation in mixed fisheries, the lack of genetic structure between these areas suggests that an alignment of these strategies and further studies may be necessary.

Conclusions and perspectives

The assessed parts of the genome considered in this study confirm a genetic panmixia between the two skipjack tuna Atlantic stocks (SKJ-E and SKJ-W) currently managed by ICCAT. Thus, we suggest that these results should be taken into consideration by the Regional Fisheries Management Organization for improving future management and conservation efforts, highlighting the need for a better understanding of how the skipjack tuna should be managed in the Atlantic Ocean. Additionally, it is possible that an alignment and reevaluation of the current strategies may be necessary. However, we recognize that these results could be limited since they were based only on two genetic fragments (control region and intron S7). Thus, an integrative investigation, joining both broad genomic assays, investigating potential loci under differential selective pressures, and non-genetic data such as ecological, otoliths, isotopes, stomach contents, and tagging, is strongly recommended to improve the comprehension of the skipjack tuna population and stock structure. This is especially critical for the Eastern Temperate Zone, represented in the present study by the Azores Archipelago. From a global perspective, a collaboration between the five Regional Fisheries Management Organizations of skipjack tuna stocks is encouraged to investigate the extension of the genetic diversity distribution along the entire range of the species. Therefore, improving a more informed system and contribute to the sustainable management of the skipjack tuna in general.

Acknowledgements We sincerely thanks to the PROTUNA project (Project to provide technical and scientific support for the development of tuna fisheries in Brazil), through which was possible to collect samples from different places during the study years and acknowledge Gisela Dionisio (Naturalist contact@naturalist.pt) for supplying the samples from the Azores. We would also like to thank the Coordination for the Improvement of Higher Education Personnel (CAPES, Brazil), of the Ministry of Education, for the PhD scholarship awarded to the first author of this scientific paper.

Author contributions MCGQB, PT and RAT conceptualized the project. Samples were collected by JIR, FA, NGCD, MJA, FNS, DA and PT. Investigation, Molecular procedures, Formal analysis, and Writing (Original Draft) was undertaken by MCGQB. PT: Funding. RAT: Supervision. All authors revised and edited the manuscript and gave final approval for publication.

Funding This research was supported by PROTUNA (Project to provide technical and scientific support for the development of tuna fisheries in Brazil), approved in the Call 22/2015—MCT/MPA/CNPq—Line 2—Tuna and tuna-like fish (Process 445810/2015–7) and by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brasil (CAPES)—Finance Code 001. JIR would like to acknowledge the Portuguese Foundation for Science and Technology (FCT) through the projects: UIDB/04292/ 2020 and UIDP/04292/2020, granted to MARE (Marine and Environmental Sciences Centre).

Data availability The data that support the finding of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors also declare that there are no intellectual, personal, or financial conflicts of interests in the present research.

References

Almada F, Francisco SM, Lima CS, FitzGerald R, Mirimin L, Villegas-Ríos D, Saborido-Rey F, Afonso P, Morato T, Bexiga S, Robalo JI (2017) Historical gene flow constraints in a Northeastern Atlantic fish: phylogeography of the ballan wrasse *Labrus bergylta* across its distribution range. R Soc Open Sci 4:160773. https://doi.org/10.1098/rsos.160773

Anderson G, Lal M, Stockwell B, Hampton J, Smith N, Nicol S, Rico C (2020) No population genetic structure of skipjack tuna (*Katsuwonus pelamis*) in the tropical Western and Central Pacific assessed using single nucleotide polymorphisms. Front Mar Sci 7:570760. https://doi.org/10.3389/fmars.2020.570760

Arregui I, Goñi N, Chifflet M (2020) Migration patterns of yellowfin, skipjack and bigeye tunas in the tropical Atlantic, based on recent tagging and recapture data. Collect Vol Sci Papers ICCAT 76:903–950

Ashida H, Tanabe T, Suzuki N, Fukui A, Tanaka S (2008) Spawning frequency and batch fecundity of skipjack tuna *Katsuwonus pelamis* in the tropical west-central Pacific Ocean. Nippon Suisan Gakkaishi (Japan) 74:802–808. https://doi.org/10.2331/suisan.74802

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. J R Stat Society B 57:289–300. https://doi.org/10.2307/23461014

Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu CH, Xie D, Suchard MA, Rambaut A, Drummond AJ (2014) BEAST 2: a software platform for Bayesian evolutionary analysis. PLoS Comput Biol 10:e1003537. https://doi.org/10.1371/journal.pcbi.1003537

Carvalho PH, Pozzobon APB, Vasconcellos AV, da Silva GB (2020) Genética do bonito-listrado na costa brasileira: conectividade e aspectos demográficos. In: Madureira LASP, Monteiro-Neto C (eds) Sustentabilidade da Pesca do Bonito-Listrado no Brasil, 1st edn. Walprint Gráfica e Editora, Rio de Janeiro, pp 89–105

Chappell J, Shackleton N (1986) Oxygen isotopes and sea level. Nature 324:137–140. https://doi.org/10.1038/324137a0

Chen W, Li C, Chen F, Li Y, Yang J, Li J, Li X (2020) Phylogeographic analyses of a migratory freshwater fish (*Megalobrama terminalis*) reveal a shallow genetic structure and pronounced effects of sea-level changes. Gene 737:144478. https://doi.org/10.1016/j.gene.2020.144478

Chow S, Hazama K (1998) Universal PCR primers for S7 ribosomal protein gene introns in fish. Mol Ecol 7:1255–1256

Clement MJ, Snell Q, Walker P, Posada D, Crandall KA (2002) TCS: estimating gene genealogies. Proceeding 16ht International Parallel Distributed Processing Symposium. 311:1110–1116. http://www.hicomb.org/papers/HICOMB2002-03.pdf

Collette BB, Nauen CE (1983) Scombrids of the world: an annotated and illustrated catalogue of tunas, mackerels, bonitos, and related species known to date. FAO Species Catalogue vol. 2.

Collette BB, Boustany A, Fox W, Graves J, Juan Jorda M, Restrepo V (2021) *Katsuwonus pelamis*. The IUCN Red List of Threatened Species 2021: e.T170310A46644566. https://doi.org/10.2305/IUCN.UK.2021-2.RLTS.T170310A46644566.en. Accessed 07 September 2022.

Corander J, Marttinen P (2006) Bayesian identification of admixture events using multilocus molecular markers. Mol Ecol 15:2833–2843. https://doi.org/10.1111/j.1365-294X.2006.02994.x

Corander J, Marttinen P, Sirén J, Tang J (2008) Enhanced Bayesian modelling in BAPS software for learning genetic structures of populations. BMC Bioinform 9:1–14. https://doi.org/10.1186/1471-2105-9-539

Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. Annu Rev Mar Sci 1:443–466. https://doi.org/10.1146/annurev.marine.010908.163757

Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. Science 311:522–527. https://doi.org/10.1126/science.1122039

Dammannagoda ST, Hurwood DA, Mather PB (2011) Genetic analysis reveals two stocks of skipjack tuna (*Katsuwonus pelamis*) in the Northwestern Indian Ocean. Canadian J Fish Aquat Sci 68:210–223. https://doi.org/10.1139/F10-136

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nat Methods 9:772. https://doi.org/10.1038/nmeth.2109

de Souza Corrêa GM, Coletto JL, Castello JP, Miller NR, de Almeida TR, Neto CM, da Costa MR (2022) Identification of fish stock based on otolith as a natural marker: The case of *Katsuwonus pelamis* (Linnaeus, 1758) in the Southwest Atlantic Ocean. Fish Res 255:106436. https://doi.org/10.1016/j.fishres.2022.106436

Després L (2019) One, two or more species? Mitonuclear discordance and species delimitation. Mol Ecol 28:3845–3847. https://doi.org/10.1111/mec.15211

Di Natale A, Srour A, Hattour A, Keskin Ç, Idrissi M, Orsi Relini L (2009) Regional study on small tunas in the Mediterranean including the Black Sea.Studies and Reviews. General Fisheries Commission for the Mediterranean. No. 85. Rome, FAO: 1–132. https://openknowledge.fao.org/items/bb8e5e2e-ceeb-4eef-af5d-b6f656e9c137

Domingues VS, Santos RS, Brito A, Almada VC (2006) Historical population dynamics and demography of the eastern Atlantic pomacentrid *Chromis limbata* (Valenciennes, 1833). Mol Phylogenet Evol 40:139–147. https://doi.org/10.1016/j.ympev.2006.02.009

Donaldson KA, Wilson RR Jr (1999) Amphi-panamic geminates of snook (Percoidei: Centropomidae) provide a calibration of the divergence rate in the mitochondrial DNA control region of fishes. Mol Phylogenet Evol 13:208–213. https://doi.org/10.1006/mpev.1999.0625

Drummond AJ, Rambaut A, Shapiro BE, Pybps OG (2005) Bayesian coalescent inference of past population dynamics from molecular sequences. Mol Biol Evol 22:1185–1192. https://doi.org/10.1093/molbev/msi103

Dueri S, Bopp L, Maury O (2014) Projecting the impacts of climate change on skipjack tuna abundance and spatial distribution. Global Change Biol 20:742–753. https://doi.org/10.1111/gcb.12460

Ely B, Viñas J, Alvarado Bremer JR, Black D, Lucas L, Covello K, Labrie AV, Thelen E (2005) Consequences of the historical demography on the global population structure of two highly migratory cosmopolitan marine fishes: the yellowfin tuna (*Thunnus albacares*) and the skipjack tuna (*Katsuwonus pelamis*). BMC Evol Biol 5:1–9. https://doi.org/10.1186/1471-2148-5-19

Erauskin-Extramiana M, Arrizabalaga H, Hobday AJ, Cabré A, Ibaibarriaga L, Arregui I, Murua H, Chust G (2019) Large-scale distribution of tuna species in a warming ocean. Global Change Biol 25:2043–2060. https://doi.org/10.1111/gcb.14630

Excoffier L, Lischer HE (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Mol Ecol Res 10:564–567. https://doi.org/10.1111/j.1755-0998.2010.02847.x

FAO (2004) *Katsuwonus pelamis*. FAO Species Fact Sheet. FAO Fisheries and Aquaculture Department Online. Rome: FAO.

FAO (2024) The State of World Fisheries and Aquaculture 2024 – Blue Transformation in action. FAO, Rome: 1–232. https://doi.org/10.4060/cd0683en

Fonteneau A (2015a) An overview of skipjack growth in the Atlantic: knowledge and uncertainties. Collect Vol Sci Pap ICCAT 71:221–229

Fonteneau A (2015b) On the movement patterns and stock structure of skipjack (*Katsuwonus pelamis*) in the

Atlantic: how many Skipjack stocks in the Atlantic Ocean. Collect Vol Sci Pap ICCAT 7:205–220

Fu Y-X (1997) Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. Genetics 147:915–925. https://doi.org/10.1093/genetics/147.2.915

Funk WC, McKay JK, Hohenlohe PA, Allendorf FW (2012) Harnessing genomics for delineating conservation units. Trends Ecol Evol 27:489–496. https://doi.org/10.1016/j.tree.2012.05.012

Gaertner D, de Molina AD, Ariz J, Pianet R, Hallier JP (2008) Variability of the growth parameters of the skipjack tuna (*Katsuwonus pelamis*) among areas in the eastern Atlantic: analysis from tagging data within a meta-analysis approach. Aquat Living Resour 21:349–356. https://doi.org/10.1051/alr:2008049

Grewe PM, Wudianto CH, Proctor CH, Adam MS, Jauhary AR, Schaefer K, Itano K, Evans K, Killian A, Foster S, Gosselin T, Feutry P, Aulich J, Gunasekera R, Lansdell M, Davies CR (2019) Population Structure and Connectivity of Tropical Tuna Species across the Indo Pacific Ocean Region. Information paper SA-IP-15 presented to the fifteenth regular session of the Western and Central Pacific Fisheries Commission Scientific Committee, 12–20 August 2019, Pohnpei, Federated States of Micronesia.

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp Ser 41:95–98

Hallier JP, Gaertner D (2006) Estimated growth rate of the skipjack tuna (*Katsuwonus pelamis*) from tagging surveys conducted in the Senegalese area (1996–1999) within a meta-analysis framework. Collect Vol Sci Pap ICCAT 59:411–420

Hallier J, Gaertner D (2008) Drifting fish aggregation devices could act as an ecological trap for tropical tuna species. Mar Ecol Prog Ser 353:55–264. https://doi.org/10.3354/meps07180

Hermida M, Cavaleiro B, Gouveia L, Saraiva A (2019) Seasonality of skipjack tuna parasites in the Eastern Atlantic provide an insight into its migratory patterns. Fish Res 216:167–173. https://doi.org/10.1016/j.fishres.2019.04.010

ICCAT (2014) Report of the 2014 ICCAT East and West Atlantic Skipjack Stock Assessment Meeting. Dakar, Senegal. ICCAT (2019) ICCAT Atlantic Ocean Tropical Tuna Tagging Programme (AOTTP)–Final narrative report evidence-based approach for sustainable management of tuna resources in the Atlantic. International Commission for the Conservation of Atlantic Tunas. Executive Summaries, Report 2014–2022. https://www.iccat.int/AOTTP/en/

ICCAT (2025) Report for biennal period, 2024-25 Part I - Vol 2 SCRS. International Commission for the Conservation of Atlantic Tuna, Madrid, Spain, 392 p. https://www.iccat.int/Documents/BienRep/REP_EN_24-25-I-2.pdf

ISSF (2024) Status of the World Fisheries for Tuna. Jul. 2024. Pittsburgh, PA, USA: ISSF Technical Report 2024–07. International Seafood Sustainability Foundation

Jatmiko I, Zedta RR, Agustina M, Setyadji B (2019) Genetic diversity and demography of skipjack tuna (*Katsuwonus pelamis*). In: southern and western part of Indonesian waters. ILMU KELAUTAN: Indones J Mar Sci 24:61–68. https://doi.org/10.14710/ik.ijms.24.2.61-68

Lee WJ, Conroy J, Howell WH, Kocher TD (1995) Structure and evolution of teleost mitochondrial control regions. J Mol Evol 41:54–66. https://doi.org/10.1007/BF00174041

Leigh JW, Bryant D (2015) Popart: full-feature software for haplotype network construction. Methods Ecol Evol 6:1110–1116. https://doi.org/10.1111/2041-210X.12410

Librado P, Rozas J (2009) DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. Bioinform 25:1451–1452. https://doi.org/10.1093/bioinformatics/btp187

Menezes MR, Ikeda M, Taniguchi N (2006) Genetic variation in skipjack tuna *Katsuwonus pelamis* (L.) using PCR-RFLP analysis of the mitochondrial DNA D-loop region. J Fish Biol 68:156–161. https://doi.org/10.1111/j.00221112.2006.00993.x

Menezes MR, Kumar G, Kunal SP (2012) Population genetic structure of skipjack tuna *Katsuwonus pelamis* from the Indian coast using sequence analysis of the mitochondrial DNA D-loop region. J Fish Biol 80:2198–2212. https://doi.org/10.1111/j.1095-8649.2012.03270.x

Moore BR, Bell JD, Evans K, Farley J, Grewe PM, Hampton J, Marie AD, Minte-Vera C, Nicol S, Piling GM, Phillips JS, Tremblay-Boyer L, Williams AJ, Smith N (2020) Defining the stock structures of key commercial tunas in the Pacific Ocean I: current knowledge and main uncertainties. Fish Res 230:105525. https://doi.org/10.1016/j.fishres.2020.105525

Muhling BA, Liu Y, Lee SK, Lamkin JT, Roffer MA, Muller-Karger F, Walter JF III (2015) Potential impact of climate change on the Intra-Americas Sea: Part 2. Implications for Atlantic bluefin tuna and skipjack tuna adult and larval habitats. J Mar Syst 148:1–13. https://doi.org/10.1016/j.jmarsys.2015.01.010

Murua H, Rodriguez-Marin E, Neilson JD, Farley JH, Juan-Jordá MJ (2017) Fast versus slow growing tuna species: age, growth, and implications for population dynamics and fisheries management. Rev Fish Biol Fish 27:733–773. https://doi.org/10.1007/s11160-017-9474-1

Neves A, Vieira AR, Sequeira V, Paiva RB, Gordo LS, Paulo OS (2020) Highly regional population structure of *Spondyliosoma cantharus* depicted by nuclear and mitochondrial DNA data. Sci Rep 10:1–11. https://doi.org/10.1038/s41598-020-61050-x

Papa Y, Oosting T, Valenza-Troubat N, Wellenreuther M, Ritchie PA (2021) Genetic stock structure of New Zealand fish and the use of genomics in fisheries management: an overview and outlook. N Z J Zool 48:1–31. https://doi.org/10.1080/03014223.2020.178861

Puerto MA, Saber S, Ortiz de Urbina JM, Gómez-Vives MJ, García-Barcelona S, Macías D (2022) Spawning area of tropical skipjack tuna, *Katsuwonus pelamis* (Scombridae) in the western Mediterranean Sea. In: Bahamon N, Domínguez-Petit R, Paramo J,F. Saborido-Rey F, and Acero-Pizarro A (eds) Iberoamerican fisheries and fish reproductive ecology, Scientia Marina, 86 (4): 1–9. https://doi.org/10.3989/scimar.05292.051

R Core Team (2017) R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Available at https://www.R-project.org/.

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarization in Bayesian phylogenetics using tracer 1.7. Syst Biol 67:901–904. https://doi.org/10.1093/sysbio/syy032

Rice WJ (1989) Analysing tables of statistical tests. Evolution 43:223–225. https://doi.org/10.2307/2409177

Richardson DE, Marancik KE, Guyon JR, Lutcavage ME, Galuardi B, Lam CH, Wildes S, Walsh HJ, Yates DA, Hare JA (2016) Discovery of a spawning ground reveals diverse migration strategies in Atlantic bluefin tuna (*Thunnus thynnus*). Proc Natl Acad Sci 113:3299–3304. https://doi.org/10.1073/pnas.152563611

Robalo JI, Farias I, Francisco SM, Avellaneda K, Castilho R, Figueiredo I (2021) Genetic population structure of the Blackspot seabream (*Pagellus bogaraveo*): contribution of mtDNA control region to fisheries management. Mitochon DNA Part A 32:115–119. https://doi.org/10.1080/24701394.2021.1882445

Rogers AR, Harpending H (1992) Population growth makes waves in the distribution of pairwise genetic differences. Mol Biol Evol 9:552–569. https://doi.org/10.1093/oxfordjournals.molbev.a040727

Schaefer KM, Fuller DW, Block BA (2007) Movements, behavior, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in the northeastern Pacific Ocean, ascertained through archival tag data. Mar Biol 152:503–525. https://doi.org/10.1007/s00227-007-0689-x

Sea Around Us (2020) Pauly D, Zeller D, Palomares MLD (eds). https://seaaroundus.org/. Accessed 14 September 2023.

Sempo G, Dagorn L, Robert M, Deneubourg JL (2013) Impact of increasing deployment of artificial floating objects on the spatial distribution of social fish species. J Appl Ecol 50:1081–1092

Sharp GD, Dizon AE (1978) The Physiological Ecology of Tunas. Proceedings of the Tuna Physiology Workshop held at the National Marine Fisheries Service Southwest Fisheries Center at La Jolla, California, Jan 10–15, 1977

Soares JB, Monteiro-Neto C, da Costa MR, Martins RRM, dos Santos Vieira FC, de Andrade-Tubino MF, Bastos AL, de Almeida TR (2019) Size structure, reproduction, and growth of skipjack tuna (*Katsuwonus pelamis*) caught by the pole-and-line fleet in the southwest Atlantic. Fish Res 212:136–145. https://doi.org/10.1016/j.fishres.2018.12.011

Stephens AM, Smith NJ, Donnelly P, Stephens CM, Li CFN (2004) Documentation for PHASE, version 2.1. https://www.animalgenome.org/bioinfo/resources/manuals/PHASE. Accessed 6 October 2020.

Tajima F (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123:585–595. https://doi.org/10.1093/genetics/123.3.585

Thompson JD, Higgins DG, Gibson TJ (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic Acids Res 22:4673–4680. https://doi.org/10.1093/nar/22.22.4673

Toews DP, Brelsford A (2012) The biogeography of mitochondrial and nuclear discordance in animals. Mol Ecol 21:3907–3930. https://doi.org/10.1111/j.1365-294X.2012.05664.x

Tortonese E (1975) Fauna d'Italia. Osteichthyes – Pesci Ossei. Ed. Calderini, Bologna, vol. IX: 367.

Vilela MJA, Castello JP (1991) Estudio de la edad y del crecimiento del barrilete *Katsuwonus pelamis*, en la region Sur y Sudeste de Brasil. Frente Marit 9:29–35

Vincent M, Pilling G, Hampton J (2019) Stock Assessment of Skipjack Tuna in the Western and Central Pacific Ocean. Pohnpei, London

Wang X, Chen Y, Truesdell S, Xu L, Cao J, Guan W (2014) The large-scale deployment of fish aggregation devices alters environmentally-based migratory behavior of skipjack tuna in the Western Pacific Ocean. PLoS One 9:e98226. https://doi.org/10.1371/journal.pone.0098226

Waples RS (1998) Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. J Hered 89:438–450. https://doi.org/10.1093/jhered/89.5.438

WCPFC (2024) Tuna Fishery Yearbook 2023. WCPFC. Western and Central Pacific Fisheries Commission, Noumea, New Caledonia