Working paper for
Indian Ocean Tuna Commission
16th Working Party on Billfish
September 4–8, 2018
Cape Town, South Africa

Genetic population structure of striped marlin (*Kajikia audax*) in the Indian Ocean, with relationship to Pacific Ocean populations

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EXECUTIVE SUMMARY

Striped marlin (*Kajikia audax*) is estimated to be heavily overfished and experiencing unsustainable levels of fishing effort in the Indian Ocean, but the development of population-specific management efforts is prohibited by a lack of information on population structure. In this study, we surveyed genetic variation across nearly 4,000 single nucleotide polymorphism (SNP) molecular markers for striped marlin sampled from the eastern and western Indian Ocean (n = 46) to provide a statistically powerful evaluation of population structure in this region. These SNPs were also surveyed across striped marlin sampled from the Pacific Ocean (n = 199) so that the relationship of Indian Ocean populations to populations in the Pacific Ocean could be assessed. We identified five genetically distinct populations, three of which corresponded with the western Indian Ocean, Oceania, and eastern central Pacific Ocean, and two of which corresponded with the North Pacific Ocean. The western Indian Ocean population displayed comparatively low genetic diversity and high genetic differentiation, suggesting a greater degree of isolation relative to other populations. The presence of a population in Oceania suggests a high level of genetic connectivity between striped marlin from the eastern Indian and western South Pacific oceans. Additionally, we found that 27.8% and 28.6% of fish sampled off Japan and Hawaii, respectively, were genetically consistent with striped marlin from Oceania, reflecting some degree of spatial connectivity among these regions. Collectively, these results provide valuable information for future assessment and management initiatives for striped marlin in the Indian Ocean, and highlight needs for additional research efforts.

BACKGROUND

Striped marlin (*Kajikia audax*) is primarily considered a non-target species of industrial fisheries throughout the Indian Ocean; however, this species is targeted in some artisanal fisheries, and is a prized target of recreational fisheries ocean-wide. A quantitative assessment of stock status for striped marlin in the Indian Ocean did not exist until 2012, when a preliminary assessment indicated that the stock was overfished and subject to overfishing. This result was confirmed in a full assessment in 2013 (IOTC WPB 2013), and the most recent assessment of stock status reported biomass at 0.24–0.62 of that required to produce maximum sustainable yield (MSY), and fishing effort at 1.32–3.04 of that necessary for MSY (IOTC WPB 2017). Given these results, the Indian Ocean Tuna Commission Working Party on Billfish identified key uncertainties challenging the management of striped marlin in the Indian Ocean, including a lack of information on stock structure. The primary purpose of the present study was to address this information gap by using a genomic approach to evaluate population structure for striped marlin throughout the species range.

Previous genetic studies of population structure for striped marlin have resolved a number of genetically distinct populations; however, these studies have been limited to the analysis of sample collections from the Pacific Ocean, and surveyed genetic variation across a small number (e.g. tens) of molecular markers (Graves and McDowell 1994, Purcell and Edmands 2011, McDowell and Graves 2008). Recent advances in molecular technology now

enable surveying thousands of molecular markers across entire genomes, regardless of the availability of prior genomic information. These methods are primarily centered on the discovery and characterization of single nucleotide polymorphisms (SNPs), single DNA basepairs that vary among individuals and provide information on population- and species-level relationships. The unprecedented level of statistical power possible in studies that survey genome-wide SNPs make such approaches a powerful tool for species conservation and management.

In the present study, we employed a genome-wide approach to address the following objectives: 1) identify the number and geographic extent of striped marlin populations in the Indian Ocean, and 2) assess the relationship of Indian Ocean populations of striped marlin to striped marlin populations in the Pacific Ocean.

METHODS

Sample collection and SNP genotyping

Tissue samples were opportunistically collected from striped marlin during the period 1992 through 2017 from locations throughout the Indian Ocean, including waters off South Africa (SAF), Kenya (KEN), and northwestern Australia (WAUS; Table 1, Figure 1). To assess the relationship of Indian Ocean striped marlin to striped marlin in the Pacific Ocean, samples were also collected from eastern Australia (EAUS), New Zealand (NZ), Japan (JAP), Taiwan (TAI), Hawaii (HAW), southern California (CAL), Baja California (BAJA), Ecuador (ECU), and Peru (PERU). DNA was extracted from tissue samples using standardized kits, and high molecular weight extractions were submitted to Diversity Arrays Technology Pty. Ltd. (DArT; Canberra, Australia) for the discovery of genome-wide SNPs using the proprietary DArTseq™ 1.0 genotyping methodology (described in Kilian et al. 2012, Sansaloni et al. 2011). SNP genotypes supplied by DArT were used for analysis in this study.

SNP filtering

SNPs underwent quality filtering using R version 3.3.1 (R Core Team 2017) and the dartR v0.93 package (Gruber et al. 2018). Samples missing ≥ 20% of genotype calls were excluded from the dataset. SNPs meeting any of the following criteria were also removed: missing ≥ 10% of genotype calls, average reproducibility < 95%, monomorphic locus, or a minor allele frequency < 0.05. In instances where more than one SNP originated from the same genomic region, only a single SNP was retained to reduce the probability of non-independently inherited markers in the dataset. Finally, loci that did not conform to the expectations of Hardy-Weinberg equilibrium (HWE) in more than one sample collection were removed.

SNPs potentially under the influence of natural selection were identified and removed prior to subsequent analyses so that non-neutral processes would not bias estimates of genetic connectivity. Putatively adaptive SNPs were identified using two distinct methods (BayeScan v2.1, Foll and Gaggiotti 2008; Arlequin v3.5, Excoffier and Lischer 2010). SNPs identified as statistically significant in both analyses were excluded from a final dataset of putatively neutral SNPs. Results based on this neutral SNP dataset are presented below; however, analyses

performed with a dataset including both neutral and putatively adaptive SNPs produced similar results (not shown).

Identification of genetically distinct populations

Samples were organized into groups representing genetically distinct populations based on results from three methods. Principal coordinate analysis (PCoA; Jombart et al. 2009) was performed using the R package adegenet v2.0.1 (Jombart 2008). The most likely number of populations (K) represented in the dataset was also inferred by testing a range of values for K in STRUCTURE v2.3.4 (Pritchard et al. 2000) and assessing results in Structure Harvester v0.6.94 (Earl and vonHoldt 2012). Finally, we performed analysis of molecular variance (AMOVA; Excoffier et al. 1992) in the program Arlequin. Because an infinite number of population structure scenarios are possible for testing with AMOVA, we used results from PCoA and STRUCTURE to assess only the most likely scenarios.

Population differentiation and diversity

After organizing samples into genetically distinct populations, the level of genetic differentiation between populations was assessed by calculating pairwise measures of F_{ST} in Arlequin. Population-level genetic diversity was also evaluated by calculating observed and expected heterozygosities in poppR v2.5.0 (Kamvar et al. 2014) and dartR, respectively, and by calculating allelic richness in PopGenReport v3.0.0 (Adamack and Gruber 2014). Finally, we used dartR to evaluate populations for the presence of private alleles.

RESULTS

SNP genotyping

The original dataset supplied by DArT contained 61,908 SNPs (Table 2). A total of 3,916 SNPs remained after quality filtering, and after removing markers that violated the expectations of HWE (n = 41) or were identified as putatively adaptive (n = 59). The final dataset comprised 245 striped marlin representing 46 fish from the Indian Ocean and 199 fish from the Pacific Ocean (Table 1).

Identification of genetically distinct populations

We employed three approaches to identify the number of genetically distinct populations represented in our dataset. Structure Harvester indicated that the most likely number of genetically distinct clusters (e.g. populations, K) represented in our dataset was five (Figure 2). These clusters corresponded with the following geographic regions and sample collections: 1) western Indian Ocean (WIO) consisting of samples from SAF and KEN, 2) Oceania consisting of samples from WAUS, EAUS, and NZ, 3) North Pacific Ocean (NPO) consisting of samples from JAP, TAI, HAW, CAL, 4) a second North Pacific Ocean population (NPO2) corresponding with a subset of fish sampled off Japan (27.8% of samples; hereafter referred to as JAP2) and Hawaii (28.6% of samples; hereafter referred to as HAW2), and 5) eastern central Pacific Ocean

(ECPO) consisting of samples from BAJA, ECU, and PERU. To improve the resolution of results for the Indian Ocean, STRUCTURE simulations were performed a second time using a smaller dataset limited to sample collections from the Indian Ocean and Oceania (Figure 3). Structure Harvester indicated that the most likely K for this dataset was three. Fish sampled from the WIO were again resolved as a distinct group in this analysis. However, the Oceania samples were resolved as two discrete groups, with samples collected off western Australia identified as separate from remaining Oceania collections (EAUS, NZ).

Results from PCoA also grouped individuals into multiple distinct clusters reflecting regional sampling location (Figure 4). PCoA axes one and two collectively explained 5.1% of total genetic variation. The clusters resolved on these axes corresponded with the five genetically distinct clusters inferred from STRUCTURE. Striped marlin sampled off WAUS were positioned relatively intermediate to the western Indian Ocean and remaining Oceania sample collections. Additionally, four fish sampled off Hawaii and three fish sampled off Ecuador grouped with Oceania collections, and one fish sampled off California grouped with ECPO collections. The placement of these eight individuals is also consistent with results from STRUCTURE (Figure 2). These eight fish likely represent migrants that were sampled in locations geographically distant from their source population. A lack of biological information for all of these samples prohibited the identification of characteristics such as size or sex that distinguish these migrants from other fish sampled in the same geographic region.

Finally, we used AMOVA to evaluate various population structure scenarios. To limit the range of possible scenarios to test with AMOVA, we only assessed scenarios that included groups consistently resolved by PCoA and STRUCTURE. These groups corresponded with WIO, ECPO, and NPO. Results from AMOVA (Table 3) indicated that differences among regions were maximized in the scenario with the following grouping: WIO, Oceania, ECPO, NPO, and NPO2. However, nearly identical results corresponded with the scenario where the same groups were recognized, except Oceania was subdivided into WAUS and EAUS+NZ.

Results from STRUCTURE, PCoA, and AMOVA consistently indicated the presence of five genetically distinct groups (e.g. populations): 1) WIO, 2) Oceania, 3) NPO, 4) NPO2, and 5) ECPO. However, these results also included evidence that Oceania may comprise two groups corresponding with western Australia and with eastern Australia and New Zealand. To account for this uncertainty, genetic differentiation and diversity metrics were calculated with Oceania grouped together, and with WAUS and EAUS+NZ grouped separately.

Population differentiation and diversity

The level of genetic differentiation between populations was assessed by calculating F_{ST} values pairwise between populations (Table 4). All F_{ST} values were statistically significant at $p = 0.000$. Within the Indian Ocean, genetic differentiation between WIO and Oceania was comparatively low ($F_{ST} = 0.0261$). For comparisons between the Indian and Pacific oceans, WIO displayed a high level of differentiation from Pacific Ocean populations other than Oceania ($F_{ST} = 0.0497–0.0836$), whereas differentiation between Oceania and other Pacific Ocean populations was

intermediate (F_{ST} = 0.0198–0.0555). These results indicate a greater degree of isolation corresponding with WIO relative to other populations resolved in this study. F_{ST} values calculated with WAUS and EAUS+NZ grouped separately included a level of genetic differentiation between these collections (F_{ST} = 0.0069; Table 5) that was less than half of that observed between all other populations (F_{ST} = 0.0169–0.0836).

Population-level genetic diversity was greatest for NPO2 (H_E = 0.204, a_R = 1.501; Table 6) but lowest for WIO (H_E = 0.147, a_R = 1.463). Oceania displayed an intermediate level of genetic diversity (H_E = 0.156, a_R = 1.488). Genetic diversity calculated for WAUS grouped separately from EAUS+NZ revealed a low level of diversity for WAUS (H_E = 0.145, a_R = 1.317; Table 7); however, this could be due to the small sample size of this collection (n = 8) relative to other populations. There were no private alleles associated with any of the populations resolved in this study.

DISCUSSION

The primary objectives of this study were to evaluate population structure for striped marlin in the Indian Ocean, and to assess the relationship of Indian Ocean and Pacific Ocean populations. To accomplish these objectives, we characterized nearly 4,000 SNPs across collections of striped marlin from locations throughout the species range. **Five genetically distinct populations were consistently resolved in this study, three of which corresponded with striped marlin in the western Indian Ocean, Oceania, and eastern central Pacific Ocean, and two of which corresponded with the North Pacific Ocean.**

Western Indian Ocean population

The presence of a genetically distinct population of striped marlin in the western Indian Ocean is consistent with biological information suggesting spawning in this region: striped marlin larvae have been collected from waters off Réunion and Mauritius, and from waters extending from Somalia to Tanzania (reviewed by Bromhead et al. 2003). Information on seasonal movements for striped marlin in the Indian Ocean are limited, but catch per unit effort data from pelagic longline fisheries operating in the western Indian Ocean suggest north-south migrations corresponding with seasonal aggregations off Kenya and off South Africa (Bromhead et al. 2003). Similarly, satellite tags deployed on striped marlin in waters off Kenya demonstrate movements restricted to the western Indian Ocean (Roy Bealey, African Billfish Foundation, *personal communication*). Conventional tagging efforts in this region include a number of tag recaptures within the western Indian Ocean, except for a single fish recaptured off Perth, Australia (Roy Bealey, African Billfish Foundation, *personal communication*). Additional tagging efforts spanning the Indian Ocean are necessary to enable a better understanding of seasonal movement patterns for striped marlin in this region.

The western Indian Ocean population of striped marlin exhibited the lowest level of genetic diversity and the highest level of genetic differentiation observed in this study. Additional study is required to determine whether this low genetic diversity is the result of

historical evolutionary events, or is due to high levels of contemporary fishing effort. Regardless, the genetic results presented here suggest a **greater degree of isolation for the western Indian Ocean relative to other populations**, and therefore a lower probability of supplementation by striped marlin from other regions, **highlighting the importance of recognizing the western Indian Ocean as a distinct assessment and management unit**.

Oceania population

The presence of a genetically distinct population of striped marlin in Oceania is supported by a number of biological observations. Striped marlin spawning has been confirmed for locations off both the eastern and western coasts of Australia, and off northern Australia in the Banda and Timor seas (reviewed by Bromhead et al. 2003). Tagging efforts in Oceania have largely been limited to waters off eastern Australia and New Zealand, and are consistent with relatively localized movements in this region, although a number of long distance migrations as far east as French Polynesia have been observed (Ortiz et al. 2003; Domeier 2006; Holdsworth et al. 2009; Sippel et al. 2011; Holdsworth and Saul 2014). No inter-oceanic movements have been reported for striped marlin; however, tagging and reporting efforts in the Indian Ocean are limited.

Some results from this study suggest that the Oceania population of striped marlin could be subdivided to reflect distinct populations in the eastern Indian Ocean (off western Australia) and in the western South Pacific Ocean (off eastern Australia and New Zealand). However, the level of genetic differentiation (e.g. F_{ST}) between these two regions was less than half of that observed between all other populations. These results suggest that **if striped marlin in Oceania comprise two biologically distinct populations, they are connected by a comparatively high degree of gene flow**, possibly facilitated by the more temperate waters inhabited by striped marlin relative to other istiophorids (20–25 ºC sea surface temperature; Howard and Ueyanagi 1965; Sippel et al. 2007). A larger sample size for striped marlin off western Australia is required to further evaluate this genetic relationship, and a better biological understanding of striped marlin off eastern and western Australia (e.g. spatiotemporal spawning, seasonal movements) is necessary to inform these genetic results.

The occurrence of **a small number of striped marlin sampled off Hawaii and Ecuador that were genetically indistinguishable from striped marlin sampled from Oceania suggests some level of spatial connectivity among these regions**. Movements between Oceania and Hawaii or Ecuador have not been reported for tagged fish; however, tagging and reporting efforts may not have been sufficient to capture such movements. These results highlight the importance of understanding seasonal movement patterns for striped marlin throughout the species range. Additionally, **sustainable management practices for striped marlin in both Indian and Pacific waters are necessary for promoting a healthy population in Oceania**. Finally, shared genetic diversity between Oceania and populations elsewhere in the Pacific Ocean highlight the **importance of Oceania as a conduit between striped marlin in the Pacific and Indian oceans**.

Concluding remarks

The genetically distinct populations of striped marlin identified in this study do not correspond with management units currently recognized for this species in the Pacific and Indian oceans (Figure 5). The single ocean-wide management unit presently used for striped marlin in the Indian Ocean should be **subdivided to reflect the presence of two genetically distinct populations in the western and eastern Indian Ocean**. Additionally, management of striped marlin in the eastern Indian Ocean should include **joint efforts by the IOTC and Western and Central Pacific Fisheries Commission to reflect a population that spans Oceania**. Even if striped marlin off western Australia warrant recognition as a biologically distinct management unit, the results of this study demonstrate a close genetic relationship with striped marlin off eastern Australia and New Zealand, necessitating management measures that consider this entire geographic region.

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Tables and Figures

Table 1. Details for striped marlin sample collections analyzed in this study.

Sampling Region	Code	Year	No. Individuals	Total
Indian Ocean				
South Africa	SAF	2017	1	11
		2016	3	
		2015	7	
Kenya	KEN	2016	13	27
		2015	14	
Western Australia	WAUS	2016	8	8
			Total:	46
Pacific Ocean				
Eastern Australia	EAUS	2015	3	35
		2012	3	
		2011	7	
		2010	6	
		1994	16	
New Zealand	NZ	2017	22	22
Japan	JAP	2015	18	18
Taiwan	TAI	2016	4	11
		2015	5	
		2014	2	
Hawaii	HAW	2015	21	21
California	CAL	2016	2	15
		2000	13	
Baja California	BAJA	2015	21	22
Ecuador	ECU	2016	22	37
		1992	15	
Peru	PERU	2016	19	19
			Total:	199
			Grand Total:	245

Table 2. Number of single nucleotide polymorphism (SNP) loci retained after each filtering step.

Filter	No. Retained Loci
Loci received from Diversity Arrays Technology Pty. Ltd.	61,908
Quality Filter	
Missing ≥ 10% genotypes	41,613
Average reproducibility < 95%	41,540
Monomorphic	11,831
More than one SNP per reduced representation locus	10,220
Minor allele frequency < 0.05	4,016
Hardy-Weinberg Equilibrium	
P < 0.006 in > 1 sample collection	3,975
Outlier Identification	
Putatively neutral	3,916
Putatively under selection	59

Table 3. Results from analysis of molecular variance (AMOVA) performed for scenarios with samples organized by sampling location or by region. Sample collections are labeled as in Table 1. Scenarios with samples grouped by region are as follows: WIO = western Indian Ocean sample collections SAF and KEN; Oceania = sample collections WAUS, EAUS, and NZ; NPO = North Pacific Ocean sample collections JAP, TAI, HAW, and CAL; NPO2 = North Pacific Ocean sample collections JAP2 and HAW2; ECPO = eastern central Pacific Ocean sample collections BAJA, ECU, and PERU. The most likely population structure scenarios are highlighted in gray.

Grouping	Source of Variation	Φ_{ST}	Percent Variation	p-value
WIO, Oceania, NPO, ECPO	Among regions	0.0300	3.00	0.000
	Among populations within regions	0.0037	0.36	0.000
	Within populations	0.0336	96.64	0.000
WIO, Oceania, NPO, NPO2, ECPO	Among regions	0.0336	3.36	0.000
	Among populations within regions	0.0029	0.28	0.000
	Within populations	0.0363	96.37	0.000
WIO, WAUS, EAUS+NZ, NPO, ECPO	Among regions	0.0299	2.99	0.000
	Among populations within regions	0.0033	0.32	0.000
	Within populations	0.0330	96.69	0.000
WIO, WAUS, EAUS+NZ, NPO, NPO2, ECPO	Among regions	0.0335	3.35	0.000
	Among populations within groups	0.0023	0.22	0.002
	Within populations	0.0358	96.42	0.000
WIO+WAUS, EAUS+NZ, NPO, ECPO	Among regions	0.0288	2.88	0.000
	Among populations within regions	0.0046	0.45	0.000
	Within populations	0.0332	96.68	0.000
WIO+Oceania, NPO, ECPO	Among regions	0.0248	2.48	0.000
	Among populations within regions	0.0103	1.00	0.000
	Within populations	0.0349	96.51	0.000
WIO, Oceania+NPO+ECPO	Among regions	0.0298	2.98	0.017
	Among populations within regions	0.0196	1.90	0.000
	Within populations	0.0488	95.12	0.000

Table 3. (*continued)*

Grouping	Source of Variation	Φ_{ST}	Percent Variation	p-value
WIO+WAUS, EAUS+NZ+NPO+ECPO	Among regions	0.0269	2.69	0.004
	Among populations within regions	0.0192	1.86	0.000
	Within populations	0.0456	95.44	0.000
WIO+Oceania, NPO+ECPO	Among regions	0.0236	2.36	0.001
	Among populations within regions	0.0156	1.52	0.000
	Within populations	0.0388	96.12	0.000

Table 4. Pairwise F_{ST} values (below diagonal) calculated between striped marlin populations. Cells are colored as a heat map ranging from green (lowest F_{ST} values) to red (highest F_{ST} values). P-values associated with each pairwise comparison are also shown (above diagonal). Sample collections are grouped as follows: WIO = western Indian Ocean sample collections SAF and KEN; Oceania = sample collections WAUS, EAUS, and NZ; NPO = North Pacific Ocean sample collections JAP, TAI, HAW, and CAL; NPO2 = North Pacific Ocean sample collections JAP2 and HAW2; ECPO = eastern central Pacific Ocean sample collections BAJA, ECU, and PERU.

	WIO	Oceania	NPO	NPO2	ECPO
WIO	--	0.000	0.000	0.000	0.000
Oceania	0.0261	--	0.000	0.000	0.000
NPO	0.0497	0.0198	--	0.000	0.000
NPO2	0.0836	0.0555	0.0394	--	0.000
ECPO	0.0580	0.0330	0.0169	0.0556	--

Table 5. Pairwise F_{ST} values (below diagonal) calculated between striped marlin populations with WAUS grouped separately. Cells are colored as a heat map ranging from green (lowest F_{ST} values) to red (highest F_{ST} values). P-values associated with each pairwise comparison are shown above diagonal. Statistical significance was assessed using a critical value (p_{crit} = 0.015) corrected for multiple pairwise comparisons (n = 15; Benjamini and Yekutieli 2001). Sample collections are grouped as follows: WIO = western Indian Ocean sample collections SAF and KEN; NPO = North Pacific Ocean sample collections JAP, TAI, HAW, and CAL; NPO2 = North Pacific Ocean sample collections JAP2 and HAW2; ECPO = eastern central Pacific Ocean sample collections BAJA, ECU, and PERU.

	WIO	WAUS	EAUS+NZ	NPO	NPO2	ECPO
WIO	--	0.000	0.000	0.000	0.000	0.000
WAUS	0.0208	--	0.006	0.000	0.000	0.000
EAUS+NZ	0.0279	0.0069	--	0.000	0.000	0.000
NPO	0.0497	0.0291	0.0195	--	0.000	0.000
NPO2	0.0836	0.0512	0.0541	0.0394	--	0.000
ECPO	0.0580	0.0380	0.0331	0.0169	0.0556	--

Table 6. Diversity metrics calculated for striped marlin populations. Cells are colored as a heat map ranging from green (lowest diversity values) to red (highest diversity values). WIO = western Indian Ocean, NPO = North Pacific Ocean, ECPO = eastern central Pacific Ocean.

Population	Sample Collections	N	a_R	H_E	H_O
WIO	SAF, KEN	38	1.463	0.147	0.144
Oceania	WAUS, EAUS, NZ	65	1.488	0.156	0.162
NPO	JAP, TAI, HAW, CAL	54	1.489	0.155	0.156
NPO2	JAP2, HAW2	11	1.501	0.204	0.304
ECPO	BAJA, ECU, PERU	77	1.472	0.154	0.160

N = number of individuals comprising population
a_R = rarefaction allelic richness
H_E = expected heterozygosity
H_O = observed heterozygosity

Table 7. Diversity metrics calculated for striped marlin populations with WAUS grouped separately. Cells are colored as a heat map ranging from green (lowest diversity values) to red (highest diversity values). WIO = western Indian Ocean, NPO = North Pacific Ocean, ECPO = eastern central Pacific Ocean.

Population	Sample Collections	N	a_R	H_E	H_O
WIO	SAF, KEN	38	1.332	0.147	0.144
	WAUS	8	1.317	0.145	0.136
	EAUS, NZ	57	1.351	0.156	0.162
NPO	JAP, TAI, HAW, CAL	54	1.350	0.155	0.156
NPO2	JAP2, HAW2	11	1.418	0.204	0.304
ECPO	BAJA, ECU, PERU	77	1.345	0.154	0.160

N = number of individuals comprising grouped collections
a_R = rarefaction allelic richness
H_E = expected heterozygosity
H_O = observed heterozygosity

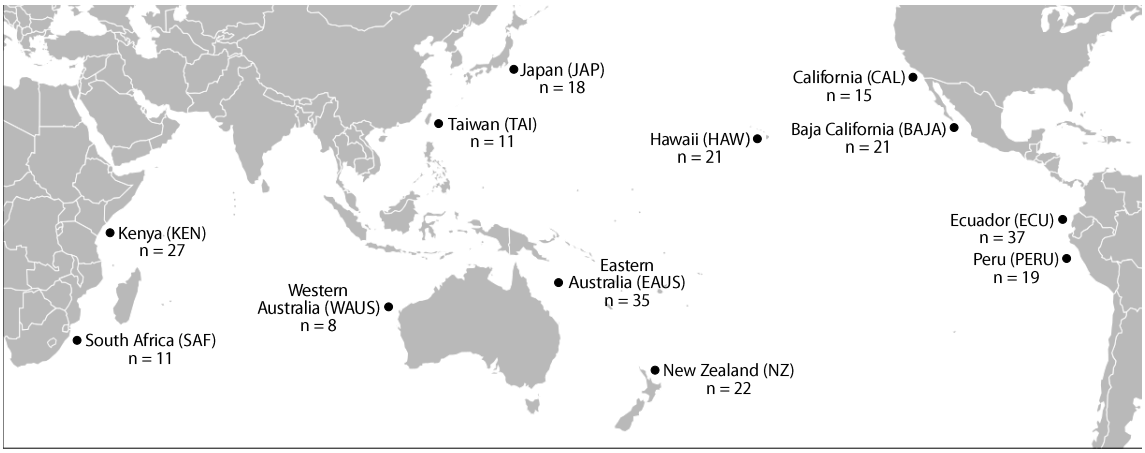

Figure 1. Map displaying geographic sampling locations and sample sizes for collections of striped marlin evaluated in this study. Points indicate representative sampling region.

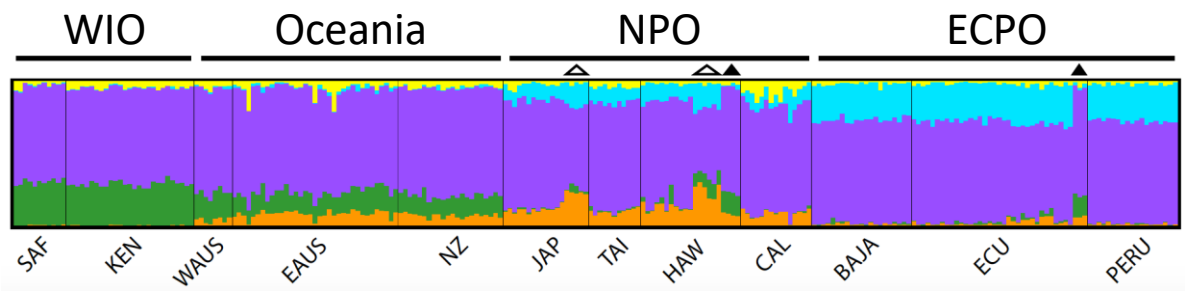

Figure 2. Results from STRUCTURE analyses performed using a K = 5, the most likely K identified by Structure Harvester. Each vertical bar represents an individual, and individuals are colored according to genetic ancestry. Sample collections are denoted at bottom of figure and groups identified as genetically distinct are denoted at top: WIO = western Indian Ocean sample collections SAF and KEN; Oceania = sample collections WAUS, EAUS, and NZ; NPO = North Pacific Ocean sample collections JAP, TAI, HAW, and CAL; ECPO = eastern central Pacific Ocean sample collections BAJA, ECU, and PERU. Open arrowheads identify the JAP2 (n = 5) and HAW2 (n = 6) samples which comprise a distinct population in the North Pacific Ocean (NPO2). Filled arrowheads indicate putative migrants consistent with Oceania but sampled off Hawaii (n = 4) and Ecuador (n = 3).

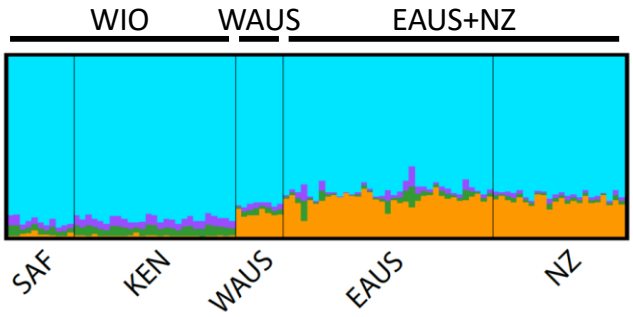

Figure 3. Results from STRUCTURE analyses performed using a dataset limited to sample collections from the Indian Ocean and Oceania. Results are from the scenario with K = 3, the most likely K identified by Structure Harvester. Each vertical bar represents an individual, and individuals are colored according to genetic ancestry. Sample collections are denoted at bottom of figure and groups identified as genetically distinct are denoted at top: WIO = western Indian Ocean sample collections SAF and KEN.

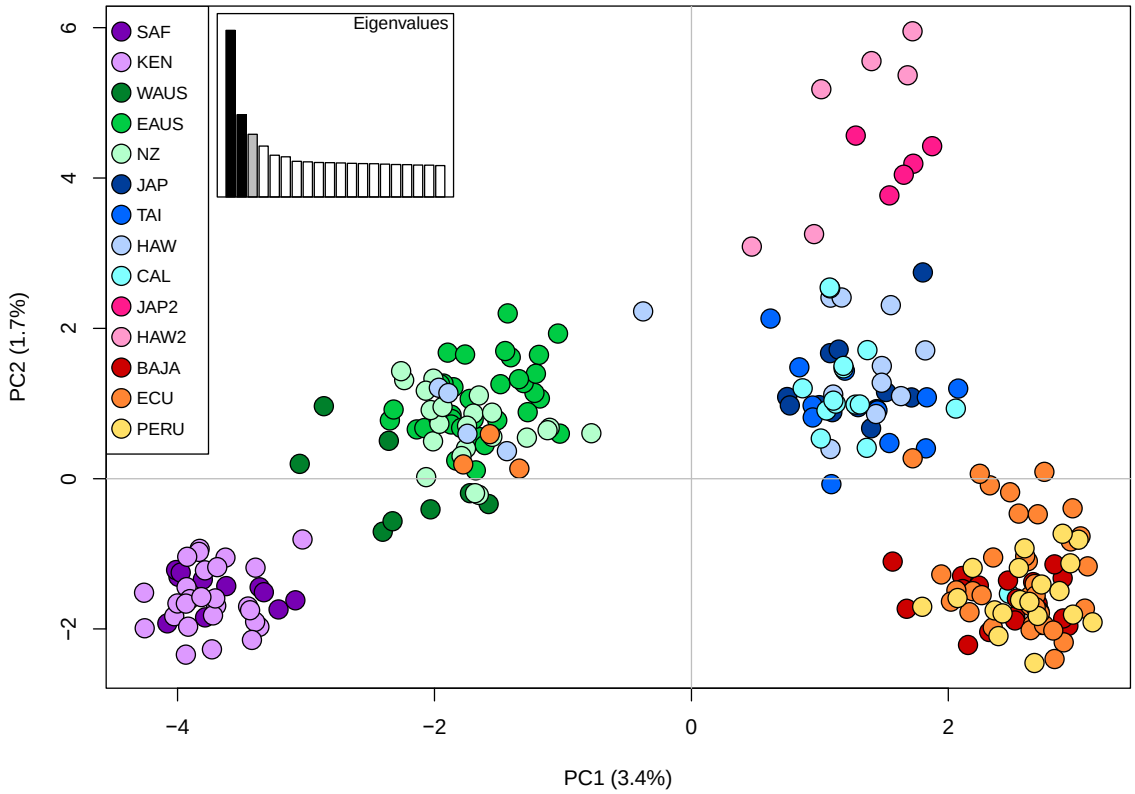

Figure 4. Two-dimensional plot of principal coordinate analysis (PCoA) axes one and two. Percentage of total genetic variation explained by each axis is shown. Sample collections are labeled as in Table 1. Each collection is represented by a unique color according to the legend at top left; similar colors (e.g. blues) are used to represent larger geographic regions. Inset at top left shows eigenvalues associated with the PCoA, including plotted axes (black bars).

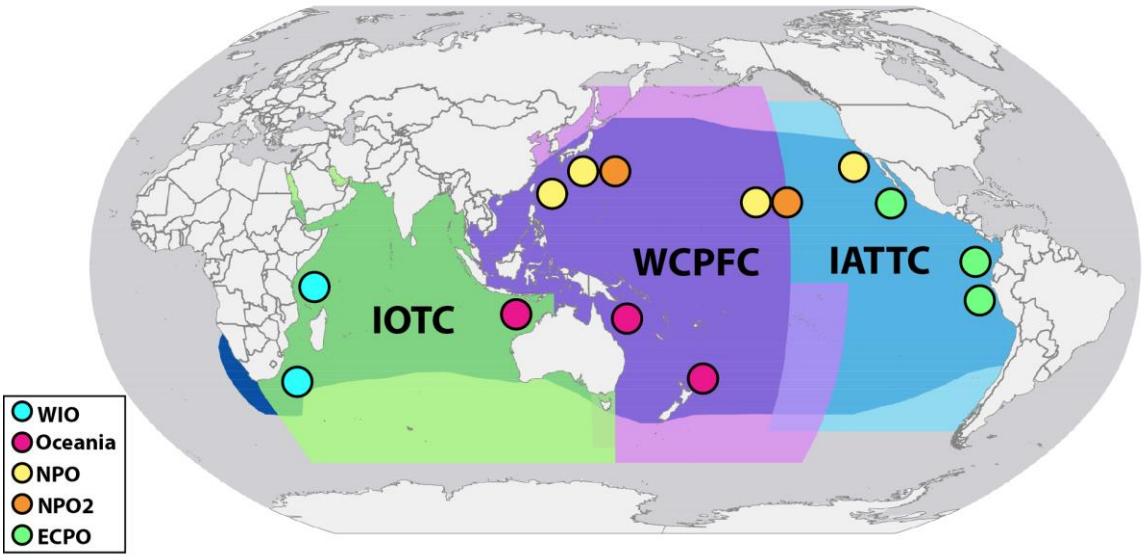

Figure 5. World map displaying spatial distribution of striped marlin (*Kajikia audax*; dark blue) overlaid with jurisdictional regions for the Indian Ocean Tuna Commission (IOTC; green), Western and Central Pacific Fisheries Commission (WCPFC; pink), and Inter-American Tropical Tuna Commission (IATTC; light blue). Points correspond with sampling locations for collections of striped marlin evaluated in the present study, and are colored according to genetically distinct population. Currently, the IOTC recognizes a single stock of striped marlin in the Indian Ocean, the WCPFC recognizes distinct stocks in the western and central North Pacific and in the western South Pacific oceans, and the IATTC recognizes a single stock in the eastern Pacific Ocean. WIO = western Indian Ocean, NPO = North Pacific Ocean, ECPO = eastern central Pacific Ocean.