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Preliminary results from an assessment of genetic population structure for striped marlin (*Tetrapturus audax*) in the Pacific and Indian oceans

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Abstract

The Indian Ocean Tuna Commission currently recognizes a single ocean-wide stock of striped marlin (*Tetrapturus audax*) due to a lack of information on the intra-oceanic stock structure of this species. Tagging efforts for striped marlin in the Indian Ocean have been limited, and previous genetic assessments of population structure have been restricted to the analysis of sample collections from the Pacific Ocean. In the Pacific Ocean, tagging and genetic studies have confirmed the presence of multiple regional stocks that coincide with geographically distant spawning grounds. A number of spawning grounds have been inferred for striped marlin in the Indian Ocean; however, the stock structure of this species in the Indian Ocean, as well as the inter-oceanic relationship of striped marlin in the Pacific and Indian oceans, is unknown. Reducing uncertainties currently associated with the management of striped marlin in the Indian Ocean is of particular importance given that this stock was recently identified as overfished ($B_{2011}/B_{MSY} = 0.416$) and experiencing overfishing ($F_{2011}/F_{MSY} = 1.28$). In this study, we assess the genetic population structure of striped marlin throughout the full species range using newly developed single nucleotide polymorphism (SNP) molecular markers that provide genome-wide representation. Preliminary results based on an exploratory dataset comprising 29 striped marlin characterized at over 9,000 SNP loci are presented in this report. These preliminary results suggest that striped marlin in the Indian Ocean represent a genetic stock distinct from Pacific Ocean fish. Evidence for stock structure within the Indian Ocean was not observed; however, sample collections from the eastern ocean basin are limited. Future work includes the assessment of additional sample collections characterized by larger sample sizes to facilitate comprehensive analysis of intra- and inter-oceanic genetic connectivity.

Introduction

Striped marlin (*Tetrapturus audax*; family Istiophoridae) is a highly migratory pelagic species distributed throughout temperate and tropical waters of the Pacific and Indian oceans. In the Indian Ocean, there is a lack of information on the population structure of striped marlin, and this species is currently assessed and managed as a single ocean-wide stock. In 2013, the Indian Ocean Tuna Commission (IOTC) Working Party on Billfish (WPB) identified striped marlin as heavily overfished and experiencing overfishing, with biomass and fishing effort in 2011 at 0.42 and 1.28 of that required to produce maximum sustainable yield, respectively (IOTC 2013). Given the stock status of striped marlin in the Indian Ocean, management would benefit from information that reduces uncertainties currently associated with the management of this species, including an improved understanding of stock structure.

Throughout the species range, striped marlin are targeted along with other billfishes in recreational sport fisheries, some of which are primarily catch-and-release. Small-scale artisanal fisheries also target striped marlin mainly for local subsistence; however, the major source of fishing mortality for this species is attributed to bycatch in pelagic longline fisheries targeting swordfish and tunas. Reporting of catches for striped marlin and other billfishes is inconsistent, including a lack of reporting for live and dead discards at time of haulback from pelagic longline fisheries. In the Indian Ocean, total catches of billfishes increased from approximately 25,000 t in the early 1990s to nearly 75,000 t in the mid-1990s, and have remained relatively stable since (IOTC 2014); striped marlin constitute a small proportion (5%) of the total billfish catch. In recent years, the majority of billfish catches in the Indian Ocean have been associated with longline vessels, but catches from gillnet fisheries are on the rise (IOTC 2014).

Striped marlin are seasonally abundant in locations throughout the Indian Ocean; additionally, a number of spawning grounds have been inferred in this region through the presence of larvae and/or reproductively active females (Figure 1). Catch data from pelagic longline fisheries suggest that striped marlin are present in low abundance in most of the species range throughout the year, but seasonal concentrations characterized by periods of increased abundance occur in four main regions (Bromhead et al. 2003):

1) Off the eastern coast of Africa from the equator to 10º S. Larvae and females with mature gonads have also been identified from this general vicinity, west of Madagascar from 6º N to 6º S (Pillai & Ueyanagi 1978).

2) In the south and western Arabian Sea.

3) In the Bay of Bengal. Mature females have also been reported from this region during the 1st and 2nd quarters (Pillai & Ueyanagi 1978).

4) Off northwestern Australia primarily from 10 to 25º S. Larvae and mature females have also been identified in this general region, from 10 to 18º S during July through December (Jones & Kumaran 1964, Ueyanagi 1974, Nakamura 1983).

In addition to the primary seasonal concentrations previously listed, which in some instances appear to be associated with spawning, striped marlin larvae have also been collected in the region southeast of Madagascar from 20 - 25º S and 55 - 60º E (Nishikawa et al. 1978), and in the Banda and Timor seas south of Indonesia during January and February (Ueyanagi & Wares 1975; Figure 1).

Tagging efforts for istiophorid billfishes in the Indian Ocean are limited, and only a small number of striped marlin recaptures have been reported (< 2%; Ortiz et al. 2003, Romanov 2016). Based on their analysis of catch per unit effort data obtained from pelagic longline fisheries, Bromhead et al. (2003) suggested the possibility of north-south seasonal migrations for striped marlin in the Indian Ocean. These movements may include migrations along the eastern coast of Africa, in the western Arabian Sea, along the western coast of Australia, and between waters off northwest Australia and the Bay of Bengal. Inter-oceanic movements of striped marlin have not been observed, though Penrith & Cram (1974) report thirteen striped marlin captured via pelagic longline in localities off the Cape of Good Hope, South Africa. In the Pacific Ocean, results from satellite tagging of striped marlin demonstrate restricted regional movements (Domeier 2006), including for individuals tagged off eastern Australia and New Zealand.

Previous genetic evaluations of population structure for striped marlin have been limited to the analysis of sample collections from the Pacific Ocean, and genetic connectivity throughout the Indian Ocean is currently unknown. In the Pacific Ocean, four genetic stocks have been collectively resolved based on the analysis of small numbers of molecular markers (McDowell & Graves 2008, Purcell & Edmands 2011). These genetic results are generally consistent with seasonal movements inferred from tagging data (Ortiz et al. 2003, Domeier 2006) and with the presence of geographically distant spawning grounds identified throughout the Pacific Ocean (Bromhead et al. 2003). However, the lack of Indian Ocean sample collections in previous

genetic studies not only limits our understanding of genetic stock structure within this ocean basin, but also prohibits comprehension of the degree of connectivity between the Pacific and Indian oceans.

Recently, the development and widespread availability of next-generation sequencing-technology has significantly improved the ability to resolve genetic population structure by facilitating the rapid and economical evaluation of large (thousands to tens of thousands) numbers of molecular markers across sizeable numbers of samples. This advancement is especially significant for pelagic fishes, for which genetic differentiation between populations, if present, is expected to be low (Waples 1998, Ward et al. 1994). In this study, next-generation sequencing-based methodology was used to discover and characterize single nucleotide polymorphism (SNP) molecular markers across collections of striped marlin sampled from locations throughout the Pacific and Indian oceans. Specific objectives of this study were to:

1) Apply next-generation sequencing methodology to discover a large number of SNPs in striped marlin.

2) Evaluate the number and geographic location of genetic populations of striped marlin in the Pacific and Indian oceans.

3) Assess the degree of genetic connectivity among populations, particularly between ocean basins.

4) Identify putative adaptive SNPs and evaluate the presence of localized adaptation.

This study is currently ongoing and the results presented in this report are preliminary. These preliminary results are based on the analysis of an exploratory dataset characterized by small sample sizes. The expected completion date for this project is May 2018, and finalized results will be made available to the IOTC WPB thereafter. Collectively, the ambition for information resulting from this study is to reduce uncertainties currently associated with the management of striped marlin in the Indian Ocean.

Methods

A total of 29 striped marlin representing collection locations throughout the Pacific and Indian oceans were included in our preliminary dataset (Figure 2). These samples consisted of

fin clips from live fish that were released after capture or muscle tissue from landed fish available in local markets. Samples were preserved in 95% ethanol or a 10% dimethyl sulfoxide solution (Seutin et al. 1991) and were stored at room temperature or in a freezer at approximately -20º C. Total genomic DNA was isolated from tissue samples using standardized kits including the ZR Genomic DNA Tissue MiniPrep Kit (Zymo Research) and the DNeasy Blood and Tissue Kit (Qiagen). DNA isolations were electrophoresed on 1.5% agarose gels to assess quality of isolated DNA. For samples qualitatively displaying high levels of high molecular weight DNA during gel electrophoresis, DNA concentrations were fluorometrically quantified using a Qubit dsDNA BR Assay Kit (Thermo Fisher Scientific). Samples with suitably high concentrations of DNA were stabilized with GenTegra-DNA (GenTegra, LLC) and sent to Diversity Arrays Technology (DArT; University of Canberra, Australia; http://www.diversityarrays.com) genotyping service for DArTseq™ analysis. Briefly, DArTseq™ is a genotyping-by-sequencing methodology similar to that described by Peterson et al. (2012), and involves the reduction of genomic complexity through restriction enzyme digestion, followed by ligation of sample-specific barcodes and enzyme-specific adapters. Samples were pooled to form a single library which was then sequenced on an Illumina next-generation sequencing platform. Resulting data were processed using proprietary DArT analytical pipelines, including the filtering of low quality sequence data. A secondary proprietary pipeline was used to identify SNPs as part of the DArTseq™ analysis.

A total of 11,850 SNPs were obtained from the DArTseq™ analysis in the form of a 0, 1, 2 genotype matrix. SNP loci missing genotype data for more than 25% of samples were excluded from further analyses and formatted for the R package adegenet v2.0.1 (Jombart 2008, Jombart et al. 2009) using a custom R script (R Core Team 2013). Loci that did not conform to the expectations of Hardy-Weinberg equilibrium were identified using the R package pegas v0.10 (Paradis 2010) and excluded from additional analyses. A total of 9,830 loci were retained for analyses after the filters for missing data and Hardy-Weinberg equilibrium were applied. Principal component analysis (PCA) was performed in adegenet using scaled mean allele frequencies to replace missing data. The Bayesian-informed clustering of individuals was completed using STRUCTURE v2.3.4 (Pritchard et al. 2000). STRUCTURE analyses were performed using an admixture model of ancestry (Falush et al. 2007, Hubisz et al. 2009) and 500,000 Markov Chain Monte Carlo repetitions for each iteration, with 25 iterations performed

for each of five clustering scenarios comprising K equal to two through six. The degree of genetic differentiation between sample collections was evaluated using pairwise F_{st} values calculated in Arlequin v3.5 (Excoffier & Lischer 2010). Sample collections were grouped as follows for calculation of pairwise F_{st} values: Indian Ocean (IO) including collections from Kenya, South Africa, and western Australia; North Pacific Ocean (NPO) including collections from Japan, Hawaii, and California; eastern Central Pacific Ocean (ECPO) including collections from Ecuador and Baja California; and Southwestern Pacific Ocean (SWPO) including a collection from eastern Australia. These groupings were informed by cluster-based results from PCA and STRUCTURE. F_{st} was also calculated pairwise between Indian Ocean and Pacific Ocean collections to assess inter-oceanic genetic divergence. Statistical significance of all pairwise F_{st} values was determined by 10,000 permutations and a critical value corrected for multiple pairwise comparisons (Benjamini & Yekutieli 2001, Narum 2006). The pooling of sample collections into larger groupings for the calculation of pairwise F_{st} values facilitated more powerful comparisons with sample sizes larger than those associated with individual sample collections.

Preliminary Results

Results from PCA of SNP data are presented in Figure 3. Principal component axes one and two explained the greatest degree of genetic variation in the preliminary dataset. A distinct cluster of individuals comprising samples from Baja California and Ecuador is evident (Figure 3). A second cluster comprising individuals from the North Pacific Ocean (Japan, Hawaii, and California) is also apparent. Sample collections from the Indian Ocean, including South Africa, Kenya and western Australia, comprise a third distinct cluster. The two individuals sampled off eastern Australia are positioned relatively intermediate to individuals from the Indian Ocean and North Pacific Ocean collections, but with slightly greater association to Indian Ocean collections.

STRUCTURE results from clustering scenarios characterized by K equal to two through four are presented in Figure 4 (Panels A–C). In the K = 2 scenario (Figure 4A), individuals sampled from the Pacific and Indian oceans correspond with ocean-specific clusters and display low degrees of individual admixture, except for the two individuals sampled off eastern Australia. The high degrees of individual admixture displayed by the two eastern Australia samples reflect genetic compositions intermediate to individuals from the Pacific and Indian

oceans. In the K = 3 scenario (Figure 4B), a distinct cluster comprising individuals from the eastern central Pacific Ocean (Ecuador and Baja California) is present. In addition, individuals comprising the Hawaiian collection display high degrees of individual admixture primarily reflective of the genetic composition associated with all Pacific Ocean collections. The pattern observed in the K = 4 scenario (Figure 4C) is similar to that observed for K = 3; however, the genetic composition of individuals sampled off Japan is highly variable.

Pairwise F_{st} values calculated between sample collections that were grouped according to cluster-based results are shown in Figure 5. Pairwise F_{st} values ranged from 0.034 to 0.081, and all comparisons were statistically significant. The minimum and maximum values of observed differences were associated with comparisons of the eastern central Pacific Ocean with the North Pacific Ocean and the Indian Ocean, respectively. The pairwise F_{st} value associated with the comparison between pooled Pacific and Indian ocean collections was 0.057 (p = 0.000).

Preliminary Conclusions

Results presented in this report are based on the analysis of a small number of individuals (n = 29) characterized across a large number of SNP loci (n = 9,830). Though a high degree of genomic representation and statistical power is afforded by the large number of loci evaluated, results based on this preliminary dataset should be interpreted with some caution given the small sample sizes per geographic location and overall. Final results based on a complete dataset comprising larger sample sizes will be made available to the IOTC WPB upon project completion.

Results from cluster-based analyses including PCA and STRUCTURE suggest the presence of multiple genetic groups of striped marlin represented by the sample collections analyzed here. Collections from the Indian Ocean appear to comprise a group genetically distinct from Pacific Ocean collections based on results from PCA and STRUCTURE (Figures 3, 4). The F_{st} value observed between pooled Indian Ocean and Pacific Ocean sample collections (F_{st} = 0.057; Figure 5) was highly significant (p = 0.000), and is consistent with the cluster-based results. Within the Indian Ocean, limited sample sizes from the eastern ocean basin prohibited a robust east-west intra-oceanic comparison of striped marlin population structure; however, results from PCA and STRUCTURE did not provide evidence to suggest that the four individuals sampled off western Australia were genetically distinct from striped marlin sampled off Kenya

(n = 3) and South Africa (n = 2). Larger sample sizes from these locations in the final dataset will enable direct evaluation of the presence of genetic differentiation between eastern and western regions of the Indian Ocean.

In the Pacific Ocean, results from cluster-based analyses suggest the presence of a distinct genetic stock comprising sample collections from the eastern central Pacific Ocean (Ecuador and Baja California), and a second genetic stock consisting of samples from the North Pacific Ocean (Japan, Hawaii, and California; Figures 3, 4). However, individuals sampled off Hawaii and off Japan display a greater degree of genetic admixture compared to individuals from other collections (Figure 4B, C). Interestingly, the two individuals sampled off eastern Australia appear genetically intermediate to striped marlin sampled from the Pacific and Indian oceans based on results from PCA and STRUCTURE (Figures 3, 4). F_{st} values associated with the pairwise comparison of the eastern Australia fish to other sample collections were all statistically significant (Figure 5); however, a more robust measure of genetic differentiation will require larger sample sizes from this region.

Collectively, these preliminary results are consistent with a single genetic stock of striped marlin in the Indian Ocean that is distinct from Pacific Ocean fish. In the Pacific Ocean, two genetic stocks were resolved, comprising sample collections from the eastern central Pacific and from across the North Pacific. The presence of a distinct genetic stock in the North Pacific Ocean is consistent with results from previous genetic assessments based on small numbers of microsatellite molecular markers and mtDNA sequences (McDowell & Graves 2008, Purcell & Edmands 2011). McDowell & Graves (2008) resolved striped marlin sampled off Ecuador as genetically distinct from fish sampled off Baja California; the incongruence between that study and the current report is likely to be the result of smaller sample sizes in our preliminary dataset, or the greater genomic resolution facilitated by the analysis of thousands of molecular markers randomly distributed throughout the genome in this preliminary study. Finally, the exact genetic relationship of striped marlin sampled off eastern Australia to striped marlin sampled from the Indian Ocean and elsewhere in the Pacific is inconclusive based on these preliminary results– additional sample sizes are required to clarify this relationship. Information from the electronic tagging of striped marlin in the southwest Pacific Ocean suggest regional movements (Domeier 2006, Sippel et al. 2011), and there have not been any tag recaptures reflecting inter-oceanic movements. Previous genetic studies have also resolved striped marlin in the southwest Pacific

Ocean as a distinct genetic stock compared to other sample collections from the Pacific Ocean (McDowell & Graves 2008, Purcell & Edmands 2011). Overall, the larger sample sizes and additional geographic locations represented in our final dataset will help to inform those uncertainties described here, and facilitate the fulfillment of additional project objectives.

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Figures

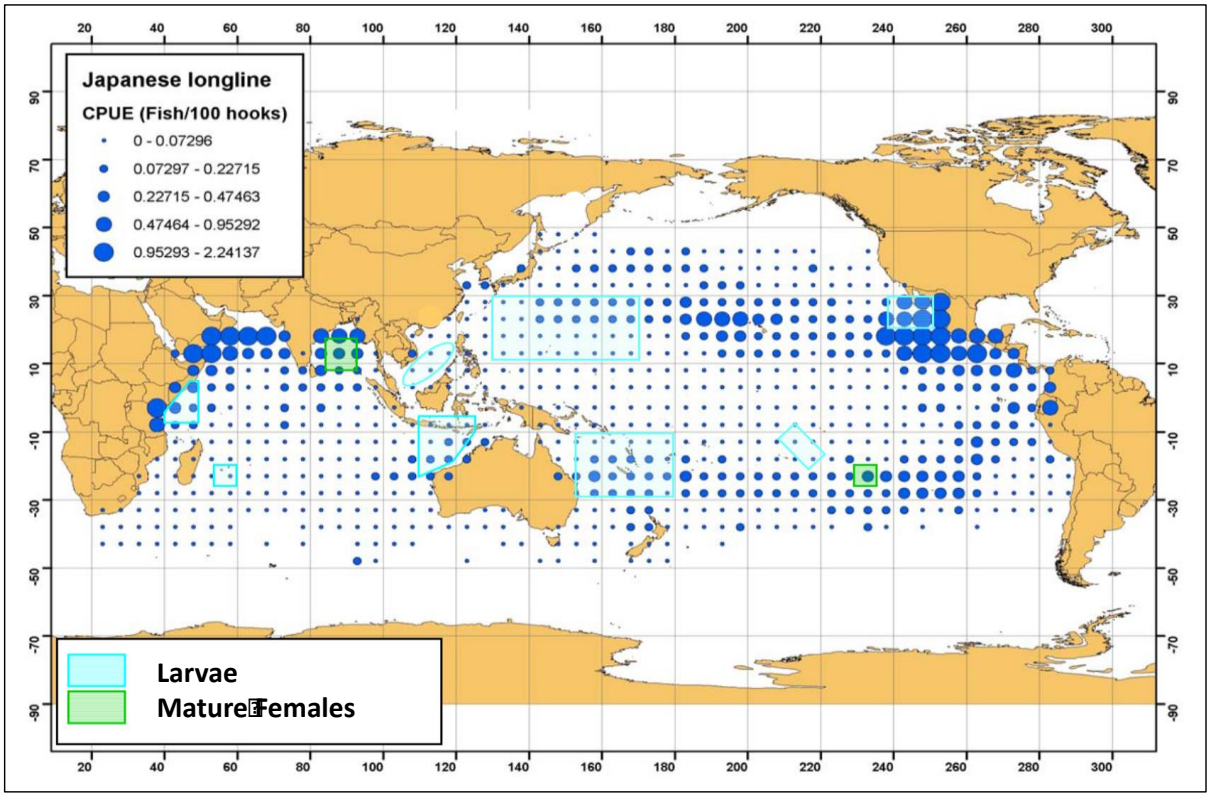


Figure 1. Spatial distribution of mean annual catch per unit effort (CPUE) for striped marlin during the period 1970 - 2000 based on Japanese pelagic longline data. Spawning grounds inferred through the presence of larvae or mature females are highlighted in turquoise and green shapes, respectively. Figure obtained from Bromhead et al. (2003).

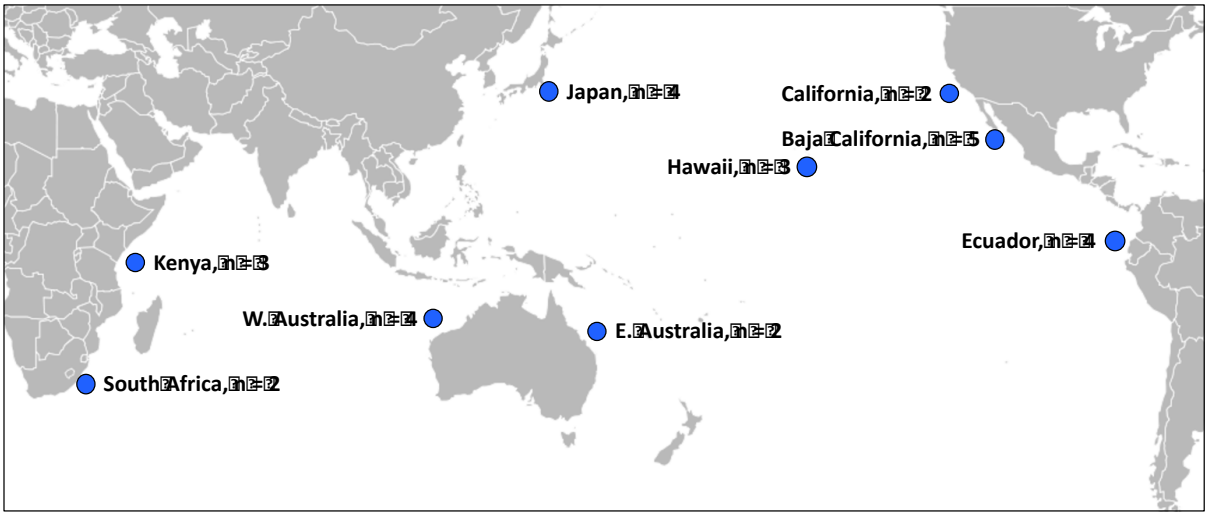


Figure 2. Map of geographic sampling locations for striped marlin individuals (n = 29 total) included in our preliminary dataset. Representative sampling locations are indicated by blue circles.

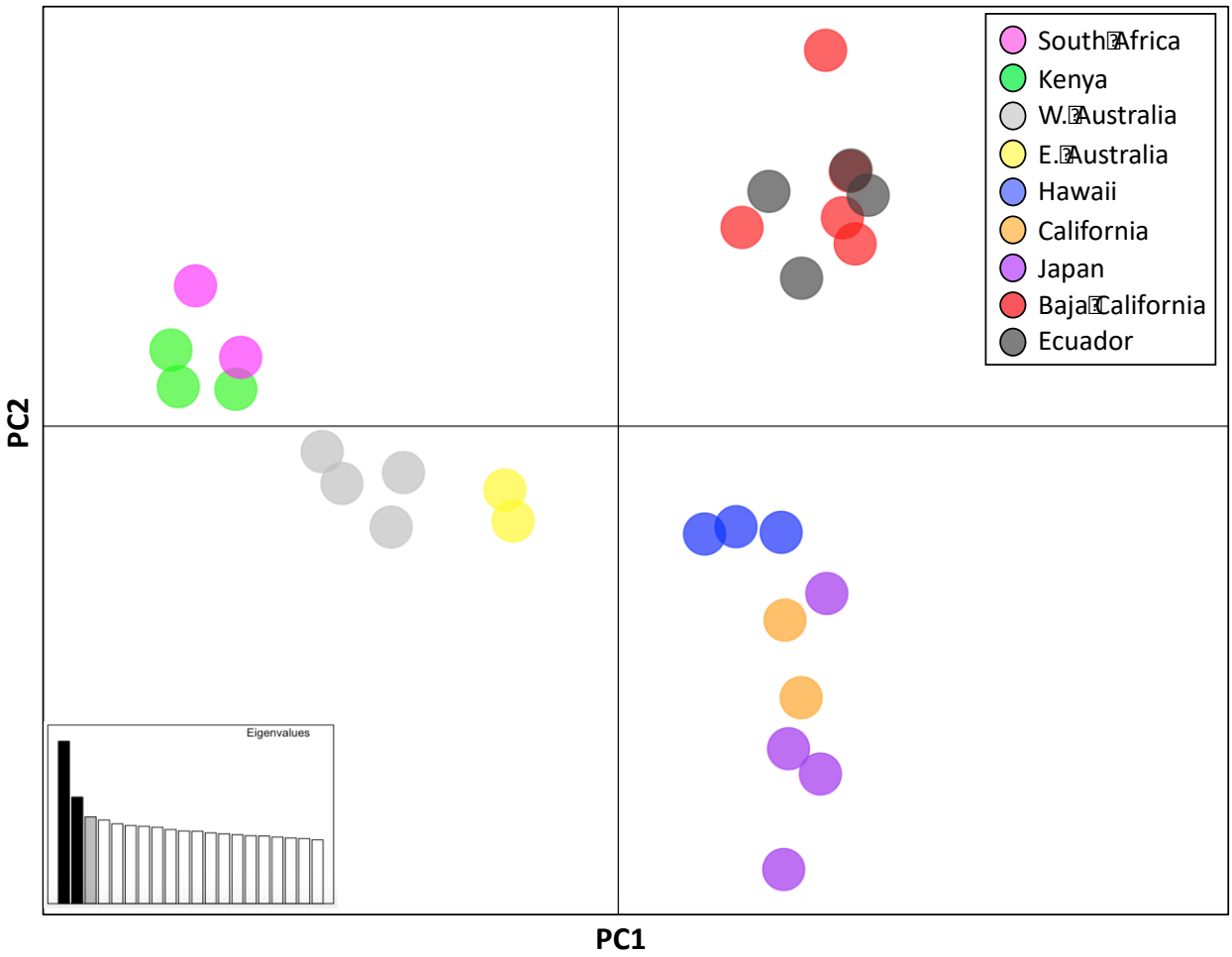


Figure 3. Two-dimensional plot of axes one and two resulting from principal component analysis of SNP data. Points are colored to reflect geographic sampling location and match the inset in the upper right corner. Plotted axes are indicated by black shading of bars representing eigen values in the lower left corner inset.

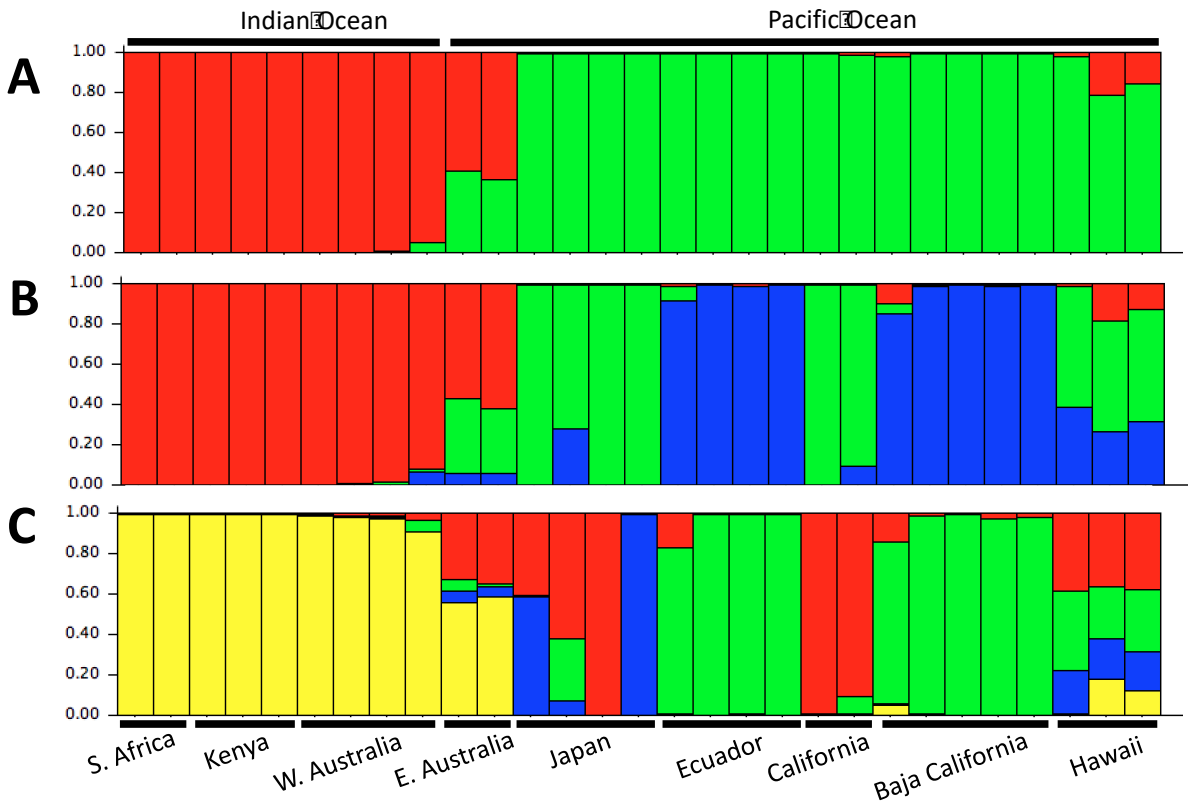
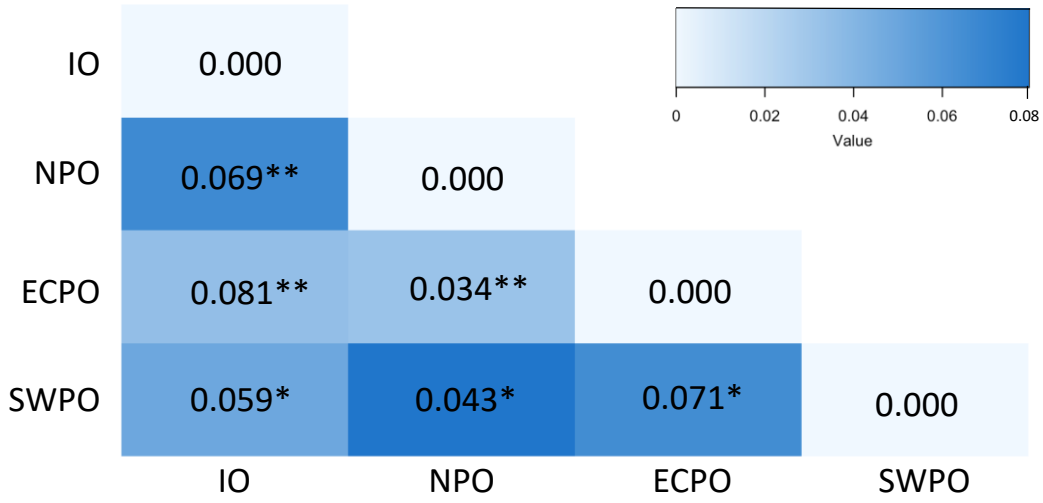


Figure 4. Barplots resulting from STRUCTURE analyses. Each bar represents and individual, and bars are colored to reflect individual admixture (i. e. genetic ancestry, generally speaking). Solid black horizontal lines at top of figure reflect ocean-scale sampling location while those at bottom reflect regional sampling location. Results are shown for scenarios evaluating the presence of two (Panel A), three (Panel B), and four (Panel C) genetic clusters.



**Statistically significant at p ≤ 0.020*

***Statistically significant at p = 0.000*

Figure 5. F_{st} values associated with the pairwise comparison of sample collections pooled based on results from PCA and STRUCTURE. IO = Indian Ocean comprising individuals sampled off Kenya (n = 3), South Africa (n = 2), and western Australia (n = 4); NPO = North Pacific Ocean comprising individuals sampled off Japan (n = 4), Hawaii (n = 3), and California (n = 2); ECPO = eastern Central Pacific Ocean comprising individuals sampled off Ecuador (n = 4) and Baja California (n = 5); SWPO = southwest Pacific Ocean comprising individuals sampled off eastern Australia (n = 2). Cells containing F_{st} values are shaded to reflect degree of genetic differentiation relative to other pairwise comparisons; associated color scale is shown at top right.