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Original Article

Global analyses of sailfish (*Istiophorus platypterus*) using next-generation sequencing reveal multiple populations

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Abstract

The sailfish (*Istiophorus platypterus*) is a mobile epipelagic billfish whose range extends across the world's tropical and subtropical oceans. Once thought to be two allopatric species, respectively inhabiting the Indo-Pacific and Atlantic oceans, molecular analyses support a single species with global distribution. Adequate sampling of widespread pelagic species presents considerable challenges, and most previous studies on sailfish used small numbers of molecular markers. As such, our understanding of their global population structure was limited. In this study, we collaborated with fisheries researchers and fishers to build a comprehensive genomic dataset of single-nucleotide polymorphisms for sailfish spanning most of its range. Here, we examined genetic variation using three filtering approaches: (i) the full-loci dataset, (ii) putatively neutral loci, and (iii) large-F_{ST} loci for 590 sailfish from 20 locations to explore contemporary population structure and connectivity in a global context. Cluster analyses of all datasets indicated three discrete populations: the Atlantic, eastern Pacific, and Indo-West Pacific oceans. For the first time, sailfish sampled from locations across the Indo-West Pacific revealed genetic connectivity throughout this region. Analyses of a subset of large-F_{ST} loci suggested a small reduction in gene flow between the western and eastern Atlantic Ocean and between the western Indian Ocean and the rest of the Indo-West Pacific. These insights into contemporary population structure can inform future stock assessments and cross-jurisdictional management of this migratory marine species.

Introduction

Billfishes (Istiophoridae) are strongly mobile, pelagic predators with widespread ranges, patchy distributions, large fecundities, and wide larval dispersal (Nakamura 1985). These characteristics make them particularly challenging to study and manage when assessing their population structure and delimiting boundaries of fisheries stocks (Graves and McDowell 2015). Billfishes are managed by regional fisheries management organizations (RFMOs) across their transnational distributions, where they interact with multiple fishery operations. Sailfish (*Istiophorus platypterus*) occur in warm epipelagic waters of tropical and subtropical oceans globally (Nakamura 1985). Most sailfish stocks are experiencing large amounts of fishing mortality and stock statuses are uncertain due to a lack of comprehensive catch data (Pons et al. 2017). In 2022, sailfish were assessed globally as Vulnerable by the IUCN Red List, and population trends for most billfish species are either decreasing or data deficient (Collette et al. 2022). While they are targeted commercially in some regions, fishing pressure is also driven by artisanal fisheries and bycatch in commercial longline and purse-seine fisheries (Pons et al. 2017).

Strong larval dispersal potential and adult movement ability in pelagic fishes, combined with few physical barriers in the open ocean, result in substantial gene flow between populations that weakens population differentiation (Waples 1998). Indeed, molecular techniques have provided strong evidence for a single circumglobal species of sailfish (Graves and McDowell 1995, Ferrette et al. 2023), where they were previously considered separate in the Atlantic (*I. albicans*) and Indo-Pacific (*I. platypterus*) (Nakamura 1983). Several studies suggest population structure in sailfish both among and within different ocean basins, including evidence for distinct

Table 1. Sailfish genetic material source locations by region with sample numbers (*n*), date range, and codes for each location.

Region	Code	Sampling location	Date range	*n*
Western Atlantic Ocean (WAO)	A1	Brazil (Espirito Santo & Cabo Frio)	2015–2017	49
	A2	Venezuela	2015–2017	30
	A3	Miami, Florida, USA	2015–2017	34
Eastern Atlantic Ocean (EAO)	A4	Liberia	2015–2017	30
	A5	Ivory Coast	2015–2017	30
	A6	Senegal	2015–2017	30
Western Indian Ocean (WIO)	I1	Kenya (Kilifi Central)	2020–2021	42
	I2	Mozambique (Pemba & Beira Sofala)	2020–2021	23
	I3	Somalia (Bosaso, Berbera & Mogadishu)	2020–2021	17
	I4	Tanzania (Nungwi)	2020–2021	40
Eastern Indian Ocean (EIO)	I5	Western Australia (Broome, Exmouth, Dampier)	2015–2022	50
Western Pacific Ocean (WPO)		Coral sea, Australia:		
	P1	North Queensland (Townsville &	2013–2022	17
	P2	Whitsundays)	2021–2022	16
		Southern Queensland (Sunshine Coast)		
	P3	Northern Australia (Darwin & Gulf of Carpentaria)	2013–2021	72
	P4	Nha Trang, Vietnam	2015	13
	P5	Kuala Rompin, Malaysia	2022	6
	P6	Lae & Madang, Papua New Guinea	2022	4
	P7	Philippine Sea, Taiwan	2017	50
	P8	New Caledonia, Fiji, Marshall Islands (SPC samples)	2001–2017	7
Eastern Pacific Ocean (EPO)	P9	Cabo San Lucas, Baja California, Mexico	2012–2014	30

mtDNA clades between the Atlantic and Indo-Pacific, and heterogeneity within the Indo-Pacific (Graves and McDowell 2003, Lu et al. 2014, Ferrette et al. 2021). Our current understanding of the global population structure of sailfish remains limited due to challenges of sampling across their vast range and the small number of molecular markers used in earlier studies (Graves and McDowell 2015, Ferrette et al. 2021). Previous studies have focused on the west Atlantic and east Pacific, which leaves unresolved questions about structure within the Indo-Pacific (McDowell 2002, Rubio-Castro et al. 2015, Ferrette et al. 2021). Heterogeneity between the east and west Pacific, as well as population structure across the west Pacific and Indian Oceans remains unclear (McDowell 2002, Lu et al. 2014, Graves and McDowell 2015).

Population structure in marine pelagic species can be driven by reproductive or feeding behaviour, as well as physical or physiological impediments to dispersal (Rocha et al. 2007, Hirschfeld et al. 2021). Some barriers, such as strong gradients in temperature or currents, may readily fluctuate over short timescales, whereas physical barriers such as land bridges may influence connectivity over multi-millennial timescales (Rocha et al. 2007, Hirschfeld et al. 2021). Different molecular markers will detect the influence of these barriers at different scales (Hirschfeld et al. 2021). Therefore, further research using next-generation sequencing and a broader sampling strategy are necessary to re-evaluate global sailfish population structure to enable their effective management (Ferrette et al. 2021). Here, we used a novel dataset of SNPs in sailfish from across their circumtropical range to investigate contemporary population structure and connectivity. First, we assessed connectivity between the global ocean basins across known biogeographic barriers to dispersal. Second, we determined whether population structure was present between and within the Indo-Pacific and Atlantic oceans.

Methods

Sample collection and genotyping

Samples were collected from either caught-and-released sailfish as fin clips, or as muscle from landed sailfish from 2001 to 2022 (Table 1). DNA was extracted from 188 samples using either a DNeasy Blood and Tissue DNA extraction kit (Qiagen), or a salting out protocol (Sunnucks and Hales 1996). Diversity Arrays Technology Pty Ltd (DArT) carried out DNA extractions for 407 samples. Genotyping was conducted using the DArTseq genome complexity reduction method for medium density sequencing (Kilian et al. 2012). Each plate contained individuals from at least two ocean basins and a replicate individual to avoid ascertainment bias during genotyping. Digestion of DNA was undertaken using restriction enzymes *Pst*I (recognition sequence 5′-CTGCA|G-3′) and *Sph*I (5′-GCATG|C-3′), followed by adapter ligation and amplification of small adapter-ligated fragments (Kilian et al. 2012). A proprietary analytical pipeline was applied by DArT to produce a SNP dataset (Kilian et al. 2012).

Quality filtering and data subsets

All visualization, manipulation, and analyses of the data were conducted in R 4.4.1 (R Core Team 2024). Genotyping errors were checked using *radiator* by assessing individual heterozygosity and the presence of duplicate genotypes (Gosselin 2023). Quality SNP filtering was applied to the global dataset as well as to two geographical subsets: the Atlantic

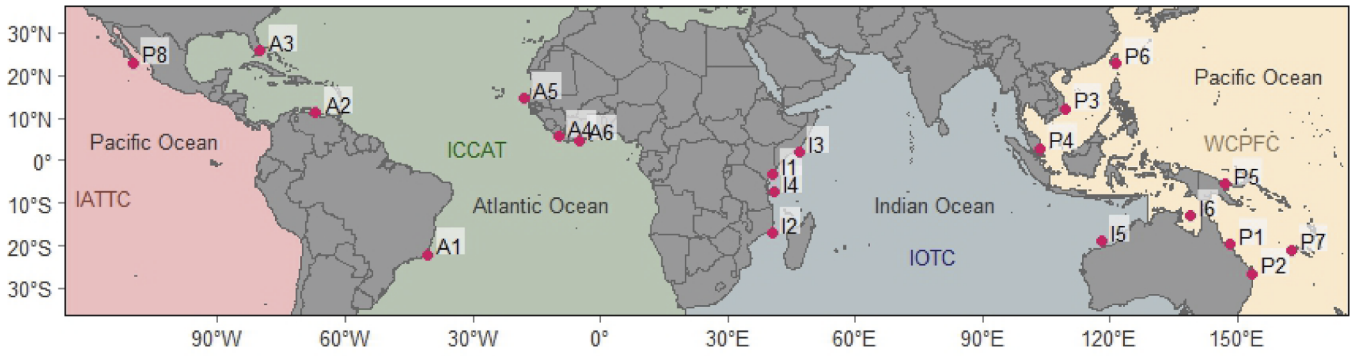

Figure 1. Global map of sampling locations with location codes as per Table 1. Jurisdictions of regional fisheries management organizations are included: Inter-American Tropical Tuna Commission (IATTC), International Commission for the Conservation of Atlantic Tunas (ICCAT), Indian Ocean Tuna Commission (IOTC), and Western and Central Pacific Fisheries Commission (WCPFC).

(AO) and Indo-Pacific (IPO). This stratification was based on previous molecular studies that showed clear genetic differentiation between these areas (Graves and McDowell 2003, Ferrette et al. 2021). Filtering of SNPs was performed using *dartRverse* 1.0.2 (Gruber et al. 2018, Mijangos et al. 2022). Details on the order of steps and thresholds applied in the filtering process are provided in Table S1. In addition, putatively neutral datasets were generated by identifying and removing loci putatively under selection to avoid violating the assumptions of neutrality (Whitlock and Lotterhos 2015). Two genome scan methods were implemented using *OutFLANK* 0.2 and *pcadapt* 4.3.5 with a *q*-value threshold of 0.05 (Whitlock and Lotterhos 2015, Privé et al. 2020). Datasets with a subset of large-F_{ST} loci were employed to increase discriminatory power with low levels of population differentiation to distinguish patterns within ocean basins (Jansson et al. 2023). The 300 loci with the largest F_{ST} values in *OutFLANK* were subset for global, IPO, and AO individuals (Whitlock and Lotterhos 2015). In total, nine datasets were produced, which included applying three filtering approaches to each set of the global, IPO and AO samples: (i) full-loci dataset, (ii) putatively neutral loci, and (iii) large-F_{ST} loci. Missing data were imputed using nearest-neighbour prior to further analyses.

Genetic diversity and differentiation

Sampling locations were grouped into larger geographic regions to provide insights into broad patterns of genetic variation and to ensure sufficient sample sizes. Regions were based on stock boundaries defined by RFMOs and include the west Atlantic Ocean (WAO), east Atlantic Ocean (EAO), west Indian Ocean (WIO), east Indian Ocean (EIO), west Pacific Ocean (WPO), and east Pacific Ocean (EPO) (Table 1, Fig. 1). Population diversities were estimated from the full-loci dataset for each region and sampling location using *dartRverse* with 1000 bootstraps (Nei 1978). A hierarchical analysis of molecular variance estimated variance among and within each genetic population, ocean basin and individual using the global full-loci dataset with 1000 permutations in *poppr* 2.9.6 (Kamvar et al. 2014). Statistical significance for the molecular variance components was calculated using 999 permutations in *ade4* 1.7–22 (Dray and Dufour 2007). Pairwise F_{ST} and statistical significance values between sampling locations and between regions were calculated from global full-loci and large-F_{ST} loci datasets with 1000 bootstrap intervals using *StAMPP* 1.6.3 (Weir and Cockerham 1984, Pembleton et al. 2013). Partial mean migration rates within and between AO, EPO, and Indo-West Pacific (IWP) were estimated using the full-loci dataset with a modified version of *BayesAss* 3.0.4 (Wilson and Rannala 2003). BA3-SNPS-autotune allows handling of large SNP datasets and was used with default settings for 1 million generations with 10% burn-in and a sampling interval of 100 (Mussman et al. 2019).

Population clustering analyses

Principal Coordinates Analyses (PCoAs) were performed on a Euclidean distance matrix of allele frequencies between individuals in *dartRverse* (Legendre and Legendre 1998). PCoAs were performed using both full-loci and large-F_{ST} loci on the global dataset, and then on AO and IPO subsets to differentiate clusters within ocean basins. Admixture analyses were performed with sparse non-negative matrix factorization (SNMF) in *LEA* 3.16.0 (Frichot and François 2015). The SNMF analyses assign individuals to ancestral populations (K) without *a priori* geographical information. Individual admixture coefficients and allele frequencies for $K = 1$–20 were estimated by SNMF using 10 repetitions for each K and 200 iterations, and entropy criteria were estimated using cross-validation to evaluate the quality of fit (Frichot and François 2015). Ancestry matrices of the runs with the smallest cross-entropy were visualized with *pophelper* 2.3.1 (Francis 2017). SNMF analyses were also performed using both full-loci and large-F_{ST} loci for each of the global dataset and AO and IPO subsets.

Results

SNP genotyping and filtering

Sampling included 590 individuals at 20 locations across the pantropical range of the sailfish that can be grouped into six regions across the three ocean basins (Table 1, Fig. 1). DArT-seq genotyping produced 33 871 SNPs from 567 sailfish. After quality filtering, the global dataset included 500 individuals with 8069 SNPs. The IPO dataset included 328 individuals and 7268 neutral loci, and the AO dataset included 174 individuals and 7838 neutral loci. Genome scans identified few outliers, which were unlikely to truly represent adaptive loci. Therefore, the full-loci dataset was used in subsequent analy-

Table 2. Diversity estimates for each region using the global full-loci dataset including number of individuals (n), observed heterozygosity (H_O) and expected heterozygosity (H_E) with standard error in parentheses, inbreeding coefficient (F_{IS}), and F_{IS} confidence interval (CI).

Region	n	H_O	H_E	F_{IS}	F_{IS} CI
WAO	87	0.095 (±0.002)	0.102 (±0.002)	0.059	0.050–0.062
EAO	84	0.093 (±0.002)	0.100 (±0.002)	0.060	0.053–0.060
WIO	96	0.087 (±0.002)	0.093 (±0.002)	0.050	0.039–0.053
EIO	105	0.089 (±0.002)	0.092 (±0.002)	0.042	0.029–0.033
WPO	110	0.091 (±0.002)	0.094 (±0.002)	0.039	0.033–0.044
EPO	18	0.081 (±0.002)	0.087 (±0.002)	0.077	0.052–0.057
AO	171	0.094 (±0.002)	0.101 (±0.002)	0.060	0.055–0.064
IWP	311	0.089 (±0.002)	0.094 (±0.002)	0.044	0.040–0.049

Table 3. Hierarchical analysis of molecular variance for the full-loci dataset showing variations across oceans, populations (IWP, AO, and EPO), and individuals.

	df	Sum sq.	Variance components (σ)	Percent variation	P	Phi (Φ)
Between oceans	2	11 176	0.343	0.084	0.346	0.001
Between populations within oceans	1	1440	16.603	4.088	0.001	0.041
Between individuals within populations	496	204 788	23.689	5.833	0.001	0.061
Within individuals	500	182 751	365.501	89.995	0.001	0.100
Total	999	400 155	406.136	100.000		

ses. An overview of each filtering step and its influence on the number of loci and individuals in each dataset is provided in Table S1.

Broad-scale trends

Genetic diversity and variation

Genetic diversity varied little among regions [observed heterozygosity (H_O) 0.081–0.095 and expected heterozygosity (H_E) 0.087–0.102] (Table 2). All regions had small inbreeding coefficients (F_{IS} = 0.039–0.077) (Table 2). The smallest H_O and H_E and the largest F_{IS} were found in the EPO region, represented by a single location (Mexico) and a smaller sample size (Table 2). Genetic variation between ocean basins was reduced (0.08%), and 4.1% was attributed to populations within ocean basins (Table 3). Most variation was within individuals (90.0%), compared to 5.8% variation between individuals within populations (Table 3).

Genetic differentiation and migration analyses among ocean basins

Pairwise F_{ST} between regions were relatively small in the full-loci dataset ($F_{ST} \leq 0.08$) but were larger in the large-F_{ST} loci dataset ($F_{ST} \leq 0.268$) (Fig. 2). Both datasets had significant differentiation in pairwise F_{ST} between AO and EPO, AO and IWP, and IWP and EPO (Fig. 2). Pairwise F_{ST} were larger between EPO and AO than between EPO and IWP (Fig. 2). Pairwise F_{ST} between sampling locations (Fig. 3) reflected the broad patterns seen between regions (Fig. 2). Mexico (EPO) differed significantly from all other locations and all locations in the Indo-West Pacific also differed significantly from all Atlantic locations (Fig. 3). Inferred migration rates were small between AO, IWP and EPO (Table 4). As such, each population consisted mostly of residents (68.3%–99.6%) (Table 4). The IWP to EPO had greater migration (30.2%), compared to all other directions (0.2%–1.6%) (Table 4).

Population clustering among ocean basins

The PCoA separated global sailfish into three main clusters: IWP, AO, and EPO (Fig. 4). The first two PCoA axes explained 5.7% of genetic variation in the full-loci dataset (Fig. 4a); however, the PCoA using large-F_{ST} loci increased the explained variation to 26.9% (Fig. 4b). Ancestry matrices from SNMF analyses also separated sailfish in IPO from AO (Fig. 5). Separation of individuals in EPO from IWP was resolved at $K = 4$ for the global datasets (Figs 5a, 5b). Minimum cross-entropy for the full-loci dataset suggested an optimum of $K = 5$ and $K = 2$–4 for the large-F_{ST} loci (Fig. S2).

Patterns within ocean basins

Genetic differentiation within ocean basins

Pairwise F_{ST} between sampling locations revealed finer-scale patterns within ocean basins. In most cases, trends within the full-loci dataset were reflected in the large-F_{ST} loci (Fig. 3). Within AO, very small yet significant differences ($F_{ST} \leq 0.01$) appeared between several locations in both datasets (Fig. 3). Brazil (WAO) was significantly different from all other AO locations, and Venezuela (WAO) had significant differences with Liberia and Ivory Coast (EAO) (Fig. 3). There were no significant differences within EAO locations (Fig. 3). Small differences were observed between locations within the Indo-West Pacific in both full-loci ($F_{ST} \leq 0.01$) (Fig. 3a) and large-F_{ST} loci ($F_{ST} \leq 0.04$) datasets (Fig. 3b). However, these differences were not always consistent between datasets (Fig. 3). For example, Somalia (WIO) had significant pairwise F_{ST} with most IWP locations in the full-loci dataset (Fig. 3a), which are not fully reflected in large-F_{ST} loci (Fig. 3b). The full-loci dataset also showed small differences between Mozambique (WIO) and WPO locations in south Queensland, Papua New Guinea, and Malaysia (Fig. 3a); however, these differences were not significant in the large-F_{ST} loci (Fig. 3b).

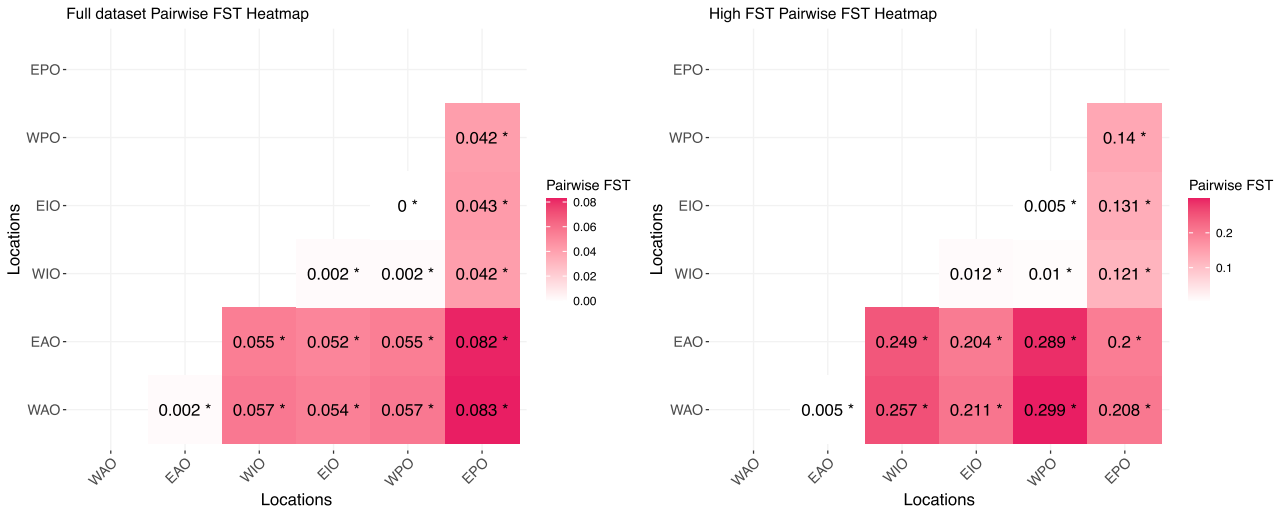

Figure 2. Heatmap matrix plot of pairwise F_{ST} between regions for (a) full-loci dataset and (b) large-F_{ST} loci dataset with region acronyms as defined in Table 1. Asterisks denote $P < 0.01$.

Population clustering within ocean basins

Individuals within the IPO subset clustered into EPO and IWP, which represented most of the variation in PCoA axes for the full-loci dataset (1.9%) and large-F_{ST} loci (11.1%) (Fig. 4d). Large-F_{ST} loci showed a slight spread of WIO individuals compared to EIO and WPO sailfish in the cluster (Figs 4d, S3). In contrast, IWP sailfish were more tightly clustered in the full-loci dataset, aside from several sailfish from Somalia (WIO) (Figs 4a, S3). There was no overlap of 90% of individuals in EAO and WAO for the AO subset of large-F_{ST} loci, with 7.8% explained variation (Fig. 4f). However, the full-loci dataset showed more clustering and had 2.4% variation explained by PCoA axes (Fig. 4e).

Ancestry matrices for the IPO subset clearly delineated EPO in both datasets, and indicated substantial shared ancestry between EIO, WIO, and WPO (Fig. 5c, d). Large-F_{ST} loci in the AO subset suggested ancestral differences between sailfish in WAO and EAO at $K = 2$ (Fig. 5f). However, this was not reflected in the full-loci dataset (Fig. 5e). Differences within AO were noticeable in samples from Brazil (A1) across most datasets (Fig. 5).

Discussion

Key findings

Our comprehensive assessment of population structure for sailfish revealed genetic connectivity throughout the IWP, based on novel high-throughput SNPs sampled across their global distribution. This connectivity suggests long-distance dispersal despite the absence of comparable movement patterns in tagging or fisheries data. AO, IWP, and EPO populations were genetically distinct. However, large-F_{ST} loci indicated reduced gene flow between the EAO and WAO, and between the WIO and the rest of the IWP. Nevertheless, the observed differentiation was insufficient to justify considering the EAO and WAO or the WIO as separate populations with different demographic histories at an evolutionary timescale. Heterozygosity was consistent with the average genome-wide heterozygosity found previously in sailfish and other billfish (Ferrette et al. 2023). Our findings highlight a need to revise boundaries for sailfish stocks managed by RFMOs.

Eastern Pacific sailfish are a discrete population

The strongest signal in our results was the differentiation between EPO and AO sailfish, consistent with the suggestion of Ferrette et al. (2021) that gene flow between Pacific and AO populations ceased ~6 million years ago. Dispersal of tropical marine species between the WAO and EPO has been largely prevented since the formation of the Isthmus of Panama at least 3 million years ago (O'Dea et al. 2016), although separation may have begun earlier during the gradual closure of the seaway and resulting oceanographic changes (Bacon et al. 2015). Our findings show EPO sailfish are genetically distinct from those in the IWP, which is supported by studies of mtDNA and nuclear microsatellites (McDowell 2002, Lu et al. 2014, Ferrette et al. 2021). Several studies of other billfishes have also found a distinct EPO population from the rest of the Pacific, including for striped marlin and swordfish (Lu et al. 2016, Mamoozadeh et al. 2019). Evidence for reduced gene flow and support for discrete stocks between the east and west Pacific has also been found using SNPs for skipjack, yellowfin, and bigeye tunas (Grewe et al. 2015, Barth et al. 2017, Grewe et al. 2019).

Although sailfish are capable of long-distance movements, no direct evidence from either tagging or fisheries data indicates crossings of ocean basins (Nakamura 1985, Braun et al. 2015, Lam et al. 2016). Sailfish associate with productive coastal waters on continental shelves rather than the open ocean (Ortiz et al. 2003, Lam et al. 2016). The east and west Pacific are not separated by a land barrier; however, the Pacific is the world's largest ocean, and the East Pacific Barrier is a well-known biogeographic break (Briggs and Bowen 2012). This barrier represents 5000–8000 km of deep water between the central Pacific islands and the continental shelf of the eastern tropical Pacific. Although the EPO population in our study was represented only by sailfish off Mexico, low levels of genetic differentiation have previously been found across several locations in the EPO (Rubio-Castro et al. 2015, Ferrette et al. 2021).

The Benguela Current is a barrier to dispersal

Separation of sailfish between the Indian and Atlantic oceans is evident in this study, which is well-supported by previous

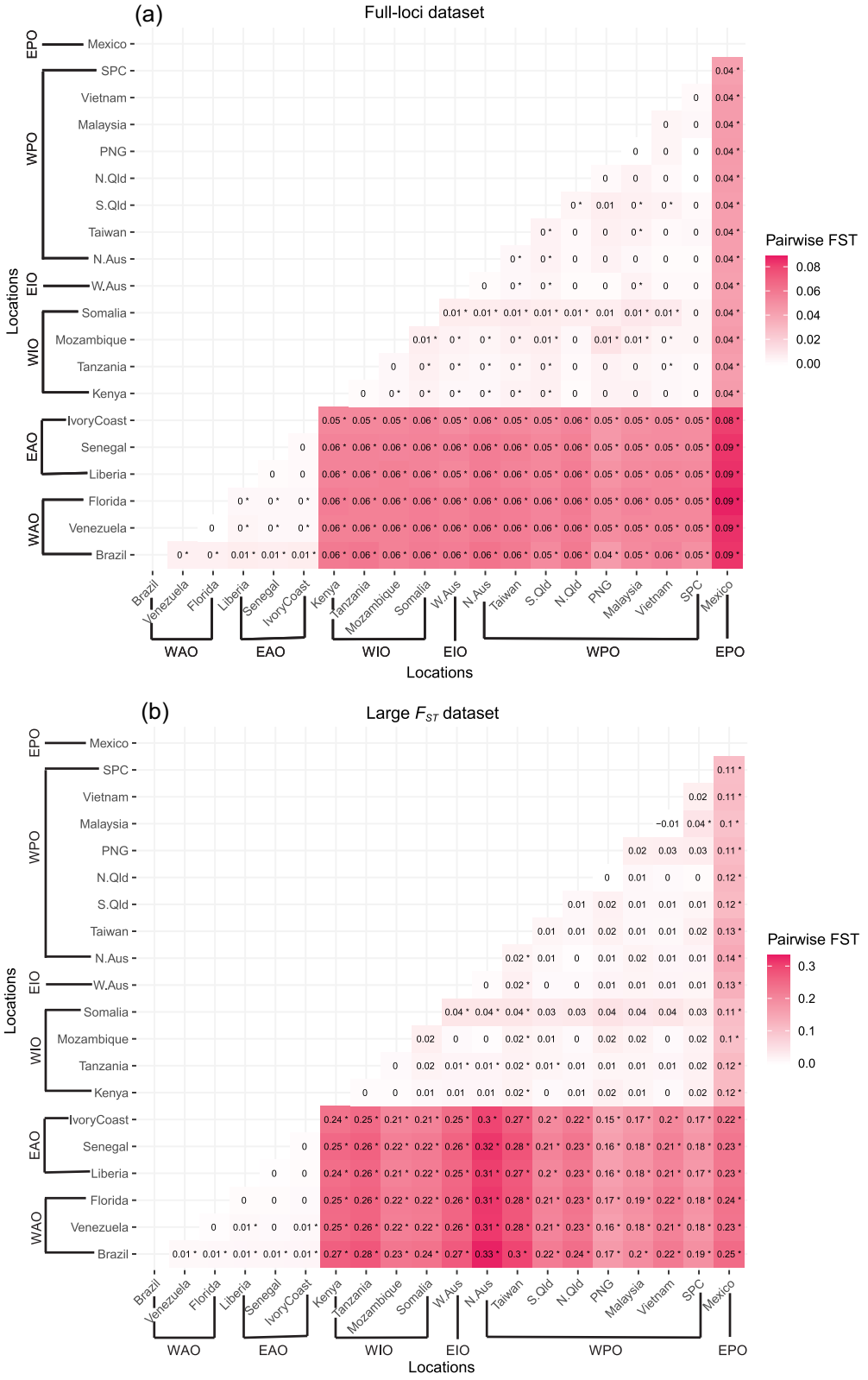

Figure 3. Heatmap matrix plot of pairwise F_{ST} between all sampling locations for (a) full-loci dataset and (b) large-F_{ST} loci with region acronyms as in Table 1. Asterisks denote $P < 0.01$.

molecular studies (e.g. McDowell 2002, Ferrette et al. 2023). Yellowfin, albacore, and bigeye tunas have similar circumtropical distributions to sailfish, and SNP analyses have also shown a clear separation between AO and IPO populations (Barth et al. 2017, Mullins et al. 2018, Weist et al. 2024). Africa is considered a barrier to movement for tropical marine species between the Indian and Atlantic oceans, due the strong and cold Benguela Current off the southwest coast of

Table 4. Estimated posterior mean migration rates between and within populations with standard deviation in parentheses.

		Source population		
		AO	IWP	EPO
Sink population	AO	0.9960 (±0.0027)	0.0019 (±0.0019)	0.0019 (±0.0019)
	IWP	0.002 (±0.0015)	0.9950 (±0.0023)	0.0033 (±0.0019)
	EPO	0.0159 (±0.0153)	0.3020 (±0.0210)	0.6830 (±0.0153)

Shaded values represent the proportion of individuals (or alleles) that originated from within the same population. Unshaded values represent the proportion of individuals in a sink population that originated from a particular source population.

Africa. Sailfish are restricted to warm waters with a preference for >22°C and are therefore unlikely to cross the Benguela Current (Braun et al. 2015, Lam et al. 2016). However, one study has suggested that sailfish may occasionally move from WIO to the EAO (Ferrette et al. 2021), which has also been proposed for yellowfin tuna (Barth et al. 2017, Mullins et al. 2018). Longline fisheries records show that black marlin have occurred in the Cape of Good Hope area and occasionally migrated into the AO, which is outside of their IPO range (Penrith and Cram 1972). Rare vagrants may cross from the WIO when warm-core eddies are shed into the AO by the Agulhas Current (Penrith and Cram 1972, Nakamura 1983).

Genetic connectivity across the Indo-West Pacific

While EPO was identified as a separate population from WPO, our study provides evidence for gene flow across the IWP. Despite the geographic spread of sampling spanning the east coast of Africa to Taiwan, our findings indicated genetic connectivity was maintained within this region. This connectivity reinforces findings from prior genomic analyses of high-coverage SNPs, but fewer samples and locations (Ferrette et al. 2023). Adult sailfish can disperse widely and spawn extensively across regions (Nakamura 1985, Graves and McDowell 2015), which may have maintained gene flow of sailfish across the IWP.

Gene flow across the WPO and Indian oceans has been suggested for several tunas and billfishes (Graves and McDowell 2015, Moore et al. 2020). A lack of stock structure within the IPO has been noted for blue marlin, which are larger and more migratory than sailfish (Graves and McDowell 2015, Williams et al. 2020). Analysis of SNPs in yellowfin and bigeye tunas did not show genetic separation between the Indian and Pacific Oceans (Barth et al. 2017, Weist et al. 2024). An IPO study of SNPs in striped marlin concluded that fish from WPO and EIO belonged to the same population, although some genetic differentiation was found between the EIO and WIO (Mamoozadeh et al. 2019). Finer-scale structure was reported for black marlin, with SNPs identifying three discrete populations within IWP, which was suggested to be driven by reproductive philopatry (Williams et al. 2015). A lack of population structure in sailfish in this region is surprising given tagging studies have reported more restricted movements in sailfish compared to other species of billfishes and tunas (Ortiz et al. 2003, Braun et al. 2015).

Site fidelity has been proposed for both sailfish and black marlin (Ortiz et al. 2003). However, this behaviour in sailfish may result from seasonal migrations into coastal subtropical waters to feed rather than from spawning-site fidelity and reproductive philopatry as in black marlin (Williams et al. 2015). Unlike black marlin, sailfish form feeding aggregations and hunt cooperatively for teleosts and squid (Herbert-Read et al. 2016). We suggest that black marlin have more defined spawning grounds and timing compared to sailfish (Domeier and Speare 2012). Sailfish are thought to spawn throughout the year in equatorial waters, and during summer months in the subtropics (Nakamura 1983, Buenafe et al. 2022). If sailfish spawning is linked to favourable environmental conditions rather than defined spawning grounds, then this may increase gene flow. Long-distance dispersal of both larval and adult sailfish in the IWP may be facilitated by currents, such as the Kuroshio Current, where sailfish have been known to spawn (Nakamura 1983).

The warm waters of the Indonesian Throughflow Current might aid dispersal of sailfish from WPO into EIO. Biogeographic barriers for marine species between WPO and Indian oceans are at smaller scales and more permeable than those between AO and IPO (Briggs and Bowen 2012, Hirschfeld et al. 2021). Gene flow in the region may have been reduced when Pleistocene glaciations led to cooler waters, and the Sunda and Sahul shelves formed land bridges among Indonesian islands and Australia and Papua New Guinea (Voris 2000). Sailfish may have continued intermixing between WPO and EIO during interglacial periods of the Pleistocene given that shallow waters do not appear to be a barrier to sailfish dispersal, as they are regularly found in shallow gulfs, such as the Gulf of Carpentaria and Arabian Gulf (Hoolihan et al. 2004). After the Pleistocene, sailfish populations across IWP expanded and established secondary contact (Ferrette et al. 2021).

Support for reduced gene flow across ocean basins

In sailfish, geographic separation across basins of the Indian Ocean and AO may have resulted in reduced dispersal, but not enough separation to result in distinct populations. The distances across these ocean basins are shorter compared to distances across the Pacific. Previous molecular studies and results from full-loci analyses in our study do not provide support for multiple populations of AO sailfish (McDowell 2002, Ferrette et al. 2021, Ferrette et al. 2023). However, we found subtle genetic differentiation in large-F_{ST} loci between the EAO and WAO, where sailfish off Brazil showed the greatest differences in both pairwise F_{ST} and ancestry matrices with EAO sailfish. Similar analyses of large-F_{ST} SNPs in yellowfin tuna also showed differentiation between the EAO and WAO, despite a lack of structure in neutral loci analyses (Pecoraro et al. 2018). The expanse of deep water known as the mid-Atlantic barrier could contribute to reduced gene flow between the east and west (Briggs and Bowen 2012, Hirschfeld et al. 2021).

Previous studies have not identified genetic structure for sailfish within the Indian Ocean, except for the Arabian Gulf, which is a semi-enclosed basin with limited mixing with the broader WIO (McDowell 2002, Hoolihan et al. 2004, Fer-

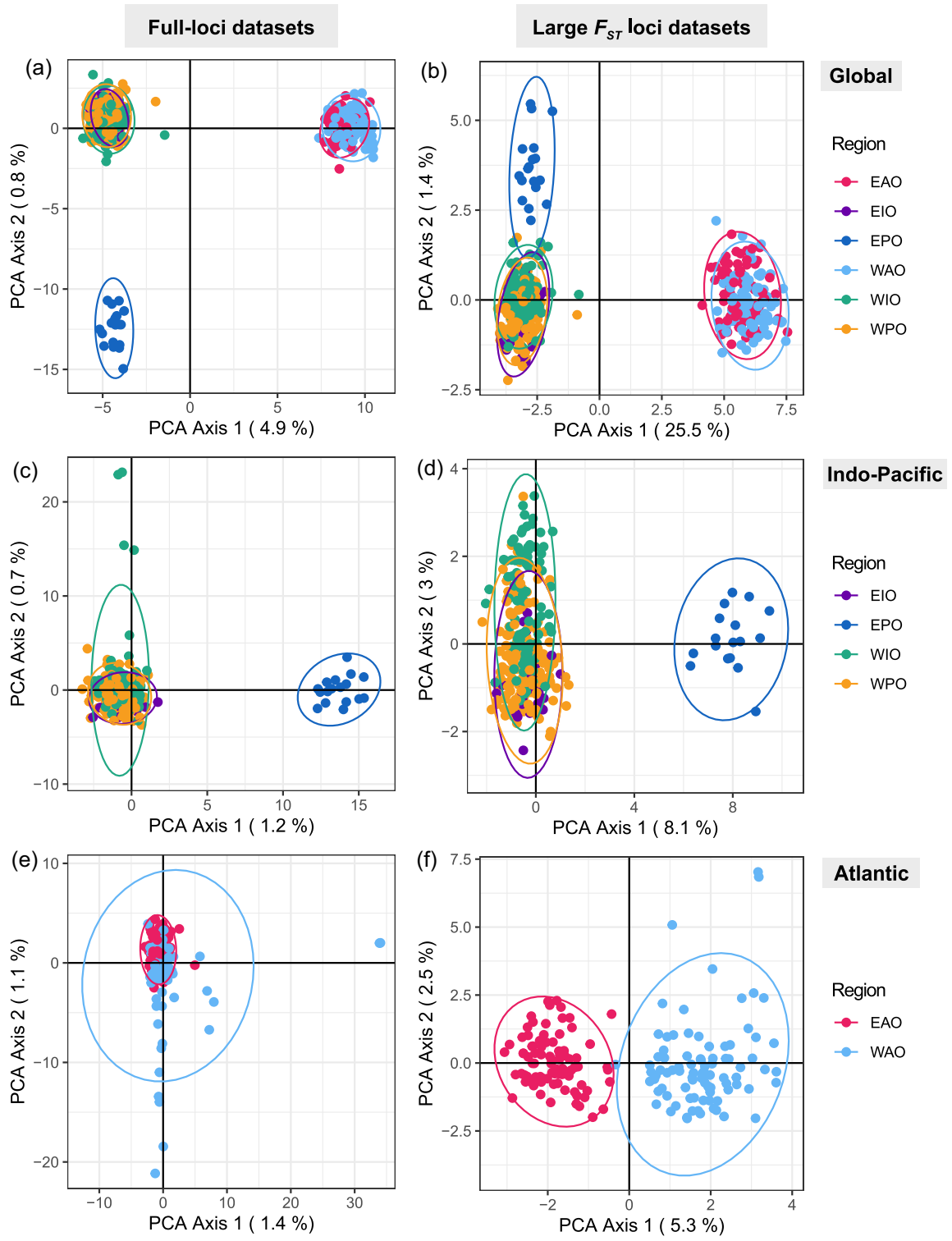

Figure 4. Principal coordinates analysis (PCoA) plots with ellipsoid encompassing 90% of individuals. Datasets are compared for global (a) full-loci dataset and (b) large-F_{ST} loci, Indo-Pacific (c) full-loci dataset and (d) large-F_{ST} loci, and Atlantic (e) full-loci dataset and (f) large-F_{ST} loci. Individuals are coloured by region as in Table 1.

rette et al. 2021). However, these studies used fewer molecular markers and had geographically limited sampling within the Indian Ocean. Suitable habitats for sailfish span the northern Indian Ocean off Sri Lanka, the Maldives, and the Seychelles and may facilitate dispersal of occasional migrants across this ocean basin. Minor genetic differences between the WIO and the rest of the IWP arose in our findings based on large-F_{ST} loci that were not evident in the full-loci dataset. Regional selective pressures, such as environmental heterogeneity, may contribute to genetic differences in marine fishes at ecological scales (Klein et al. 2024). Genetic differences have been found using putatively adaptive SNPs in both

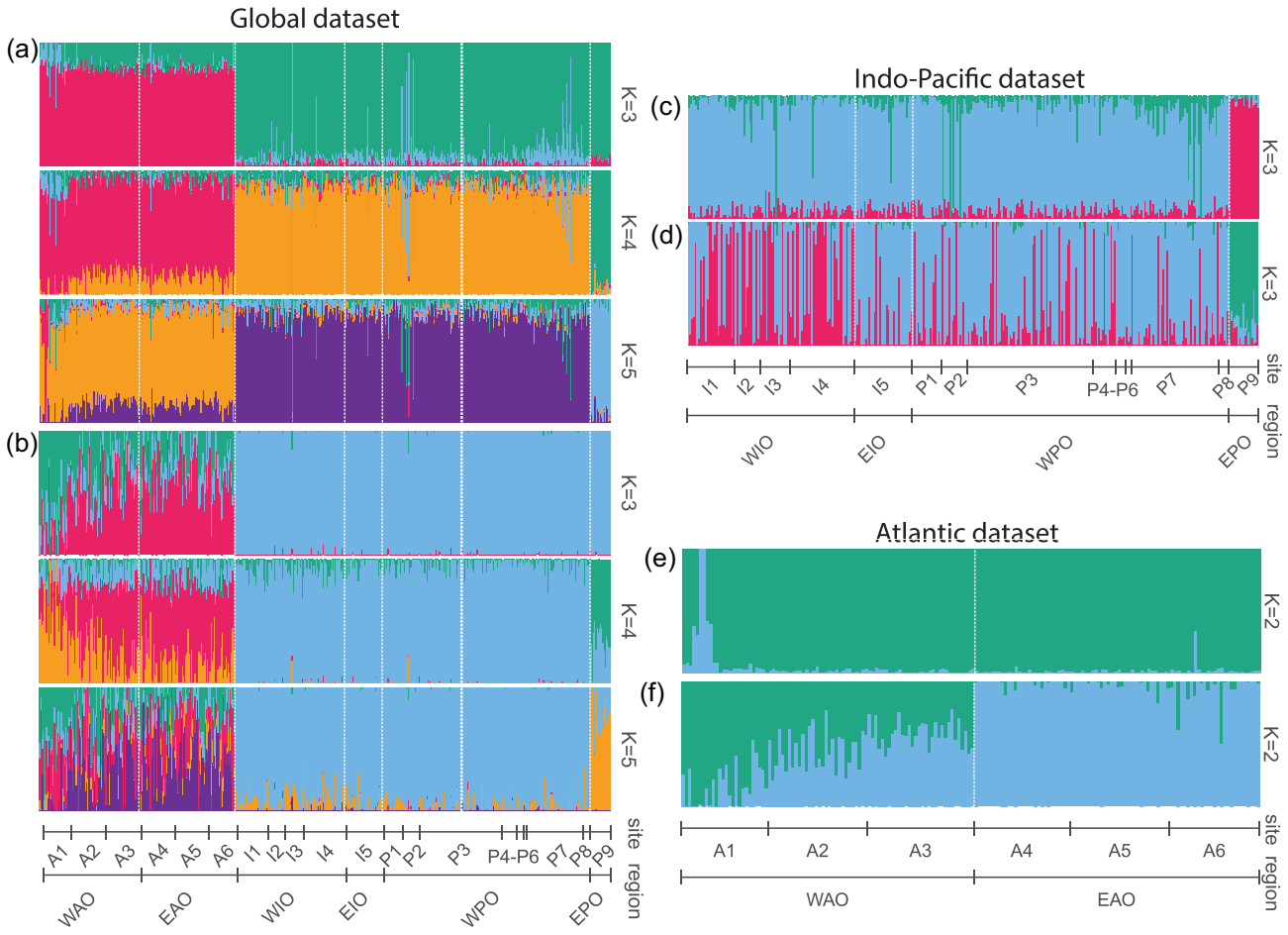

Figure 5. Ancestry matrices of global dataset with $K = 3$–5 for the (a) full-loci dataset and (b) large-F_{ST} loci, the Indo-Pacific dataset for (c) full-loci dataset and (d) large-F_{ST} loci dataset with $K = 3$, and the Atlantic dataset for (e) full-loci dataset and (f) large-F_{ST} loci dataset with $K = 2$. Region acronyms and location codes as per Table 1.

striped marlin within the Indian Ocean (Mamoozadeh et al. 2019), and yellowfin tuna within the Pacific (Grewe et al. 2015).

Conclusion and implications for management

Our study provides the most thorough genomic assessment of sailfish population structure to-date with increased representation of IPO samples. The implications of this study are important for organizations that manage recreational, artisanal and commercial fisheries around the world. We have reviewed the alignment of genetic populations with operational fisheries management stocks given continued global fishing pressure on sailfish. We suggest that RFMOs in the Pacific and Indian oceans should work together to ensure consistency in the management of sailfish across the IWP as they are a single genetic population. Although long-distance dispersal will counter the effects of genetic drift and loss of genetic diversity, overharvesting of seasonal aggregations of sailfish in one region can affect geographically distant but connected areas if they are part of the same population.

We suggest that sailfish should continue to be managed as a separate stock in EPO, given they are genetically distinct from the rest of the Pacific. Reduced genetic diversity within this region and its geographic isolation may make these sailfish more vulnerable to climate change, such as the predicted increase in oxygen minimum zones (Rubio-Castro et al. 2015, Logan et al. 2022). Populations in the EAO and WAO are currently managed as separate stocks. Our findings suggest that reduced dispersal between EAO and WAO sailfish populations may be at recent ecological timescales. However, this pattern is not reflected at evolutionary timescales, as shown in our full-loci results and in studies of mtDNA, microsatellites, and whole-genome sequencing (McDowell 2002, Ferrette et al. 2021, 2023). We suggest that AO sailfish could be managed as east and west stocks that are recognized as genetically connected.

In summary, results from this study provided evidence for connectivity across the IWP and a discrete EPO population. We confirmed strong genetic differentiation between AO and IPO with an indication of reduced gene flow between EAO and WAO. We anticipate that our study will inform the delineation of biologically meaningful sailfish stocks in fisheries management.

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Author contributions

Laura Marion Smith (Conceptualization [lead], Data curation [lead], Formal Analysis [lead], Funding acquisition [lead], Investigation [lead], Methodology [lead], Data curation [lead], Formal Analysis [lead], Project administration [lead], Resources [lead], Validation [lead], Visualization [lead], Writing – original draft [lead], Writing – review & editing [lead]), Samuel Williams (Conceptualization [equal], Formal Analysis [supporting], Funding acquisition [equal], Investigation [supporting], Methodology [supporting], Resources [supporting], Supervision [equal], Writing – review & editing [equal]), Bruno Ferrette (Methodology [supporting], Resources [supporting], Writing – review & editing [supporting]), Bonnie J. Holmes (Conceptualization [supporting], Supervision [supporting], Writing – review & editing [supporting]), Nelly Isigi Kadagi (Funding acquisition [supporting], Resources [supporting], Writing – review & editing [supporting]), Ching-Ping Lu (Resources [supporting], Writing – review & editing [supporting]), Sofia Ortega-Garcia (Resources [supporting], Writing – review & editing [supporting]), Julian Pepperell (Conceptualization [supporting], Funding acquisition [equal], Supervision [equal], Writing – review & editing [supporting]), Ian R Tibbetts (Conceptualization [supporting], Funding acquisition [supporting], Investigation [supporting], Project administration [supporting], Supervision [equal], Writing – review & editing [supporting]), Nina Wambiji (Funding acquisition [supporting], Resources [supporting], Writing – review & editing [supporting]), Sammy Wambua (Resources [supporting], Writing – review & editing [supporting]), Christine Dudgeon (Conceptualization [equal], Data curation [supporting], Formal Analysis [supporting], Investigation [supporting], Methodology [supporting], Resources [supporting], Supervision [equal], Writing – review & editing [equal]).

Supplementary data

Supplementary material is available at the *ICES Journal of Marine Science* online.

Conflict of interest: The authors have no conflicts of interest to declare.

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Data availability

SNP data used in this study is available on the University of Queensland eSpace (https://doi.org/10.48610/c1ba0c1). Raw data and code will be shared upon reasonable request to the corresponding author.

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