Molecular Ecology

WILEY

MOLECULAR ECOLOGY

ORIGINAL ARTICLE OPEN ACCESS

Larval Genomics as a Viable, Fisheries-Independent Tool for Investigating Population Structure in Tropical Pacific Tunas

Jacob E. Jaskiel[1,2,3] | Hannah E. Aichelman[1,2,4] | Giulia Anderson[5] | Louw Claassens[6,7] | James E. Fifer[1,8] | Christina M. Hernandez[9,10] | Alexa K. Huzar[1,11] | Joel K. Llopiz[10,†] | Jan W. Witting[12] | Sean P. Mullen[1] | Randi D. Rotjan[1,2,3]

[1]Department of Biology, Boston University, Boston, Massachusetts, USA | [2]Biology Department, Tufts University, Medford, Massachusetts, USA | [3]Blue Nature Alliance, Arlington, Virginia, USA | [4]Genomics Research Center, University of Rochester, Rochester, New York, USA | [5]Oceanic Fisheries Programme, Fisheries Aquaculture and Marine Ecosystems Division, Pacific Community (SPC), Noumea, New Caledonia | [6]Palau International Coral Reef Center, Koror, Palau | [7]Department of Zoology & Entomology, Rhodes University, Makhanda, South Africa | [8]Department of Ecology, Behavior, and Evolution, School of Biology, University of California San Diego, La Jolla, California, USA | [9]Department of Biological Sciences, Old Dominion University, Norfolk, Virginia, USA | [10]Biology Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA | [11]Department of Integrative Biology, University of Texas at Austin, Austin, Texas, USA | [12]Sea Education Association, Falmouth, Massachusetts, USA

Correspondence: Jacob E. Jaskiel (jaskielj@bu.edu)

Received: 29 August 2025 | **Revised:** 16 February 2026 | **Accepted:** 23 March 2026

Keywords: evolutionary ecology | larval genomics | next-generation sequencing | population genomics | population structure | tuna fisheries

ABSTRACT

Understanding how dispersal, life history, and environmental variability shape genetic connectivity in the open ocean remains a central challenge in evolutionary biology. Highly migratory marine predators like tunas have traditionally been considered genetically homogeneous across ocean basins, yet emerging genomic evidence suggests that cryptic population structure can persist even in species with high gene flow and large effective population sizes. We used 2bRAD sequencing of 348 larval and subadult skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*), and bigeye tuna (*T. obesus*) collected from the central Pacific across 7 years of sampling to examine species boundaries, population genetic information, genetic structure, and connectivity. Larval sampling revealed consistent spawning by all three species and enabled unbiased detection of genetic patterns prior to recruitment bottlenecks. We found strong divergence amongst species, no evidence of structuring within skipjack or bigeye, and a divergent yellowfin population detected in 2 consecutive sampling years north of American Samoa. Comparisons between larvae and subadults suggest that sampling early life history stages can be a valuable tool for assessing population genetic information before recruitment bottlenecks, selective harvest by fisheries, adult dispersal, and selective pressures acting on adult populations, thereby contributing novel insights to the research and effective management of these species. These results highlight how larval genomics can complement traditional population genomic studies of adult tunas and reveal fine-scale structure in highly vagile species, providing new perspectives on connectivity in the open ocean.

1 | Introduction

Tunas comprise some of the most valuable wild-capture fisheries in the world, supplying an average of $USD 40 Billion per year at final point of sale and providing food and job security for millions of people (FAO 2024). Much of the global tuna supply is derived from the western and central Pacific Ocean (WCPO), a region that supplies roughly 50%–60% of the world's

[†]Posthumous Contribution

tuna (Hare et al. 2022; Senina et al. 2018) and is dominated by tropical tunas, including (in descending order of landings) skipjack (*Katsuwonus pelamis*: ~1.75 million metric tonnes per year), yellowfin (*Thunnus albacares*: ~720 thousand mt year^{-1}), and bigeye (*T. obesus*: ~140 thousand mt year^{-1}; Day et al. 2023; Magnusson et al. 2023; Teears et al. 2025). Skipjack and yellowfin, which are characterized by fast generation times, high reproductive output, and large population sizes relative to other tunas, are the dominant catch and are primarily targeted by purse seine fleets to supply canneries throughout the region (Artetxe-Arrate et al. 2021; FAO 2024). Bigeye have slower generation times, smaller population sizes, and are typically found at greater depths, making them targets of longline fisheries that supply high quality tuna to sushi and sashimi markets (Artetxe-Arrate et al. 2021; Campling et al. 2017). In addition to their socio-economic benefits, tunas provide valuable ecosystem services through top-down ecosystem regulation (Baum and Worm 2009; Heithaus et al. 2008; Miller et al. 2018), carbon sequestration via deadfalls (Mariani et al. 2020; Mouillot et al. 2023), and via nutrient transport between pelagic and mesophotic environments (Bernal et al. 2017; Schaefer and Fuller 2010).

Skipjack tuna can reach sexual maturity in as little as 6 months (Ashida et al. 2017; Ohashi et al. 2019) and spawn as much as once per day during the spawning season, which can be year-round in the tropics and involve up to 1.87 million eggs per female during spawning events (Ohashi et al. 2019). Skipjack have a maximum lifespan of 8–10 years, although most of the catch from industrial fisheries encompasses individuals less than 4 years old (Teears et al. 2025). Skipjack are relatively small bodied compared to other commercially harvested tunas, reaching maximum sizes of 90–100 cm (Teears et al. 2025). Yellowfin tuna generally reach sexual maturity at about 2 years of age in the WCPO (Itano 2000), and spawn continuously throughout the year within 10 degrees of latitude from the equator, with reproductively active females releasing up to 4 million eggs per spawning event, which can occur nearly daily in the tropics (Itano 2000; Schaefer 1996). Yellowfin can reach considerably larger body sizes than skipjack, with some individuals growing up to 180 cm and living up to 15 years (Magnusson et al. 2023). Bigeye reach sexual maturity later than the other tropical tunas, with most individuals beginning to spawn from 2 to 5 years of age depending on the sampling region (Farley et al. 2017). Spawning can occur almost daily in reproductively active females and take place year-round in the tropics as in skipjack and yellowfin, but large females are capable of releasing upwards of 8 million eggs per spawning event (Farley et al. 2017; Sun et al. 2013). Bigeye are capable of growing up to 200 cm and living as long as 14–16 years (Day et al. 2023). While all three of these species are capable of retaining metabolic body heat (Ciezarek et al. 2019; Dizon and Brill 1979; Schaefer et al. 2009), bigeye are particularly adept due to their additional heat-exchangers that permit more frequent and deeper dives below the thermocline (Ciezarek et al. 2019; Holland et al. 1992; Thygesen et al. 2016).

All tropical tunas are traditionally considered highly migratory by fisheries managers (United Nations 1982), even though some studies have shown evidence of site fidelity (Filous et al. 2020; Schaefer and Fuller 2009; Schaefer and Fuller 2022; Sibert and Hampton 2003). Still, tropical tunas can travel over 1200 miles between tagging recoveries (Fonteneau and Hallier 2015), traversing Exclusive Economic Zones (EEZs) of different nations as well as the high seas, making international cooperation important for the scientific study and management of these species (Allen et al. 2010; Bayliff et al. 2005). There are five tuna Regional Fisheries Management Organizations (tRFMOS) tasked with studying, managing, and enforcing regulations for tunas within their jurisdictions, with the Western and Central Pacific Fisheries Commission (WCPFC) managing the largest and most productive tuna fisheries in the world (Hare et al. 2022). Since the expansion of industrial commercial tuna fishing in the 1950s, there has been a nearly ten-fold increase in global catch (Juan-Jordá et al. 2011), mainly from the expansion of purse seine fisheries (Barclay 2014; Miyake et al. 2004). The most recent estimates suggest an improvement in tuna stock health, suggesting that 74% of all tuna stocks are in a healthy state (up from 65% in 2025), 0% overfished (down from 9% in 2025; measured by harvest > maximum sustainable yield), and the remaining 26% have remained steadily at an intermediate level based on data from class 4, 5, and 6 industrial vessels (ISSF 2025, 2026). Skipjack, yellowfin, and bigeye tuna are all managed by the WCPFC based on stock assessment models and input from fishing nations and other participating entities. Presently, none of these species are considered to be overfished in the WCPO, and the latest assessments of spawning stock biomass for skipjack, yellowfin, and bigeye are 51%, 47%, and 35% of estimates of unfished levels, respectively (Day et al. 2023; Magnusson et al. 2023; Teears et al. 2025). However, these species are still considered by the International Union for Conservation of Nature to be declining in adult abundance, with bigeye tuna considered a globally vulnerable species (Collette et al. 2021a, 2021b, 2021c).

Previous studies leveraging molecular techniques including mtDNA and microsatellite sequencing led to hypotheses that tunas represented single stocks within ocean basins, with no genetic population structure within tRFMO jurisdictions (Grewe 1997; Kumar and Kocour 2015; Ward et al. 1994). Tropical tunas have long been assumed to be panmictic due to their large population sizes, fast generation times, high migratory potential, and subsequent high levels of gene flow and low genetic drift (Anderson et al. 2020; Funk et al. 2012). Management delineations for stocks therefore reflected the historical economic development of each fishery rather than the biological characteristics of each stock (Moore et al. 2020). However, recent studies leveraging high-throughput DNA sequencing and single-nucleotide polymorphisms (SNPs) as molecular markers have provided evidence of fine-scale regional population structure based on analysis of loci under potential selection (LUPS) that may reflect local adaptations to environmental gradients within ocean basins in yellowfin, and to a lesser extent in bigeye (Grewe et al. 2015; Pecoraro et al. 2018; Weist et al. 2024) but likely not in skipjack (Anderson et al. 2020). The ability to detect genetic structure is dependent on several factors, including spatiotemporal scope of sampling and sequencing methods (Anderson et al. 2019). Despite numerous studies reporting intra-basin structure based on LUPS, it is important to note that divergence at outlier loci is not necessarily sufficient to confirm true genetic structure, and sampling design, sequencing errors, or statistical artefacts can lead to observable divergence and apparent structuring without confirming the roles of such genes and their influence on

individual fitness (Pardo-Diaz et al. 2015). Such studies typically fail to observe intra-basin genetic structuring when using neutral SNPs (Grewe et al. 2015; Pecoraro et al. 2018). Nevertheless, the potential existence of subpopulations within tRFMO management areas raises concerns of the possibility to overfish subpopulations with cryptic genetic diversity if not accounted for in management frameworks (Begg et al. 1999).

Here, we use 2bRAD sequencing to demonstrate the utility of larval genomics in assessing population genetic information of commercially important tropical tunas. We use these data to confirm which species are utilizing the central Pacific as a spawning habitat, compare population genetic information, and investigate patterns in population structure and connectivity within skipjack, yellowfin, and bigeye tuna collected from the Phoenix Islands Protected Area (PIPA) and the surrounding waters spanning over 30 degrees of latitude and 16 degrees of longitude, as well as the Palau National Marine Sanctuary (PNMS). We also compare our findings from larval genomics to those of adult yellowfin and bigeye collected from PIPA to explore the benefits and drawbacks of larval genomics as a method of studying tuna populations and aiding fisheries management.

2 | Materials and Methods

2.1 | Field Sampling, Sequencing, and Genotyping

2.1.1 | Study Sites—Phoenix Islands Protected Area, Palau National Marine Sanctuary

The Phoenix Islands are located in the central equatorial Pacific and are comprised of islands, atolls, and seamounts that interact with equatorial currents to create hotspots of upwelling and primary productivity that attract a high diversity of coral reef, pelagic, and deep sea organisms (Auscavitch et al. 2020; Rotjan et al. 2014). In 2015, the Republic of Kiribati elevated PIPA to a fully no-take MPA, preventing commercial fishing and other extractive activities until PIPA was re-opened in January 2023 (Kittinger et al. 2024). Skipjack, yellowfin, and bigeye tuna have all been observed to use the Phoenix Islands as a spawning area (Hernández et al. 2019). Due to the Phoenix Archipelago's physical location in the central equatorial Pacific, it may represent an area of mixing between different populations of tunas, such as eastern and western stocks which are managed by different tRFMOs, particularly during El Nino Southern Oscillation (ENSO) conditions when much of the tuna biomass in the western Pacific follows the warm pool eastwards towards the Phoenix Islands (Lehodey et al. 1997; Tseng et al. 2010). Consequently, the Phoenix Islands Archipelago is an ideal location to assess population demographics and structure of tunas in the region. Additionally, opportunistic sampling in the PNMS provides a geographic outgroup to test for connectivity between the Marine Protected Areas (MPAs), and allows for an assessment of population structure of PNMS tuna, consistent with the management and research priorities identified in the PNMS Monitoring and Science Strategy (Claassens et al. 2023). The PNMS was enacted in 2015 and came into effect in 2020, when 80% of Palau's EEZ was closed to all extractive activities with the remaining 20% of the EEZ open for artisanal fishing. Similar to the establishment of PIPA, the formation of the PNMS aimed to protect offshore and deep-sea habitats while maintaining cultural ties to the pelagic environment.

2.1.2 | Larval Sampling and Lab Processing

Larval sampling primarily occurred on board the SSV *Robert C Seamans* (Sea Education Association) along similar cruise tracks and sampling dates in 2015 (July 8 to August 7), 2016 (July 5 to August 6), 2017 (July 11 to August 9), 2018 (July 8 to August 10), and 2019 (July 7 to August 5; Figure 1a). Sampling took place over the entire cruise track and encompassed 18.9° N to 12.2° S and 159.1° W to 175.2° W, with 147/272 (54%) of the total sampling stations occurring within the PIPA boundary, and the remaining 125 (46%) during transit to and from PIPA spanning the areas from American Samoa to 6.6° S, and from 1° S to Hawaii (Figure 1a). Up to 3 different zooplankton net deployments occurred at each station, with 2 or more conducted at each station inside the boundary of PIPA. Nets were towed for roughly 30 min at a speed of approximately 2 knots. A Tucker Trawl with a 1 m^2 opening and 333 μm mesh was first towed obliquely to the thermocline (approximately 100–150 m) to sample the mixed layer. The Tucker Trawl net was then used again to sample the upper 50 m, where larval tuna are typically most abundant (Boehlert and Mundy 1994), using a double oblique tow (Wiebe et al. 2015). Lastly, a 0.5 × 1 m Neuston net was used to sample the upper 0.25 m of the surface waters. Sampling took place at roughly local noon and local midnight every day. Zooplankton samples were fixed in 95% ethanol before being shipped to Boston University, Boston, MA.

Larval fish were separated from the general zooplankton biomass under a Leica M165FC stereomicroscope. Tuna larvae were separated and identified as either skipjack tuna (*Katsuwonus pelamis*) or true tunas in the genus *Thunnus* using morphological characteristics (Nishikawa and Rimmer 1987; Richards 2005; Figure S1). Each larva was photographed and total length was measured using a Leica DFC550 digital camera with Leica Application Suite v4.9.0. Prior to DNA extraction, the gut of each larva was excised using a sterilized surgical scalpel to avoid contamination of sequencing results from potential prey.

Larvae were also opportunistically collected from October 7–23, 2022 in the PNMS by the Palau International Coral Reef Center. Sampling was concentrated in three regions within the Palau EEZ: PNMS North and South (both fully protected), and the Domestic Fishing Zone (open to commercial fishing; Figure 1b). Within each sampling region, 2–3 sites separated by at least 15 nautical miles (nm) were sampled with 3 net deployments at each site, with all deployments occurring at least 2 nm apart. In total, 6 tows were conducted in the north, 3 tows were conducted in the west, and 12 tows were conducted in the south ($N = 21$ total deployments). For each deployment, a 2 m^2 plankton net with 333 μm mesh was lowered to a depth of at least 50 m and pulled at 2 kts. Once at the desired depth, the net was slowly brought back to the surface via a winch, and this process was repeated two more times to conduct a triple oblique/towyo deployment (Wiebe et al. 2015). A SeaGear Flowmeter and depth logger were also attached to the net to record the volume of water filtered and confirm the depth of each net deployment. Upon recovery of the net, zooplankton biomass was fixed in 95% ethanol and sorted

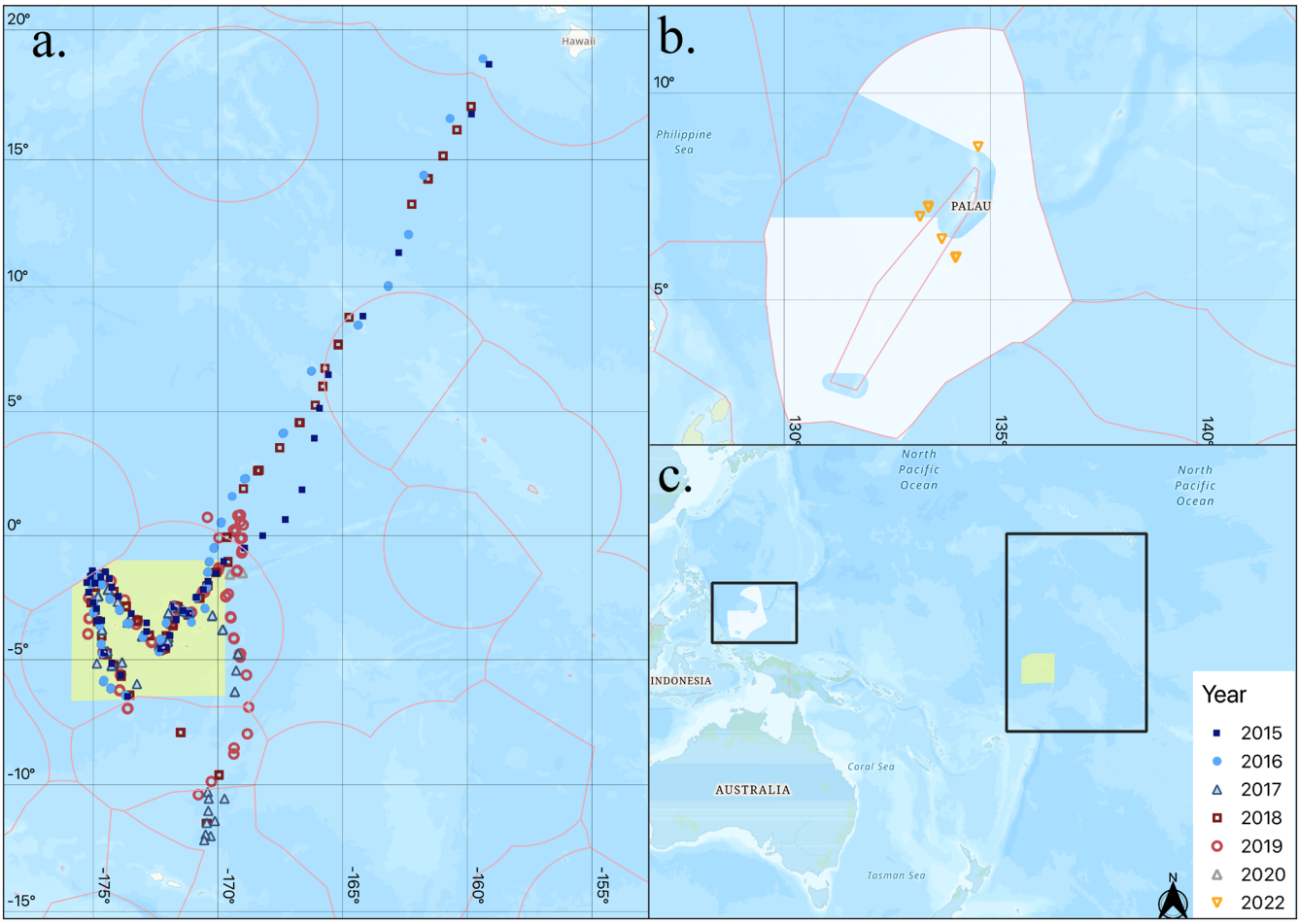

FIGURE 1 | Maps of sampling locations. (a) Map of sampling locations from 2015 to 2020 within the Phoenix Islands Protected Area (PIPA) and surrounding waters with Exclusive Economic Zones (EEZs) shown in orange. (b) Map of sampling locations from 2022 within the Palau National Marine Sanctuary (PNMS) with EEZs shown in orange. (c) Map of the broader western and central pacific with map extents (black boxes) showing sampling regions.

for tuna larvae (for additional details, see Claassens et al. 2024). Larvae were then shipped to Boston University, Boston, MA for genomic analysis. Processing of PNMS larval tuna prior to DNA extraction followed the same protocols as above.

2.1.3 | Adult Sampling

Fin clips from subadult and adult (79–121 cm) bigeye (*T. obesus*) and yellowfin (*T. albacares*) tuna were collected from September 13–16, 2020 from sampling stations within the PIPA boundary (Figure 1a) by the Secretariat of the Pacific Community during a tagging survey for the WCPFC. Sampling occurred with pole and line near oceanographic data moorings and drifting fish aggregating devices at night. Fin clips were fixed in RNAlater before they were shipped to Boston University, Boston, Massachusetts.

2.1.4 | DNA Extraction and 2bRADseq Library Preparations

Larval and adult tuna DNA was extracted using Qiagen DNEasy Blood and Tissue Kits (Qiagen, Hilden, Germany) following manufacturer's instructions, except a smaller volume of elution buffer was used to increase DNA concentrations. The resulting DNA was quantified using a Quant-iT PicoGreen dsDNA assay kit (Thermo Fisher Scientific) and prepared for 2bRAD sequencing (Wang et al. 2012). 60 technical replicates were used to account for downstream sequencing batch effects that may arise due to multiple sequencing runs. In total, 466 samples were successfully sequenced, with 180 samples sequenced across 2 lanes of Illumina HiSeq2500 using single-end 50 bp sequencing, and 286 samples sequenced across 3 lanes of Illumina NovaSeq6000 using single-end 100 bp sequencing at the Tufts University Core Facility in Boston, Massachusetts. Sample metadata and information on sequencing depth and coverage can be found in Data S2.

2.1.5 | Genotype Calling and Detection of Technical Replicates

Initial processing of 2bRAD-seq data followed the pipeline outlined at https://github.com/z0on/2bRAD_denovo (accessed February 2023). Adapters and barcodes were trimmed, and raw reads were demultiplexed using the provided trimming/demultiplexing perl script. Cutadapt v. 4.1 (Martin 2011) was used to remove reads with Phred quality score less than 15

and reads less than 25 bp in length. All reads were mapped to a *T. albacares* reference genome (Accession: GCF_914725855.1; Wellcome Sanger Tree of Life Programme, 2023) using bowtie2 v2.5.1 with default parameters (Langmead and Salzberg 2012). Genotyping and identification of single nucleotide polymorphisms (SNPs) were conducted using maximum likelihood estimates produced by ANGSD v0.935 (Korneliussen et al. 2014). The following genotyping filters were used for initial identification of technical replicates: retained loci were present in at least 50 individuals, had a minimum mapping quality Phred score of 20, minimum quality Phred score of 25, strand bias p-value $> 1 \times 10^{-5}$, heterozygosity bias p-value $> 1 \times 10^{-5}$, SNP p-value (probability a site is truly variable) $< 1 \times 10^{-5}$, minimum minor allele frequency > 0.05, excluded triallelic sites, and excluded reads with multiple best hits (Figure S2; see Table S1 for the genotyping filters for each analysis and subsequent number of loci retained). Additionally, individuals that had less than 40% of their sites with $> 5\times$ coverage were removed from downstream analyses ($n = 46$). Four larval samples from PNMS did not cluster with any known species group and were therefore excluded from subsequent analyses. Sequences from technical replicates were then merged with samtools v1.12 (Danecek et al. 2021). The full analysis pipeline can be found open source at https://github.com/jaskielj/Jaskiel_et_al_2025_Tuna_2bRAD.

2.2 | Interspecific Analyses

2.2.1 | Species Identification and Validation

Putative species groups were assigned using a hierarchical clustering dendrogram (Figure S3a) constructed based on a pairwise identity by state (IBS) matrix produced via ANGSD using the following filters: loci must have been present in at least 80% of individuals, individual sequencing depth had to be 5× or greater per locus, loci had a minimum mapping quality Phred score of 20, minimum quality Phred score of 25, strand bias p-value $> 1 \times 10^{-5}$, heterozygosity bias p-value $> 1 \times 10^{-5}$, SNP p-value $< 1 \times 10^{-5}$, minimum minor allele frequency > 0.05, excluded triallelic sites, and excluded reads with multiple best hits (Table S1). A Principal Coordinate Analysis (PCoA) based on resulting IBS matrices was conducted in R(R Core Team 2024) using the *capscale* function (package = *vegan*; Oksanen et al. 2022) to confirm species groups assigned via hierarchical clustering (Figure 2). ADMIXTURE v1.3.0 (Alexander et al. 2009) was used to validate the optimal number of species clusters (K) using Evanno's ΔK (Evanno et al. 2005) and the least cross validation error with 10 replicates for each value of K, from $K = 1$ to $K = 10$. However, admixture plots for the most probable numbers of population clusters were produced using NGSadmix v32 (Skotte et al. 2013) based on PCoA and cluster dendrogram results, as Evanno's ΔK and least CV error did not agree on the optimal number of population clusters (Figure 3; Figure S4).

2.2.2 | Genetic Divergence of Tropical Tuna Species

Before calculating genetic differentiation between species, sequences were grouped according to their cluster assignment and the following filters were used to produce sets of SNPs without distorted allele frequencies: loci must have been present in at least 80% of individuals, had a minimum mapping quality Phred score of 20, minimum quality Phred score of 25, strand bias p-value $> 1 \times 10^{-5}$, heterozygosity bias p-value $> 1 \times 10^{-5}$, excluded triallelic sites, excluded reads with multiple best hits, and no minimum minor allele frequency or SNP p-value filters were used (Table S1). ANGSD was then used to calculate the Site Allele Frequency (SAF) for each species group's panel of SNPs. RealSFS was then used to calculate folded 1d Site Frequency Spectra (1dSFS) for each pairwise species comparison. SAFs

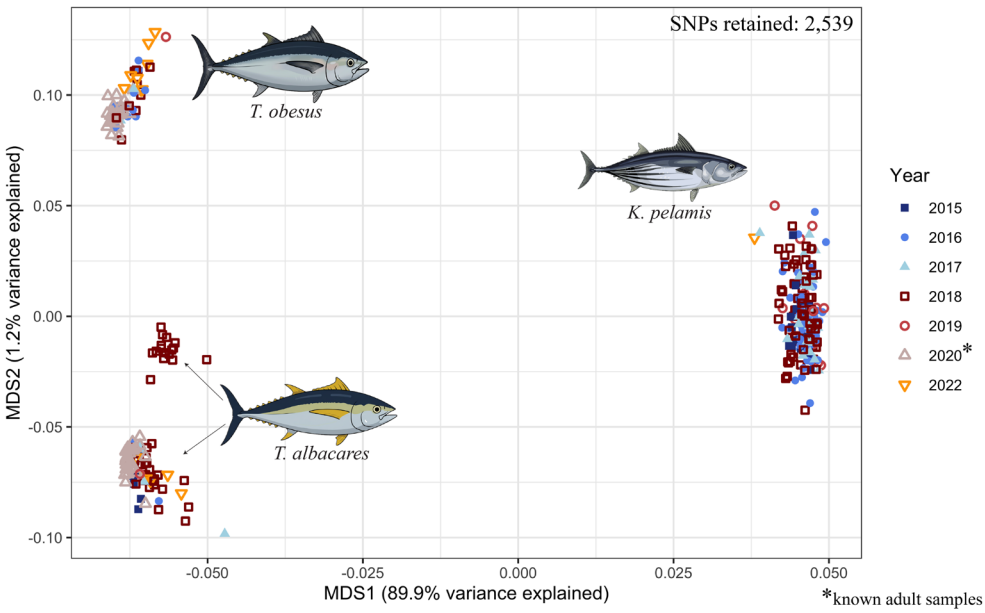

FIGURE 2 | Principal Coordinate Analysis (PCoA) of all samples ($N = 356$) based on the identity by state matrix using a panel of 2539 single-nucleotide polymorphisms (SNPs). Clusters represent skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*), and bigeye tuna (*T. obesus*). The asterisk indicates known adult samples of *T. albacares* and *T. obesus* collected from PIPA in 2020.

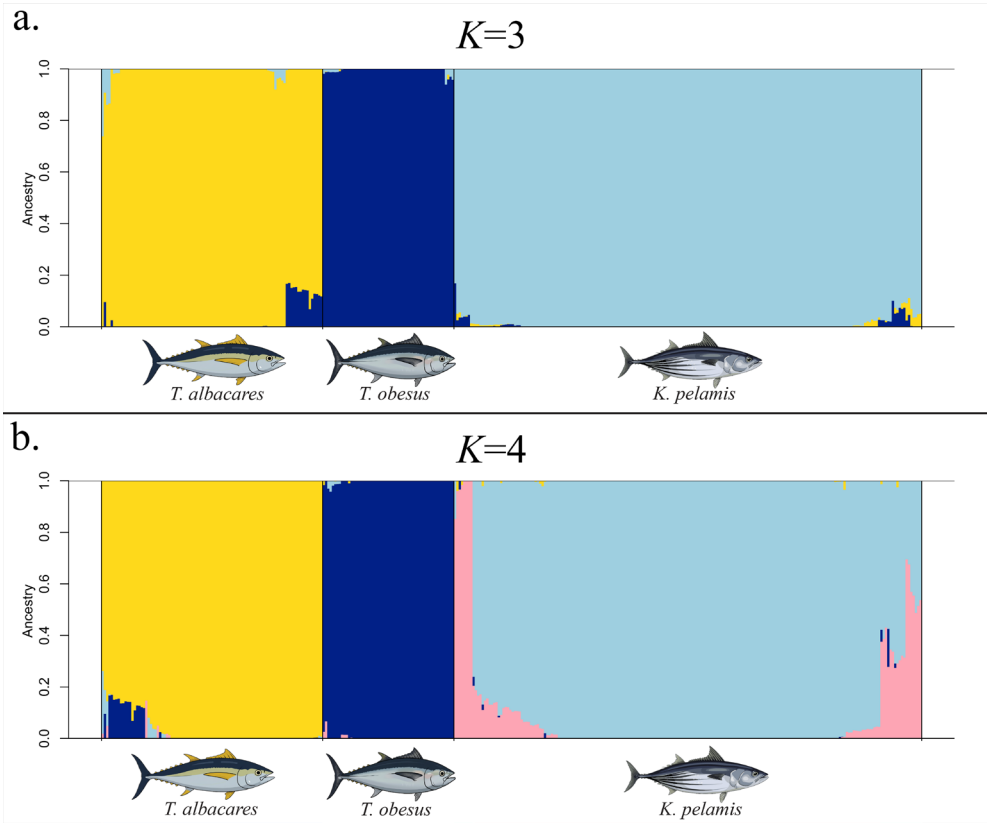

FIGURE 3 | (a) Admixture plot of all samples ($N = 356$) grouped by putative species cluster with $K = 3$ populations. (b) Admixture plot of samples grouped by putative species cluster with $K = 4$ populations.

and SFSs were used to calculate weighted global F_{ST} for each pairwise species comparison (Figure S3b).

2.3 | Intraspecific Analyses

2.3.1 | Linkage Disequilibrium Filtering, Detection of Related Individuals, and Outlier Detection

Before analysing species groups individually, loci in Linkage Disequilibrium (LD) were detected with ngsLD (Fox et al. 2019) and sites in linkage were removed based on the LD decay curve for each species (Figure S5; max distance = 5 kb, min $r^2 = 0.2$ for each) using the provided LD pruning script (https://github.com/fgvieira/prune_graph). Following the removal of linked sites, related individuals were detected with NGSrelate v2 (Hanghøj et al. 2019), and dyads with pairwise relatedness exceeding 0.125 (corresponding to first cousins) were identified (Figure S6). The individual with the lowest sequencing coverage was removed from each dyad, as presence of close kin can influence observed patterns of population structure (Selwyn et al. 2016) or indicate cross-contamination of samples (Anderson et al. 2023). Finally, outlier sites were detected for each species cluster with the R package *pcadapt* v4.4.1 (Luu et al. 2017; Privé et al. 2020), which uses robust Mahalanobis distances to identify SNPs that are highly correlated with the most explanatory principle components from PCA and does not rely on prior population assignments. SNPs with q-values < 0.05 (false discovery rate less than 5%) using the Benjamini-Hochberg Procedure were considered to be outliers, and were removed to produce panels of neutral SNPs for analysis of population genetic statistics, structure, and connectivity.

2.3.2 | Genetic Divergence and Demographics Within Tropical Tuna Species

To assess the degree of genetic divergence between years of sampling within individual species clusters, the following set of genotyping filters were applied: neutral, unlinked loci must have been present in at least 80% of unrelated individuals, and no minimum minor allele frequency or SNP p-value filters were applied (Table S1). Resulting SNPs were then used to calculate SAFs and corresponding folded 1dSFS for each year of sampling for each species group. Weighted pairwise F_{ST} between sampling years for each species cluster was calculated in realSFS using the 1dSFS (Figure 4) only for year-classes with 4 or more individuals to avoid inflated F_{ST} as a consequence of low sample size. Expected heterozygosity (H_e) was calculated with realSFS's expectation maximization algorithm using genotype likelihoods generated by ANGSD (Figure S7). Welch's two sample t-tests were used to determine differences between H_e values calculated for each year of sampling within species clusters. Nucleotide diversity (π) and thetas were acquired in ANGSD by first taking the folded SFS produced earlier for each species and calculating thetas for each chromosome with realSFS. Then, Watterson's Theta (θ_W) and Tajima's D (Tajima 1989) were calculated for each species (Table 1). Effective population size (N_e) was calculated using $\theta = 4N_e\mu$, where $\theta = \theta_W$ (Table 1). The mutation rate μ has been estimated for yellowfin to be 7.3×10^{-9} mutations per

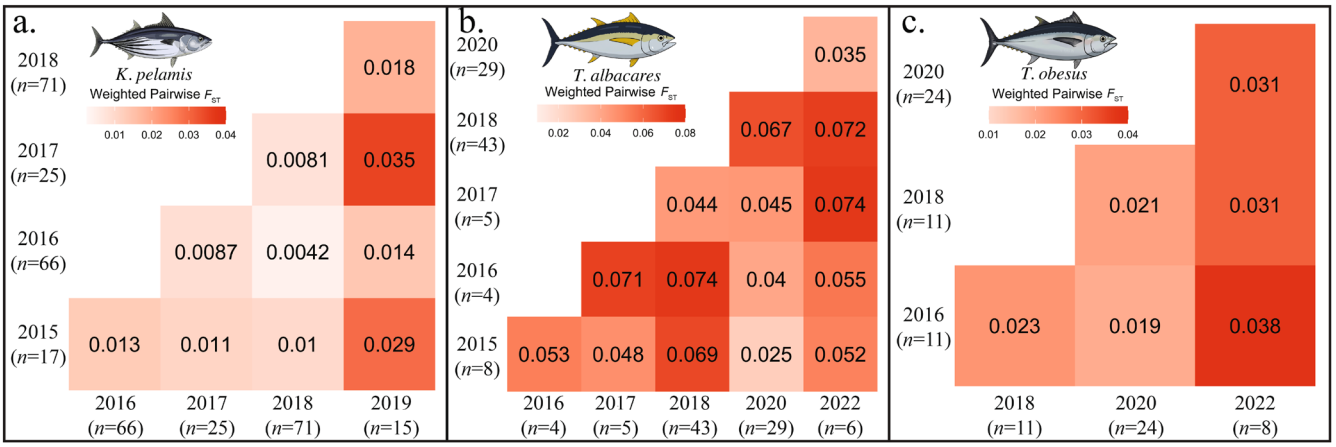

FIGURE 4 | Weighted pairwise F_{ST} across sampling years for (a) *K. pelamis*, (b) *T. albacares*, and (c) *T. obesus*.

TABLE 1 | Population demographic summary statistics for each focal species. Statistics are based on neutral, unlinked SNPs present in at least 80% of unrelated individuals, and no minimum minor allele frequency or SNP *p*-value filters were applied. Included are average expected heterozygosity (H_e), average observed heterozygosity (H_o), nucleotide diversity (π), Watterson's theta (θ_W), Tajima's *D*, and estimated effective population size (N_e) calculated using $N_e = \theta_W/4\mu$, where μ was assumed to be 7.3×10^{-9} for yellowfin (Barth et al. 2017), and approximate corrections of μ for skipjack and bigeye were 5.1×10^{-9} and 9.5×10^{-9}, respectively.

Species	Expected heterozygosity (H_e)	Observed heterozygosity (H_o)	Nucleotide diversity (π)	Watterson's theta (θ_W)	Tajima's *D*	Effective population size (N_e)
K. pelamis	0.031	0.028	0.030	0.089	−2.03	4,362,745
T. albacares	0.033	0.026	0.033	0.071	−1.75	2,431,507
T. obesus	0.030	0.027	0.028	0.073	−2.07	1,921,053

site per generation (Barth et al. 2017), and we applied approximate 30% corrections for skipjack and bigeye mutation rates (5.1×10^{-9} and 9.5×10^{-9}, respectively) to account for life history differences like generation times and fecundity, which influence per site per generation mutation rates (Bergeron et al. 2023). Average H_e and observed heterozygosity (H_{obs}) were derived from allele frequencies under Hardy–Weinberg Equilibrium for each species group (Table 1), where $H_e = 2pq$, $H_{obs} = H_e - F(H_e)$, and F is the inbreeding coefficient estimated by ANGSD.

2.3.3 | Analyses of Population Genetic Structure

To investigate intraspecific population genetic structure across years of sampling, the following genotyping filters were used in ANGSD to filter SNPs: neutral, unlinked loci were present in at least 80% of unrelated individuals, had an individual sequencing depth of 5× or greater per locus, had a minimum mapping quality Phred score of 20, minimum quality Phred score of 25, strand bias p-value $> 1 \times 10^{-5}$, heterozygosity bias p-value $> 1 \times 10^{-5}$, SNP p-value $< 1 \times 10^{-5}$, minimum minor allele frequency > 0.05, excluded triallelic sites, and excluded reads with multiple best hits (Table S1). The resulting IBS matrices were used to create PCoA plots and cluster dendrograms for each species in R using the *capscale* function in the package *vegan* (Figure 5). ADMIXTURE was used to infer ancestry proportions within species, and the least cross validated error was used to determine the optimal number of clusters/populations within each species group using 10 replicates for each K (Figure S8). In order to assess connectivity between MPAs and determine whether physical distance drove genetic divergence between samples, isolation by distance plots were produced in R, and Mantel tests were conducted to quantify the relationship between pairwise geographic and genetic distances using 9999 permutations (Figure 6).

The differences in population genetic parameters between the main yellowfin cluster and the putative subpopulation were explored by separating the sequences for each population and calculating pairwise F_{ST}, H_e, H_{obs}, π, and θ_W as above (Table 2). The same population genetic parameters were calculated separately for adults and larvae of both yellowfin and bigeye to assess whether fisheries-independent sampling of larvae yielded comparable values to adult samples (Table 3).

3 | Results

3.1 | Interspecific Analyses

3.1.1 | Technical Replicate Detection and Species Identification

A dendrogram corresponding to all samples ($N = 466$; Figure S2) with the initial set of genotyping filters (31,694 SNPs; Table S1) was initially used to validate sequencing

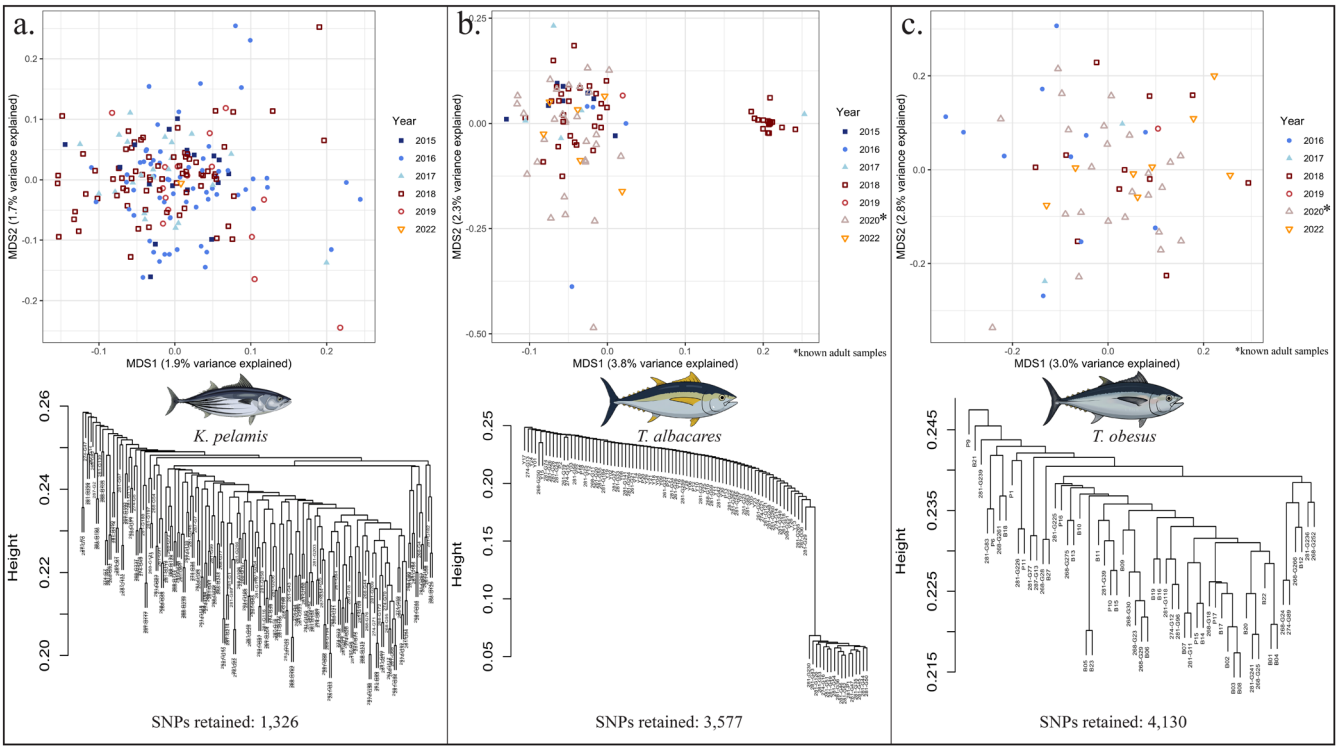

FIGURE 5 | Principal coordinate analysis (PCoA) and corresponding cluster dendrograms of individual species groups based on identity by state matrices. (a) PCoA and cluster dendrogram of skipjack based on 1326 neutral single-nucleotide polymorphisms (SNPs) (b) PCoA and cluster dendrogram of yellowfin based on 3577 neutral SNPs (c) PCoA and cluster dendrogram of bigeye based on 4130 neutral SNPs.

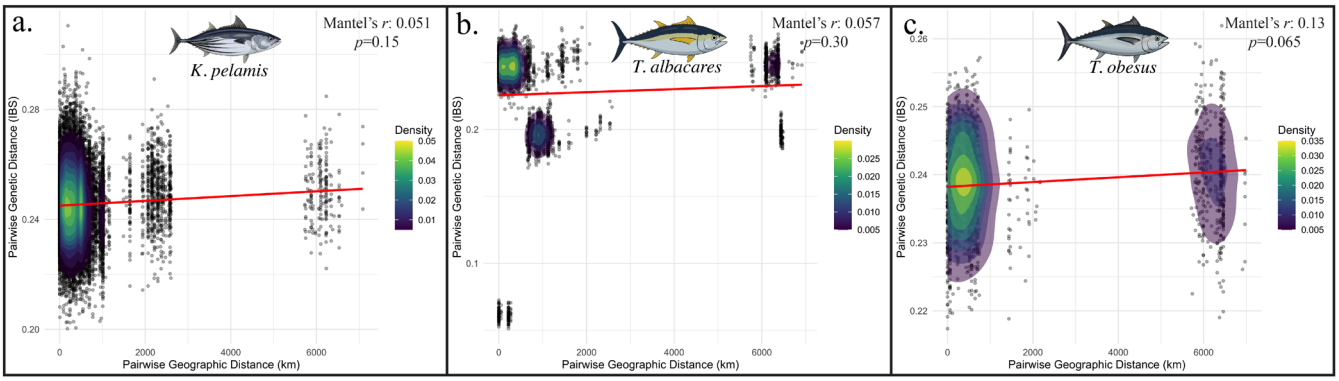

FIGURE 6 | Isolation by distance plots comparing pairwise geographic distances between sampling locations to pairwise genetic distances for (a) skipjack, (b) yellowfin, and (c) bigeye tuna. Mantel's *r*, associated *p*-values, and best fit lines are included to show the relationship between geographic and genetic distances.

TABLE 2 | Population genetic parameters (H_e, H_{obs}, PW F_{ST}, π, and θ_W) calculated separately for the main yellowfin cluster and the putative yellowfin subpopulation.

Yellowfin population	Expected heterozygosity (H_e)	Observed heterozygosity (H_o)	Pairwise F_{ST}	Nucleotide diversity (π)	Watterson's theta (θ_W)
Main	0.029	0.026	0.39	0.028	0.054
Subpop	0.027	0.024		0.024	0.036

accuracy based on identification of technical replicates, whose sequences were ultimately merged for downstream analysis after ensuring batch effects were not apparent. Technical replicates were confirmed to have much higher similarity to their replicate than to other samples. Additionally, no notable differences in sequencing coverage or depth were observed

TABLE 3 | Population genetic parameters (H_e, H_{obs}, PW F_{ST}, π, and θ_W) calculated for adult and larval samples of yellowfin and bigeye tuna.

Species/life stage	Expected heterozygosity (H_e)	Observed heterozygosity (H_o)	Pairwise F_{ST}	Nucleotide diversity (π)	Watterson's theta (θ_W)
Adult *T. albacares*	0.029	0.026	0.033	0.028	0.049
Larval *T. albacares*	0.034	0.025		0.034	0.069
Adult *T. obesus*	0.031	0.027	0.012	0.029	0.059
Larval *T. obesus*	0.029	0.026		0.028	0.060

between sequencing runs (Data S2), and samples clustered according to putative species group rather than by sequencing run, further indicating batch effects were not present. Removal of individuals with poor sequencing coverage (less than 40% of sites covered at > 5× depth) and samples that did not cluster with known species groups resulted in a total of 356 individuals retained, including 288 larvae and 53 adult tuna from PIPA, and 15 larvae from PNMS (Tables S2 and S3). The PCoA and dendrogram of the resulting 356 tuna with more stringent genotyping filters (2539 SNPs; Table S1) yielded 4 clusters representing 3 putative species groups, including one cluster of skipjack, one cluster of bigeye, and 2 clusters of yellowfin (Figure 2; Figure S3a). While skipjack larvae are identifiable to species level morphologically, *Thunnus* larvae are not easily distinguishable; therefore, species level identification for larval yellowfin and bigeye was confirmed using cluster assignment with known adult samples.

3.1.2 | Genetic Divergence of Tropical Tuna Species

Weighted pairwise global F_{ST} values between putative species clusters indicated high divergence between species (Figure S3b; skipjack/yellowfin = 0.25, skipjack/bigeye = 0.28, yellowfin/bigeye = 0.32). The optimal number of species clusters according to least CV error was 7 (Figure S4a), while Evanno's ΔK was maximized at $K = 2$ with 10 replicates for each K (Figure S4b). Consequently, the values of K used in admixture plots were based on the number of species groups ($K = 3$) and the number of clusters from the PCoA and cluster dendrogram of all samples ($K = 4$), since least CV error can often be minimized at higher values of K due to overfitting (Bradburd et al. 2018), while Evanno's ΔK can underestimate K with uneven sampling of hierarchically structured populations (Puechmaille 2016). Admixture ancestry proportions of individuals based on species assignments showed some limited mixing between clusters. For $K = 3$ and $K = 4$, the divergent group of yellowfin larvae appeared to have mixed ancestry proportions with the bigeye lineage (Figure 3). Skipjack were assigned to 2 lineages with mixed ancestry for some individuals when $K = 4$.

3.1.3 | Linkage Disequilibrium, Related Individuals, and Outlier Detection

Patterns in linked loci were very similar across all three species clusters, with the line of best fit indicating rapid LD decay and relatively weak linkage amongst loci (Figure S5). The number of SNPs retained after removal of linked sites is reported for each species group in Table S1. After calculating relatedness and kinship coefficients with NGSrelate v2, 9 dyads representing 17 individuals within skipjack samples were found to have pairwise relatedness values exceeding the threshold of 0.125 (Figure S6), and the individual with the lowest sequencing coverage in each dyad was removed from subsequent analyses ($n = 8$). No samples from the yellowfin or bigeye sample groups were found to have pairwise relatedness or kinship above the threshold corresponding to first-cousin levels of relatedness.

No outlier sites were detected within skipjack sequences using *pcadapt* with a false discovery rate of 5% (q-values < 0.05) using the Benjamini-Hochberg Procedure, and therefore all subsequent analyses with skipjack were conducted with the full panel of filter-passing SNPs that were assumed to be neutral ($n = 1326$). Conversely, yellowfin had 2265 SNPs identified as outliers using the same thresholds, which were consequently removed from the dataset and resulted in 3577 neutral SNPs for downstream analysis. Under the same thresholds, bigeye only had 3 sites flagged as outliers, which were also removed and resulted in a panel of 4130 neutral SNPs for downstream analysis.

3.2 | Intraspecific Analysis—Genetic Divergence, Demographics, and Population Structure

3.2.1 | Skipjack

Weighted pairwise F_{ST} values calculated across 5 years of larval skipjack collections revealed generally low divergence between groups (Figure 4a). Weighted pairwise F_{ST} ranged from 0.0042–0.035, and was generally highest in comparisons involving the skipjack collected in 2019. Average H_e and H_{obs} were 0.031 and 0.028, respectively (Table 1), and skipjack collected in 2019 exhibited significantly higher H_e than all other years of sampling except 2015 based on Welch's two sample t-tests ($p < 0.05$; Figure S7a). Skipjack had intermediate values of nucleotide diversity ($\pi = 0.030$) and Tajima's D ($D = -2.03$) compared to the other species analysed, and had the highest observed values of Watterson's Theta ($\theta_W = 0.089$) and estimated effective population size ($N_e = 4{,}362{,}745$; Table 1). The dendrogram displaying hierarchical clustering of pairwise IBS values for skipjack along with the corresponding PCoA (Figure 5a) showed no distinct patterns in ordination that would indicate population structuring based on an analysis of all neutral sites that passed a stringent set of genotyping filters and excluded related individuals (1326 SNPs retained).

Additionally, the most probable number of populations observed across all samples based on least CV error with 10 replicates was 1 (Figure S8a). Skipjack showed no significant relationship between pairwise geographic and genetic distances based on a Mantel test ($r = 0.051$, $p = 0.15$; Figure 6a).

3.2.2 | Yellowfin

Weighted pairwise F_{ST} values calculated across the 6 years of yellowfin sampling had the highest range and maximum value of the three species included in this study. Pairwise F_{ST} ranged from 0.025 to 0.074, and the highest values generally involved samples collected in 2016 and 2018 (Figure 4b). Yellowfin had the highest average expected heterozygosity ($H_e = 0.033$), but the lowest average observed heterozygosity ($H_{obs} = 0.026$) amongst the three species (Table 1). Comparisons of average H_e across years of yellowfin sampling yielded few statistically significant differences; however, samples collected in 2017 had the highest average H_e, while samples collected in 2022 from PNMS had significantly lower H_e than all years except 2016 ($p < 0.05$; Figure S7b). Yellowfin also exhibited the highest values of nucleotide diversity ($\pi = 0.033$) and Tajima's D (−1.75) compared to skipjack and bigeye, but had the lowest calculated Watterson's Theta ($\theta_W = 0.071$) and effective population size ($N_e = 2{,}431{,}507$; Table 1).

The dendrogram for the analysis of yellowfin and the corresponding PCoA based on strict genotyping filters (Figure 5b; 3577 neutral SNPs retained) displayed divergence within yellowfin that suggests apparent population structure within this group driven by 17 samples from 2017 ($n = 1$) and 2018 ($n = 16$). The most probable value of K with 10 replicates based on least CV error was 2 (Figure S8b), further supporting the presence of 2 populations of yellowfin across the sampling areas. The putative subpopulation of yellowfin exhibited lower expected ($H_e = 0.027$) and observed ($H_{obs} = 0.024$) heterozygosities compared to the main population ($H_e = 0.029$; $H_{obs} = 0.026$), and weighted pairwise F_{ST} was high between the two populations ($F_{ST} = 0.39$; Table 2). Additionally, the subpopulation had lower values of nucleotide diversity ($\pi = 0.024$) and Watterson's Theta ($\theta_W = 0.036$) than the main population ($\pi = 0.028$; $\theta_W = 0.054$; Table 2). Despite the divergence, there was no significant relationship between pairwise geographic and genetic distances according to the Isolation by Distance plot (Mantel's $r = 0.057$, $p = 0.30$; Figure 6b), suggesting population connectivity between PIPA and PNMS yellowfin.

Yellowfin larvae exhibited higher average expected heterozygosity ($H_e = 0.034$) and lower observed heterozygosity ($H_{obs} = 0.025$) when compared to adults ($H_e = 0.029$; $H_{obs} = 0.026$; Table 3). Larvae also exhibited higher values of nucleotide diversity ($\pi = 0.034$) and Watterson's Theta ($\theta_W = 0.069$) than adult yellowfin ($\pi = 0.028$; $\theta_W = 0.049$; Table 3). Pairwise F_{ST} between adult and larval samples was relatively low ($F_{ST} = 0.033$).

3.2.3 | Bigeye

The values of weighted pairwise F_{ST} across years of bigeye sampling were generally lower than those of yellowfin but higher than those observed in skipjack, and were the most stable across sampling years (Figure 4c). Values ranged from 0.019 to 0.038, and the highest values were observed in comparisons involving samples collected in 2022 from PNMS. When compared to the other species groups, bigeye had intermediate values of expected and observed heterozygosities ($H_e = 0.030$; $H_{obs} = 0.027$; Table 1). Expected heterozygosity in 2022 was significantly lower than all other years of sampling for bigeye tuna ($p < 0.05$; Figure S7c). Compared to skipjack and yellowfin samples, bigeye had the lowest values of nucleotide diversity ($\pi = 0.028$) and Tajima's D (−2.07), and intermediate values of Watterson's Theta ($\theta_W = 0.073$) and estimated effective population size ($N_e = 1{,}921{,}053$; Table 1). The dendrogram and PCoA (Figure 5c) of bigeye based on strict genotyping filters (4130 neutral SNPs retained) provided no evidence of genetic structuring within this population. The most probable value of K observed across the sampling region according to least CV error with 10 replicates was 1 (Figure S8c). Bigeye additionally exhibited no statistically significant relationship between pairwise geographic and genetic distance (Mantel's $r = 0.13$; $p = 0.065$; Figure 6c).

Expected and observed heterozygosities were comparable between larval ($H_e = 0.029$; $H_{obs} = 0.026$) and adult bigeye ($H_e = 0.031$; $H_{obs} = 0.026$), and there was little genetic divergence between adults and larvae (PW $F_{ST} = 0.012$; Table 3). Similarly, nucleotide diversity and Watterson's Theta values were comparable between larval bigeye ($\pi = 0.028$; $\theta_W = 0.060$) and adults ($\pi = 0.029$; $\theta_W = 0.059$; Table 3).

4 | Discussion

The contrasting genetic patterns we observed amongst skipjack, yellowfin, and bigeye tuna provide an opportunity to examine how life history, dispersal potential, and population size interact to shape genetic structure and connectivity in pelagic predators. These three species span multiple continua of life history characteristics, from the small-bodied, fast-maturing skipjack to the intermediate yellowfin, and the slower-growing, deeper-dwelling bigeye. In theory, such differences should influence the relative roles of genetic drift, selection, and gene flow in maintaining or eroding population structure. Our results generally align with this expectation: skipjack, with their large effective population size, high dispersal capacity, and rapid generation time, showed no detectable genetic structure; yellowfin, with intermediate life history traits, exhibited a clear though localized genetic subdivision; and bigeye, despite a longer generation time, observed site fidelity in some tagging studies, and smaller effective population size, displayed no genetic structure in our dataset. These contrasts suggest that neutral genetic differentiation in highly migratory pelagic fishes is not solely a function of dispersal potential or N_e alone, but may also depend on behavioural ecology, spawning-site fidelity, and the spatiotemporal stability of oceanographic features that could influence larval retention and recruitment in the WCPO. By considering these life-history differences alongside our species-specific genomic results, we can better interpret the observed patterns of connectivity and apparent local structuring within the broader evolutionary context of how highly mobile marine predators interact with their physical and ecological environments.

4.1 | Intraspecific Analysis of Divergence and Population Structure

In our analysis of population structure, we find evidence for two populations of yellowfin, but only one population of skipjack and bigeye. This is consistent with some genomic studies of these species within the WCPO that have found intra-basin genetic structuring in yellowfin (Grewe et al. 2015; Pecoraro et al. 2018), but little evidence of structure observed in skipjack or bigeye (Anderson et al. 2020; Chiang et al. 2006; Natasha et al. 2022; but see Weist et al. 2024 for bigeye divergence at adaptive loci). However, it must be noted that numerous other studies have failed to detect intra-basin structuring within yellowfin tuna using a variety of genetic markers (Anderson et al. 2023; Appleyard et al. 2001; Barth et al. 2017; Muñoz-Abril et al. 2022; Nomura et al. 2014). All 17 genetically divergent yellowfin in this study were larvae found at the southernmost sampling locations ~135–162 nm north of American Samoa exactly 1 year apart (Figure S9) and may be a genetically divergent subpopulation that is distinct from the main WCPO stock represented by the Phoenix Islands and PNMS samples. Our calculations of pairwise F_{ST} between sampling years of yellowfin indicated relatively high divergence in comparisons involving 2017 and 2018, likely driven by this putative subpopulation. Although low sample sizes may inflate F_{ST} (Holsinger and Weir 2009), using > 1000 SNPs on sample sizes as low as 4–6 can yield accurate results (Willing et al. 2012), and given these pairwise comparisons used ~100,000 SNPs, this divergence is not likely an artefact of low sample sizes. Additionally, while H_{obs} was lower than H_e in each species group (Table 1), the difference was larger in yellowfin, indicating possible genetic drift or substructuring consistent with the Wahlund effect. This difference was lessened when the two putative populations were separated (Table 2) and further exaggerated when analysing yellowfin larvae only (Table 3). Future genetic studies and tagging efforts of tropical Pacific tunas should emphasize sampling in this region as cryptic subpopulations may be prone to overfishing if not accounted for in management frameworks (Begg et al. 1999). In addition, future studies should expand sampling efforts longitudinally across the equatorial Pacific, as our dataset encompassed greater latitudinal rather than longitudinal sampling coverage.

The divergent population of yellowfin may be a consequence of spawning or site fidelity that sufficiently restricted gene flow and facilitated divergence from the main WCPO stock. Indeed, yellowfin have been studied for their magnetic homing capabilities (Walker et al. 1984); fidelity to schoolmates, islands, and/or favourable oceanographic conditions (Klimley and Holloway 1999; Schaefer et al. 2007); and migratory displacements of 340–380 nm (Sibert and Hampton 2003) that could promote site fidelity and result in sufficient genetic drift for divergence. However, other constraints on gene flow must be present given the migratory potential of yellowfin, which have been observed to travel 948 nm or more (Fonteneau and Hallier 2015; Wright et al. 2021). Barriers to dispersal like suboptimal conditions for adults (e.g., lack of preferred habitat or forage) and lower tolerance for environmental fluctuations in larvae (Reglero et al. 2014) may therefore contribute to the maintenance of structure in yellowfin if present. Based on our analysis of isolation by distance, there was no statistically significant relationship between pairwise geographic and genetic relatedness for any species analysed, indicating that such barriers to adult or larval dispersal could have contributed to the observed divergence rather than distance alone.

Differences in life histories and dispersal potential likely contributed to the lack of observed population structure within skipjack and bigeye. Skipjack, with their quick generation times, large population sizes, and general lack of site or school fidelity (Bayliff 1988; Hilborn 1991), consequently appear to maintain high rates of gene flow that prevent significant genetic divergence within the WCPO. Bigeye did not display population structure in our analysis despite their smaller effective population size and observed fidelity to physical features such as islands (Sibert et al. 2003). However, while site fidelity has been observed in this species, their capacity for long-distance migrations could still result in sufficient gene flow to prevent genetic divergence from occurring. Indeed, a comprehensive tagging study of bigeye migrations in the central Pacific indicated that median linear displacements of fish at liberty for more than 30 days was 936 nm, and while migrations were limited latitudinally, they were longitudinally extensive along the equator (Schaefer et al. 2014). Such substantial longitudinal mixing along the equator likely maintains gene flow within the WCPO. Additionally, thermoregulatory abilities in bigeye tuna may represent another potential mechanism that allows for migrations between geographically isolated populations and subsequently limits genetic divergence. Bigeye tuna have a greater capacity to maintain elevated body temperatures than yellowfin, permitting frequent deep foraging dives which allows bigeye to more efficiently exploit productive deep-water habitat in areas with stratified, oligotrophic surface waters (Ciezarek et al. 2019; Holland et al. 1992; Thygesen et al. 2016). The epipelagic environment around the Samoan Archipelago is mainly influenced by the South Equatorial Current, which transports nutrient-poor surface waters from the eastern Pacific and south Pacific gyre westward. Catches of surface schools of tuna in the purse seine fishery are low in this region, while the deep-water longline fishery is more active, particularly for albacore and to a lesser extent bigeye (Domokos 2009). Albacore, like bigeye, have adapted to maintain visceral heat and exploit deep waters for foraging (Ciezarek et al. 2019). In the case of bigeye, such adaptations may expand feeding and migratory corridors within the South Equatorial Current, thereby maintaining connectivity and gene flow, and preventing sufficient divergence for intra-basin population structure to occur.

4.2 | Utility of Larval Genomics in Population Genomics of Tunas

Numerous studies have leveraged high-throughput DNA sequencing using various techniques and genetic markers in order to elucidate evolutionary relationships, population demographic information, or assess stock structure of commercially harvested tropical tunas, but very few incorporate fisheries-independent sampling, particularly of early life history stages (but see Johnstone et al. 2021; Romdon et al. 2020). However, such sampling may be beneficial in studying the population genetics of tunas and other commercially exploited fishes because it potentially reduces biases in adult sampling due to fishing methods and gear type (Okemwa et al. 2023), samples

larvae before recruitment bottlenecks (Shropshire et al. 2022), and can help identify areas with elevated spawning activity that could represent priorities for spatial management (Hernández et al. 2019). Furthermore, sampling larvae and early life stages may allow for detection of more structure than in adult samples because of reduced mobility and admixture early in life (Anderson et al. 2023). Additionally, a better understanding of early life history dynamics can better parameterize stock assessment models and possibly provide useful estimates of spawning output and recruitment at regional scales to aid in management decisions (Kolody et al. 2019).

Despite the numerous benefits, there are several caveats associated with the use of larval tunas and other pelagic broadcast spawners for population genomics that could violate assumptions about independence of sampling. Larvae of broadcast spawners can be part of related cohorts or families via inbreeding, and highly related individuals could skew estimates of population structure and lead to erroneous conclusions on the level of divergence between samples (Selwyn et al. 2016). Additionally, larval samples can represent siblings even in the absence of inbreeding if sampling occurs shortly after a spawning event where related offspring are transported together via currents or retained in small water masses like oceanic fronts or eddies (Broquet et al. 2013; Veliz et al. 2006). In spite of these potential limitations, only 9 dyads representing 17 skipjack larvae were identified as related in the present study, and their pairwise relatedness values indicated a degree of similarity corresponding to first-cousins. No yellowfin or bigeye were identified as related based on the chosen threshold, which encourages the use of larvae as a means to assess various population genetic parameters. A study of western Atlantic larval bluefin (*T. thynnus*) identified a modest level of sibship within samples, but not enough to discourage their use in close-kin mark-recapture studies, even in a species with a discrete spawning ground and shorter spawning season that increases the likelihood of detecting relatives compared to the tropical species included in the present study (McDowell et al. 2022). Since sample contamination can also lead to high levels of pairwise relatedness and kinship (Anderson et al. 2023; Dimens et al. 2023), it is always important to test for relatedness to ensure independence of sampling, particularly in larval studies.

4.3 | Implications for Fisheries Management and Marine Spatial Planning

The study of tuna population genomics using larval samples can provide additional context to aid in the research, conservation, and management of these species. For instance, one of the fundamental tasks for fisheries managers is estimating the population sizes of commercially harvested tunas. Our estimates of effective population size using larvae may allow for additional insights into the long-term number of breeding fish to complement mark-recapture studies, and comparing such estimates with more traditional, fisheries-derived samples may reveal patterns in selection, recruitment, and fisheries impacts that are otherwise difficult to detect. Our estimates of N_e for skipjack, yellowfin, and bigeye were roughly 4.4, 2.4, and 1.9 million respectively based on our calculations of θ_W and the equation $N_e = \theta_W/4\mu$, using the estimated nuclear mutation rate for yellowfin of 7.3×10^{-9} (Barth et al. 2017) with approximate adjustments to this rate for skipjack and bigeye based on differences in life history traits like generation times (Bergeron et al. 2023). Our estimates were therefore sensitive to the estimated values of μ, and higher mutation rates than assumed here would result in lower estimates of N_e. These long-term coalescent estimates are generally high when compared with contemporary adult studies that estimate N_e with values ranging from several hundreds of individuals to tens of thousands (Anderson et al. 2020; Barth et al. 2017; Gonzalez et al. 2008; see Laconcha et al. 2015 for albacore), while estimates using heterozygote excess resulted in estimates of infinite N_e (Anderson et al. 2020). Ely et al. (2005) used mtDNA-based demographic reconstructions to estimate long-term female N_e for skipjack and yellowfin, with estimates of 98 million and 10 million, respectively. Waples et al. (2018) used close-kin mark-recapture data of southern bluefin, in conjunction with genetic and demographic estimates of N_e, to estimate the relationship between effective and census population size, and concluded the N_e/N_c ratio likely ranges from 0.1 to 0.5 in southern bluefin. Given the extremely large census population sizes for the species analysed in the present study (particularly skipjack), our calculations of larval genetic parameters sampled before recruitment bottlenecks may therefore reflect the number of breeding fish if a similar N_e/N_c ratio is applied. However, our estimates more likely reflect long-term coalescent N_e, and these results should not replace traditional close-kin mark-recapture studies and genetic estimates using a variety of techniques (Delord et al. 2024).

The lack of apparent population structure in skipjack and bigeye suggests high genetic connectivity between the two surveyed MPAs within the WCPO, and supports the current management delineations in the Pacific, whereby skipjack and bigeye are assumed to consist of western/central and eastern Pacific stocks that are managed separately. However, the divergent population of yellowfin in this study raises interesting questions surrounding stock structure and management in the central Pacific, particularly because each individual in the divergent population was collected exactly 1 year apart in 2017 and 2018 ~135–162 nm north of American Samoa (Figure S9), suggesting the possibility of multiple subpopulations within the jurisdiction of the WCPFC. Although the current levels of commercial fishing around American Samoa are low, the tuna biomass in the central and eastern Pacific is forecasted to increase under various climate change scenarios and as a consequence of increasingly frequent ENSO events (Lehodey et al. 1997, 2011; Senina et al. 2018), and the region's exposure as a fisheries target is likely to grow with time. Consequently, more research is needed to resolve the regional population structure of tunas (particularly yellowfin) and avoid possible localized depletions in genetic diversity (Begg et al. 1999). However, since the degree of intra-basin population structuring within these species remains unclear and differs by molecular marker and spatio-temporal scope of sampling, future research should prioritize whole-genome sequencing of tuna collected from both fisheries dependent and independent sampling efforts across their entire Pacific ranges to fully capture the genetic diversity within each population. Additionally, if LUPS are used to differentiate populations, their roles and influence on fitness should be thoroughly investigated before drawing conclusions about adaptive genetic population structuring.

Much of the recent population demographic work on tropical tunas has discussed philopatry, or fidelity to specific natural features like islands, seamounts, or oceanic fronts (Richardson et al. 2018; Rooker et al. 2016; Schaefer et al. 2007, 2014) and/or man-made objects like fish aggregating devices (Dupaix et al. 2024; Filous et al. 2020; Itano and Holland 2000), as philopatry has many implications for spatial management and conservation of these species (Relano and Pauly 2022). As the world works towards protecting 30% of the oceans by 2030, conservation of tunas via MPAs has emerged as a contentious topic, with some arguing that the high migratory potential of tropical tunas, which can travel over 1200 miles between tag recoveries (Fonteneau and Hallier 2015), prevents effective conservation through spatial closures despite observable increases to local spawning biomass by MPAs (Hampton et al. 2023; Lynham and Villaseñor-Derbez 2024). To adjust spatial management to benefit highly migratory pelagics like tunas, some advocate for large networks of reserves (Allan et al. 2021; Hooker et al. 2011) or shifting spatial closures dependent on oceanographic conditions (Gilman et al. 2019). Yet, tagging surveys of tropical tunas have pointed to lower lifetime migratory displacements than previously assumed, suggesting the potential for philopatry and/or locally-managed stocks. Indeed, skipjack have been observed to display lifetime median displacements of 420–470 nm, with yellowfin exhibiting displacements of only 340–380 nm (Sibert and Hampton 2003). In another study, yellowfin were found to have an average straight-line displacement of 195 ± 244 nm from the PNMS (Filous et al. 2020). Additionally, bigeye in the eastern Pacific were observed to have average lifetime displacements of 300 nm (Schaefer and Fuller 2009). Such migratory displacements are on the same scale as MPAs, challenging the assumption that spatial closures would be ineffective management tools for tuna conservation.

5 | Conclusion

In this study, we demonstrate the utility of reduced representation genome-wide sequencing in assessing information on population genetics of commercially significant tunas, primarily using larvae from fisheries-independent sources. We found evidence of population structuring in yellowfin, but not in skipjack or bigeye, which generally aligns with other genomic studies of these species in the WCPO. Our results highlight the need to resolve the extent to which tuna populations in the Pacific are genetically structured, and showcase how studies using early life history stages from fisheries-independent sources can contribute to the already-rich area of research. Our findings also raise a set of broader evolutionary questions that extend beyond the immediate context of tuna management: what evolutionary or behavioural mechanisms (e.g., natal homing) might maintain the genetically distinct yellowfin cluster we detected despite the species' high dispersal potential? Are such patterns stable features of population connectivity or transient responses to interannual environmental variability such as ENSO? Do adaptive differences emerge in the absence of strong neutral genetic structure, and how might these differences be linked to gradients in temperature, oxygen, or prey availability across the WCPO? More generally, what can the differences in life histories demonstrated by skipjack, yellowfin, and bigeye tell us about the balance between drift, selection, and gene flow in highly mobile pelagic predators? And, how have the selective pressures on life history characteristics changed over time, and in an era of contemporary industrial use? Addressing these questions will require integrating genomics, tagging, oceanographic modelling on all life stages to understand the processes that generate and maintain genetic structure in the open ocean, and to predict how such patterns may shift under changing climatic and oceanographic regimes.

Author Contributions

Conceptualization: R.D.R., S.P.M. and J.E.J.; funding acquisition: R.D.R. and S.P.M.; investigation: J.K.L., C.M.H., J.W.W., J.E.J., G.A., L.C, J.E.F., A.K.H. and H.E.A.; formal analysis: J.E.J., H.E.A. and J.E.F.; visualization: J.E.J.; supervision: J.E.J., R.D.R., S.P.M. and H.E.A.; writing – original draft: J.E.J.; writing – review and editing: J.E.J., H.E.A., G.A., L.C., J.E.F., C.M.H., A.K.H., J.K.L., J.W.W., S.P.M. and R.D.R.

Acknowledgements

We gratefully acknowledge the Blue Nature Alliance (grant #CI-113205 awarded to R. Rotjan) and the Waitt Foundation (grant #55207252 awarded to R. Rotjan and S. Mullen) for providing funding and support for this work. We extend our appreciation to the Sea Education Association and to the crew and students aboard the SSV *Robert C. Seamans* during transits S261, S268, S274, S281, and S287 for collecting, preserving, and facilitating the transport of larval tuna samples (PIPA Research Permits 02/2015, 1/16, 3/17, and 2/18). We extend our deep thanks to the Republic of Kiribati and the PIPA Implementation Office for their support of this research, in accordance with the previously mentioned permits. We especially thank our on-board observers Toaea Beiateuea (S261), Taremon Korere (S268), Kareati Waysang (S274), Moamoa Kabuati (S281), and Miita Ribabaiti (S287), noting Ms. Waysang, Ms. Kabuati, and Mr. Ribabaiti participated in these cruises in dual roles, both as Kiribati Observers and as students taking college courses onboard. We are also deeply grateful to Mr. Tukabu Teroroko and Mr. Tiiroa Roneti for helping with the permit process and helping to select and train onboard observers. We acknowledge and thank the Palau International Coral Reef Center (PICRC) for providing additional larval samples to aid in this study. We also extend our appreciation to Simon Nicol, the Oceanic Fisheries Programme of the Pacific Community, and the crew of the FV *Gutsy Lady* for facilitating the collection and transport of (sub)adult yellowfin and bigeye samples under PIPA permit application #PFA3. We also acknowledge the many plankton sorters in the Rotjan Lab, particularly Allie Cole, Emma Martin, Abigail Grassick, and Ding Xin, for their work in processing zooplankton samples and identifying larval tunas. The authors would like to acknowledge the 1S10OD032203-01 (Tufts University Core Facility Genomics Core) for the support of the included NGS analysis. We thank Quentin Hanich for helpful conversations surrounding this work, for encouraging international collaboration, and for connecting us with our SPC collaborators. We acknowledge Mikhail Matz, Sarah Davies, and Maria Valdez Ingersoll for their technical assistance during the library preparation and analysis associated with this project. Finally, we extend our gratitude to the Boston University Shared Computing Cluster, which supported all computational work.

Funding

This work was supported by Blue Nature Alliance, CI-113205; Waitt Foundation, 55207252.

Disclosure

Benefits generated: This work addresses research priorities of commercially important tuna species to benefit their conservation and management. As described above, all data, sequences, and code associated with

this research are publicly available in their appropriate repositories. A collaboration between several institutions/organizations was developed, and collaborators are included as co-authors.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All sequence data used for this project can be found in NCBI's SRA (BioProject ID = PRJNA1303678). All code and supporting materials associated with the analysis of these data can be found on Zenodo (DOI: 10.5281/zenodo.16944919) and on GitHub (https://github.com/jaskielj/Jaskiel_et_al_2026_Tuna_2bRAD).

References

Alexander, D. H., J. Novembre, and K. Lange. 2009. "Fast Model-Based Estimation of Ancestry in Unrelated Individuals." *Genome Research* 19, no. 9: 1655–1664. https://doi.org/10.1101/gr.094052.109.

Allan, J. C., K. F. Beazley, and A. Metaxas. 2021. "Ecological Criteria for Designing Effective MPA Networks for Large Migratory Pelagics: Assessing the Consistency Between IUCN Best Practices and Scholarly Literature." *Marine Policy* 127: 104219. https://doi.org/10.1016/j.marpol.2020.104219.

Allen, R., J. Joseph, and D. Squires. 2010. *Conservation and Management of Transnational Tuna Fisheries*. Wiley-Blackwell.

Anderson, G., E. Holland, and C. Rico. 2019. "Meta-Analysis of Factors Influencing Population Differentiation in Yellowfin Tuna (*Thunnus albacares*)." *Reviews in Fisheries Science & Aquaculture* 27, no. 4: 517–532. https://doi.org/10.1080/23308249.2019.1633270.

Anderson, G., M. Lal, B. Stockwell, et al. 2020. "No Population Genetic Structure of Skipjack Tuna (*Katsuwonus pelamis*) in the Tropical Western and Central Pacific Assessed Using Single Nucleotide Polymorphisms." *Frontiers in Marine Science* 7: 570760. https://doi.org/10.3389/fmars.2020.570760.

Anderson, G., J. I. Macdonald, M. Lal, J. Hampton, N. Smith, and C. Rico. 2023. "Sample Contamination Explains Evidence of Close Kin Proximity in Yellowfin Tuna (*Thunnus albacares*) in the Western and Central Pacific Ocean." *Frontiers in Marine Science* 10: 1204884. https://doi.org/10.3389/fmars.2023.1204884.

Appleyard, S., P. Grewe, B. Innes, and R. Ward. 2001. "Population Structure of Yellowfin Tuna (*Thunnus albacares*) in the Western Pacific Ocean, Inferred from Microsatellite Loci." *Marine Biology* 139, no. 2: 383–393. https://doi.org/10.1007/s002270100578.

Artetxe-Arrate, I., I. Fraile, F. Marsac, et al. 2021. "A Review of the Fisheries, Life History and Stock Structure of Tropical Tuna (Skipjack *Katsuwonus pelamis*, Yellowfin *Thunnus albacares* and Bigeye *Thunnus obesus*) in the Indian Ocean." In *Advances in Marine Biology*, vol. 88, 39–89. Elsevier. https://doi.org/10.1016/bs.amb.2020.09.002.

Ashida, H., T. Tanabe, and N. Suzuki. 2017. "Difference on Reproductive Trait of Skipjack Tuna Katsuonus Pelamis Female Between Schools (Free vs. FAD School) in the Tropical Western and Central Pacific Ocean." *Environmental Biology of Fishes* 100: 935–945. https://doi.org/10.1007/s10641-017-0621-2.

Auscavitch, S. R., M. C. Deere, A. G. Keller, R. D. Rotjan, T. M. Shank, and E. E. Cordes. 2020. "Oceanographic Drivers of Deep-Sea Coral Species Distribution and Community Assembly on Seamounts, Islands, Atolls, and Reefs Within the Phoenix Islands Protected Area." *Frontiers in Marine Science* 7: 42. https://doi.org/10.3389/fmars.2020.00042.

Barclay, K. 2014. "History of Industrial Tuna Fishing in the Pacific Islands." In *Historical Perspectives of Fisheries Exploitation in the Indo-Pacific*, edited by J. Christensen and M. Tull, vol. 12. Springer. https://doi.org/10.1007/978-94-017-8727-7_8.

Barth, J. M. I., M. Damerau, M. Matschiner, S. Jentoft, and R. Hanel. 2017. "Genomic Differentiation and Demographic Histories of Atlantic and Indo-Pacific Yellowfin Tuna (*Thunnus albacares*) Populations." *Genome Biology and Evolution* 9, no. 4: 1084–1098. https://doi.org/10.1093/gbe/evx067.

Baum, J. K., and B. Worm. 2009. "Cascading Top-Down Effects of Changing Oceanic Predator Abundances." *Journal of Animal Ecology* 78, no. 4: 699–714. https://doi.org/10.1111/j.1365-2656.2009.01531.x.

Bayliff, W. H. 1988. "Integrity of Schools of Skipjack Tuna, *Katsuwonus pelamis*, in the Eastern Pacific Ocean, as Determined From Tagging Data." *Fishery Bulletin* 86, no. 4: 631–643.

Bayliff, W. H., J. L. Moreno, and J. Majkowski. 2005. "Management of Tuna Fishing Capacity: Conservation and Socio-Economics." In *Second Meeting of the Technical Advisory Committee of the FAO Project Management of Tuna Fishing Capacity: Conservation and Socio-Economics: 15–18 March 2004*. Food and Agriculture Organization of the United Nations.

Begg, G. A., K. D. Friedland, and J. B. Pearce. 1999. "Stock Identification and Its Role in Stock Assessment and Fisheries Management: An Overview." *Fisheries Research* 43, no. 1: 1–8. https://doi.org/10.1016/S0165-7836(99)00062-4.

Bergeron, L. A., S. Besenbacher, J. Zheng, et al. 2023. "Evolution of the Germline Mutation Rate Across Vertebrates." *Nature* 615, no. 7951: 285–291. https://doi.org/10.1038/s41586-023-05752-y.

Bernal, D., R. W. Brill, K. A. Dickson, and H. A. Shiels. 2017. "Sharing the Water Column: Physiological Mechanisms Underlying Species-Specific Habitat Use in Tunas." *Reviews in Fish Biology and Fisheries* 27, no. 4: 843–880. https://doi.org/10.1007/s11160-017-9497-7.

Boehlert, G., and B. Mundy. 1994. "Vertical and Onshore-Offshore Distributional Patterns of Tuna Larvae in Relation to Physical Habitat Features." *Marine Ecology Progress Series* 107: 1–13. https://doi.org/10.3354/meps107001.

Bradburd, G. S., G. M. Coop, and P. L. Ralph. 2018. "Inferring Continuous and Discrete Population Genetic Structure Across Space." *Genetics* 210, no. 1: 33–52. https://doi.org/10.1534/genetics.118.301333.

Broquet, T., F. Viard, and J. M. Yearsley. 2013. "Genetic Drift and Collective Dispersal Can Result in Chaotic Genetic Patchiness." *Evolution* 67, no. 6: 1660–1675. https://doi.org/10.1111/j.1558-5646.2012.01826.x.

Campling, L., A. Lewis, and M. McCoy. 2017. *The Tuna Longline Industry in the Western and Central Pacific Ocean and Its Market Dynamics*. Pacific Islands Forum Fisheries Agency.

Chiang, H. C., C. C. Hsu, H. D. Lin, G. C. Ma, T. Y. Chiang, and H. Y. Yang. 2006. "Population Structure of Bigeye Tuna (*Thunnus obesus*) in the South China Sea, Philippine Sea and Western Pacific Ocean Inferred From Mitochondrial DNA." *Fisheries Research* 79, no. 1–2: 219–225. https://doi.org/10.1016/j.fishres.2005.11.026.

Ciezarek, A. G., O. G. Osborne, O. N. Shipley, et al. 2019. "Phylotranscriptomic Insights Into the Diversification of Endothermic *Thunnus* Tunas." *Molecular Biology and Evolution* 36, no. 1: 84–96. https://doi.org/10.1093/molbev/msy198.

Claassens, L., A. Gupta, E. Hartge, and K. Sam. 2023. *Palau National Marine Sanctuary Science and Monitoring Strategy: 2024–2034*, 56. Palau International Coral Reef Center.

Claassens, L., C. M. Hernández, P. Biondi, et al. 2024. "Navigating Large Scale Ocean Science in a Pacific Small Island Developing State." *Pacific Conservation Biology* 30, no. 6: PC24062. https://doi.org/10.1071/PC24062.

Collette, B. B., A. Boustany, W. Fox, J. Graves, M. Juan Jorda, and V. Restrepo. 2021a. "*Katsuwonus pelamis*. The IUCN Red List of Threatened Species." https://doi.org/10.2305/IUCN.UK.2021-2.RLTS.T170310A46644566.en.

Collette, B. B., A. Boustany, W. Fox, J. Graves, M. Juan Jorda, and V. Restrepo. 2021b. "*Thunnus albacares*. The IUCN Red List of Threatened Species." https://doi.org/10.2305/IUCN.UK.2021-2.RLTS.T21857A46624561.en.

Collette, B. B., A. Boustany, W. Fox, J. Graves, M. Juan-Jordá, and V. Restrepo. 2021c. "*Thunnus obesus*. The IUCN Red List of Threatened Species." https://doi.org/10.2305/IUCN.UK.2021-2.RLTS.T21859A46912402.en.

Danecek, P., J. K. Bonfield, J. Liddle, et al. 2021. "Twelve Years of SAMtools and BCFtools." *GigaScience* 10, no. 2: giab008. https://doi.org/10.1093/gigascience/giab008.

Day, J., A. Magnusson, T. Teears, et al. 2023. "Stock Assessment of Bigeye Tuna in the Western and Central Pacific Ocean: 2023." Scientific Committee, 19th Regular Session, WCPFC-SC19-SA-WP-05. Western and Central Pacific Fisheries Commission.

Delord, C., S. Arnaud-Haond, A. Leone, J. Rolland, and N. Nikolic. 2024. "Unraveling the Complexity of the N e/N c Ratio for Conservation of Large and Widespread Pelagic Fish Species: Current Status and Challenges." *Evolutionary Applications* 17, no. 10: e70020. https://doi.org/10.1111/eva.70020.

Dimens, P., L. Reynal, C. Pau, et al. 2023. "Weak Range-Wide Population Structure in the Blackfin Tuna (*Thunnus atlanticus*) Revealed by Analysis of Genome-Wide SNPs." *ICES Journal of Marine Science* 80, no. 4: 941–952. https://doi.org/10.1093/icesjms/fsad012.

Dizon, A. E., and R. W. Brill. 1979. "Thermoregulation in Tunas." *American Zoologist* 19, no. 1: 249–265. https://doi.org/10.1093/icb/19.1.249.

Domokos, R. 2009. "Environmental Effects on Forage and Longline Fishery Performance for Albacore (*Thunnus alalunga*) in the American Samoa Exclusive Economic Zone." *Fisheries Oceanography* 18, no. 6: 419–438. https://doi.org/10.1111/j.1365-2419.2009.00521.x.

Dupaix, A., F. Ménard, J. D. Filmalter, et al. 2024. "The Challenge of Assessing the Effects of Drifting Fish Aggregating Devices on the Behaviour and Biology of Tropical Tuna." *Fish and Fisheries* 25, no. 3: 381–400. https://doi.org/10.1111/faf.12813.

Ely, B., J. Viñas, J. R. Alvarado Bremer, et al. 2005. "Consequences of the Historical Demography on the Global Population Structure of Two Highly Migratory Cosmopolitan Marine Fishes: The Yellowfin Tuna (*Thunnus albacares*) and the Skipjack Tuna (*Katsuwonus pelamis*)." *BMC Evolutionary Biology* 5: 19. https://doi.org/10.1186/1471-2148-5-19.

Evanno, G., S. Regnaut, and J. Goudet. 2005. "Detecting the Number of Clusters of Individuals Using the Software Structure: A Simulation Study." *Molecular Ecology* 14, no. 8: 2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x.

FAO. 2024. *The State of World Fisheries and Aquaculture 2024—Blue Transformation in Action*. Food and Agriculture Organization of the United Nations. https://doi.org/10.4060/cd0683en.

Farley, J., P. Eveson, K. Krusic-Golub, et al. 2017. "Age, Growth and Maturity of Bigeye Tuna in the Pacific." Technical Report WCPFC-SC13–2017/SA-WP-01, Rarotonga, Cook Islands, 9–17 August 2017.

Filous, A., A. M. Friedlander, L. Griffin, et al. 2020. "Movements of Juvenile Yellowfin Tuna (*Thunnus albacares*) Within the Coastal FAD Network Adjacent to the Palau National Marine Sanctuary: Implications for Local Fisheries Development." *Fisheries Research* 230: 105688. https://doi.org/10.1016/j.fishres.2020.105688.

Fonteneau, A., and J.-P. Hallier. 2015. "Fifty Years of Dart Tag Recoveries for Tropical Tuna: A Global Comparison of Results for the Western Pacific, Eastern Pacific, Atlantic, and Indian Oceans." *Fisheries Research* 163: 7–22. https://doi.org/10.1016/j.fishres.2014.03.022.

Fox, E. A., A. E. Wright, M. Fumagalli, and F. G. Vieira. 2019. "*ngsLD*: Evaluating Linkage Disequilibrium Using Genotype Likelihoods." *Bioinformatics* 35, no. 19: 3855–3856. https://doi.org/10.1093/bioinformatics/btz200.

Funk, W. C., J. K. McKay, P. A. Hohenlohe, and F. W. Allendorf. 2012. "Harnessing Genomics for Delineating Conservation Units." *Trends in Ecology & Evolution* 27, no. 9: 489–496. https://doi.org/10.1016/j.tree.2012.05.012.

Gilman, E., M. J. Kaiser, and M. Chaloupka. 2019. "Do Static and Dynamic Marine Protected Areas That Restrict Pelagic Fishing Achieve Ecological Objectives?" *Ecosphere* 10, no. 12: e02968. https://doi.org/10.1002/ecs2.2968.

Gonzalez, E. G., P. Beerli, and R. Zardoya. 2008. "Genetic Structuring and Migration Patterns of Atlantic Bigeye Tuna, *Thunnus obesus* (Lowe, 1839)." *BMC Evolutionary Biology* 8, no. 1: 252. https://doi.org/10.1186/1471-2148-8-252.

Grewe, P. M. 1997. "An Assessment of Bigeye (*Thunnus obesus*) Population Structure in the Pacific Ocean, Based on Mitochondrial DNA and DNA Microsatellites Analysis." Working Paper WPYRG7/15, 7th Meeting of the Western Pacific Yellowfin Tuna Research Group, 18–20 June 1997, Nadi, Fiji.

Grewe, P. M., P. Feutry, P. L. Hill, et al. 2015. "Evidence of Discrete Yellowfin Tuna (*Thunnus albacares*) Populations Demands Rethink of Management for This Globally Important Resource." *Scientific Reports* 5, no. 1: 16916. https://doi.org/10.1038/srep16916.

Hampton, J., P. Lehodey, I. Senina, S. Nicol, J. Scutt Phillips, and K. Tiamere. 2023. "Limited Conservation Efficacy of Large-Scale Marine Protected Areas for Pacific Skipjack and Bigeye Tunas." *Frontiers in Marine Science* 9: 1060943. https://doi.org/10.3389/fmars.2022.1060943.

Hanghøj, K., I. Moltke, P. A. Andersen, A. Manica, and T. S. Korneliussen. 2019. "Fast and Accurate Relatedness Estimation From High-Throughput Sequencing Data in the Presence of Inbreeding." *GigaScience* 8, no. 5: giz034. https://doi.org/10.1093/gigascience/giz034.

Hare, S. R., P. G. Williams, J. C. Castillo, et al. 2022. *The Western and Central Pacific Tuna Fishery: 2021 Overview and Status of Stocks* Tuna Fisheries Assessment Report No. 22. Pacific Community.

Heithaus, M. R., A. Frid, A. J. Wirsing, and B. Worm. 2008. "Predicting Ecological Consequences of Marine Top Predator Declines." *Trends in Ecology & Evolution* 23, no. 4: 202–210. https://doi.org/10.1016/j.tree.2008.01.003.

Hernández, C. M., J. Witting, C. Willis, S. R. Thorrold, J. K. Llopiz, and R. D. Rotjan. 2019. "Evidence and Patterns of Tuna Spawning Inside a Large No-Take Marine Protected Area." *Scientific Reports* 9, no. 1: 10772. https://doi.org/10.1038/s41598-019-47161-0.

Hilborn, R. 1991. "Modeling the Stability of Fish Schools: Exchange of Individual Fish Between Schools of Skipjack Tuna (*Katsuwonus pelamis*)." *Canadian Journal of Fisheries and Aquatic Sciences* 48: 1081–1091.

Holland, K. N., R. W. Brill, R. K. C. Chang, J. R. Sibert, and D. A. Fournier. 1992. "Physiological and Behavioural Thermoregulation in Bigeye Tuna (*Thunnus obesus*)." *Nature* 358, no. 6385: 410–412. https://doi.org/10.1038/358410a0.

Holsinger, K. E., and B. S. Weir. 2009. "Genetics in Geographically Structured Populations: Defining, Estimating and Interpreting FST." *Nature Reviews Genetics* 10, no. 9: 639–650. https://doi.org/10.1038/nrg2611.

Hooker, S. K., A. Cañadas, K. D. Hyrenbach, C. Corrigan, J. J. Polovina, and R. R. Reeves. 2011. "Making Protected Area Networks Effective for Marine Top Predators." *Endangered Species Research* 13: 203–218. https://doi.org/10.3354/esr00322.

ISSF. 2025. *Status of the World Fisheries for Tuna* ISSF Technical Report 2025–01. International Seafood Sustainability Foundation.

ISSF. 2026. *Status of the World Fisheries for Tuna* ISSF Technical Report 2026–01. International Seafood Sustainability Foundation.

Itano, D. 2000. "The Reproductive Biology of Yellowfin Tuna (*Thunnus albacares*) in Hawaiian Waters and the Western Tropical Pacific Ocean: Project Summary." Joint Institute for Marine and Atmospheric Research Report, 00–328.

Itano, D. G., and K. N. Holland. 2000. "Movement and Vulnerability of Bigeye (*Thunnus obesus*) and Yellowfin Tuna (*Thunnus albacares*) in Relation to FADs and Natural Aggregation Points." *Aquatic Living Resources* 13, no. 4: 213–223. https://doi.org/10.1016/S0990-7440(00)01062-7.

Johnstone, C., M. Pérez, E. Malca, et al. 2021. "Genetic Connectivity Between Atlantic Bluefin Tuna Larvae Spawned in the Gulf of Mexico and in the Mediterranean Sea." *PeerJ* 9: e11568. https://doi.org/10.7717/peerj.11568.

Juan-Jordá, M. J., I. Mosqueira, A. B. Cooper, J. Freire, and N. K. Dulvy. 2011. "Global Population Trajectories of Tunas and Their Relatives." *Proceedings of the National Academy of Sciences* 108, no. 51: 20650–20655. https://doi.org/10.1073/pnas.1107743108.

Kittinger, J. N., R. D. Rotjan, Q. Hanich, B. Pasisi, and C. Rambourg. 2024. "Balancing Protection and Production in Ocean Conservation." *npj Ocean Sustainability* 3, no. 1: 24. https://doi.org/10.1038/s44183-024-00062-w.

Klimley, A. P., and C. F. Holloway. 1999. "School Fidelity and Homing Synchronicity of Yellowfin Tuna, *Thunnus albacares*." *Marine Biology* 133, no. 2: 307–317. https://doi.org/10.1007/s002270050469.

Kolody, D. S., J. P. Eveson, A. L. Preece, C. R. Davies, and R. M. Hillary. 2019. "Recruitment in Tuna RFMO Stock Assessment and Management: A Review of Current Approaches and Challenges." *Fisheries Research* 217: 217–234. https://doi.org/10.1016/j.fishres.2018.11.031.

Korneliussen, T. S., A. Albrechtsen, and R. Nielsen. 2014. "ANGSD: Analysis of Next Generation Sequencing Data." *BMC Bioinformatics* 15, no. 1: 356. https://doi.org/10.1186/s12859-014-0356-4.

Kumar, G., and M. Kocour. 2015. "Population Genetic Structure of Tunas Inferred From Molecular Markers: A Review." *Reviews in Fisheries Science & Aquaculture* 23, no. 1: 72–89. https://doi.org/10.1080/23308249.2015.1024826.

Laconcha, U., M. Iriondo, H. Arrizabalaga, et al. 2015. "New Nuclear SNP Markers Unravel the Genetic Structure and Effective Population Size of Albacore Tuna (*Thunnus alalunga*)." *PLoS One* 10, no. 6: e0128247. https://doi.org/10.1371/journal.pone.0128247.

Langmead, B., and S. L. Salzberg. 2012. "Fast Gapped-Read Alignment With Bowtie 2." *Nature Methods* 9, no. 4: 357–359. https://doi.org/10.1038/nmeth.1923.

Lehodey, P., M. Bertignac, J. Hampton, A. Lewis, and J. Picaut. 1997. "El Niño Southern Oscillation and Tuna in the Western Pacific." *Nature* 389, no. 6652: 715–718. https://doi.org/10.1038/39575.

Lehodey, P., J. Hampton, R. W. Brill, et al. 2011. "Vulnerability of Oceanic Fisheries in the Tropical Pacific to Climate Change." Vulnerability of Tropical Pacific Fisheries and Aquaculture to Climate Change, 433–492.

Luu, K., E. Bazin, and M. G. B. Blum. 2017. "Pcadapt: An R Package to Perform Genome Scans for Selection Based on Principal Component Analysis." *Molecular Ecology Resources* 17, no. 1: 67–77. https://doi.org/10.1111/1755-0998.12592.

Lynham, J., and J. C. Villaseñor-Derbez. 2024. "Evidence of Spillover Benefits From Large-Scale Marine Protected Areas to Purse Seine Fisheries." *Science* 386, no. 6727: 1276–1281. https://doi.org/10.1126/science.adn1146.

Magnusson, A., J. Day, T. Teears, et al. 2023. "Stock Assessment of Yellowfin Tuna in the Western and Central Pacific Ocean: 2023." Scientific Committee, 19th Regular Session, WCPFC-SC19-SA-WP-04. Western and Central Pacific Fisheries Commission.

Mariani, G., W. W. L. Cheung, A. Lyet, et al. 2020. "Let More Big Fish Sink: Fisheries Prevent Blue Carbon Sequestration—Half in Unprofitable Areas." *Science Advances* 6, no. 44: eabb4848. https://doi.org/10.1126/sciadv.abb4848.

Martin, M. 2011. "Cutadapt Removes Adapter Sequences From High-Throughput Sequencing Reads." *EMBnet.Journal* 17, no. 1: 1. https://doi.org/10.14806/ej.17.1.200.

McDowell, J. R., M. Bravington, P. M. Grewe, et al. 2022. "Low Levels of Sibship Encourage Use of Larvae in Western Atlantic Bluefin Tuna Abundance Estimation by Close-Kin Mark-Recapture." *Scientific Reports* 12, no. 1. https://doi.org/10.1038/s41598-022-20862-9.

Miller, M. G. R., N. Carlile, J. S. Phillips, F. McDuie, and B. C. Congdon. 2018. "Importance of Tropical Tuna for Seabird Foraging Over a Marine Productivity Gradient." *Marine Ecology Progress Series* 586: 233–249. https://doi.org/10.3354/meps12376.

Miyake, M., N. Miyabe, and H. Nakano. 2004. *Historical Trends of Tuna Catches in the World*. Vol. 467. Food & Agriculture Org.

Moore, B. R., J. D. Bell, K. Evans, et al. 2020. "Defining the Stock Structures of Key Commercial Tunas in the Pacific Ocean I: Current Knowledge and Main Uncertainties." *Fisheries Research* 230: 105525. https://doi.org/10.1016/j.fishres.2020.105525.

Mouillot, D., S. Derminon, G. Mariani, et al. 2023. "Industrial Fisheries Have Reversed the Carbon Sequestration by Tuna Carcasses Into Emissions." *Global Change Biology* 29, no. 17: 5062–5074. https://doi.org/10.1111/gcb.16823.

Muñoz-Abril, L., M. d. L. Torres, C. A. Valle, et al. 2022. "Lack of Genetic Differentiation in Yellowfin Tuna Has Conservation Implications in the Eastern Pacific Ocean." *PLoS One* 17, no. 8: e0272713. https://doi.org/10.1371/journal.pone.0272713.

Natasha, J., B. L. Stockwell, A. D. Marie, et al. 2022. "No Population Structure of Bigeye Tunas (*Thunnus obesus*) in the Western and Central Pacific Ocean Indicated by Single Nucleotide Polymorphisms." *Frontiers in Marine Science* 9: 799684. https://doi.org/10.3389/fmars.2022.799684.

Nishikawa, Y., and D. W. Rimmer. 1987. "Identification of Larval Tunas, Billfishes and Other Scombroid Fishes (Suborder Scombroidei): An Illustrated Guide." *CSIRO Reports* 186: 1–20.

Nomura, S., T. Kobayashi, Y. Agawa, et al. 2014. "Genetic Population Structure of the Pacific Bluefin Tuna *Thunnus orientalis* and the Yellowfin Tuna *Thunnus albacares* in the North Pacific Ocean." *Fisheries Science* 80, no. 6: 1193–1204. https://doi.org/10.1007/s12562-014-0789-8.

Ohashi, S., Y. Aoki, F. Tanaka, K. Fujioka, A. Aoki, and H. Kiyofuji. 2019. *Reproductive Traits of Female Skipjack Tuna (Katsuwonus pelamis) in the Western Central Pacific Ocean (Wcpo)* Technical Report WCPFC-SC15-2019/SA-WP-10. Federated States of Micronesia.

Okemwa, G. M., A. A. Abubakar, F. Mzingirwa, et al. 2023. "Characterizing Gear-Based Exploitation Patterns of Artisanal Tuna Fisheries in the Western Indian Ocean: A Snapshot From Kenya." *Regional Studies in Marine Science* 61: 102877. https://doi.org/10.1016/j.rsma.2023.102877.

Oksanen, J., G. Simpson, F. Blanchet, et al. 2022. "vegan: Community Ecology Package." R Package Version 2.6–4. https://CRAN.R-project.org/package=vegan.

Pardo-Diaz, C., C. Salazar, and C. D. Jiggins. 2015. "Towards the Identification of the Loci of Adaptive Evolution." *Methods in Ecology and Evolution* 6, no. 4: 445–464. https://doi.org/10.1111/2041-210X.12324.

Pecoraro, C., M. Babbucci, R. Franch, et al. 2018. "The Population Genomics of Yellowfin Tuna (*Thunnus albacares*) at Global Geographic Scale Challenges Current Stock Delineation." *Scientific Reports* 8, no. 1: 13890. https://doi.org/10.1038/s41598-018-32331-3.

Privé, F., K. Luu, B. J. Vilhjálmsson, and M. G. B. Blum. 2020. "Performing Highly Efficient Genome Scans for Local Adaptation With R Package Pcadapt Version 4." *Molecular Biology and Evolution* 37, no. 7: 2153–2154. https://doi.org/10.1093/molbev/msaa053.

Puechmaille, S. J. 2016. "The Program Structure Does Not Reliably Recover the Correct Population Structure When Sampling Is Uneven: Subsampling and New Estimators Alleviate the Problem." *Molecular Ecology Resources* 16, no. 3: 608–627. https://doi.org/10.1111/1755-0998.12512.

R Core Team. 2024. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Reglero, P., D. P. Tittensor, D. Alvarez-Berastegui, A. Aparicio-González, and B. Worm. 2014. "Worldwide Distributions of Tuna Larvae: Revisiting Hypotheses on Environmental Requirements for Spawning Habitats." *Marine Ecology Progress Series* 501: 207–224. https://doi.org/10.3354/meps10666.

Relano, V., and D. Pauly. 2022. "Philopatry as a Tool to Define Tentative Closed Migration Cycles and Conservation Areas for Large Pelagic Fishes in the Pacific." *Sustainability* 14, no. 9: 9. https://doi.org/10.3390/su14095577.

Richards, W. J. 2005. *Early Stages of Atlantic Fishes: An Identification Guide for the Western Central North Atlantic*. CRC Press. https://doi.org/10.1201/9780203500217.

Richardson, A. J., K. J. Downes, E. T. Nolan, et al. 2018. "Residency and Reproductive Status of Yellowfin Tuna in a Proposed Large-Scale Pelagic Marine Protected Area." *Aquatic Conservation: Marine and Freshwater Ecosystems* 28, no. 6: 1308–1316. https://doi.org/10.1002/aqc.2936.

Romdon, A., A. Sembiring, N. P. D. Pertiwi, et al. 2020. "Description and Identification of Tuna Larvae Based on Genetic and Morphological Analysis." *IOP Conference Series: Earth and Environmental Science* 618, no. 1: 12035. https://doi.org/10.1088/1755-1315/618/1/012035.

Rooker, J. R., R. J. David Wells, D. G. Itano, S. R. Thorrold, and J. M. Lee. 2016. "Natal Origin and Population Connectivity of Bigeye and Yellowfin Tuna in the Pacific Ocean." *Fisheries Oceanography* 25, no. 3: 277–291. https://doi.org/10.1111/fog.12154.

Rotjan, R., R. Jamieson, B. Carr, et al. 2014. "Chapter Eight—Establishment, Management, and Maintenance of the Phoenix Islands Protected Area." In *Advances in Marine Biology*, edited by M. L. Johnson and J. Sandell, vol. 69, 289–324. Academic Press. https://doi.org/10.1016/B978-0-12-800214-8.00008-6.

Schaefer, K. M. 1996. "Spawning Time, Frequency, and Batch Fecundity of Yellowfin Tuna, *Thunnus albacares*, Near Clipperton Atoll in the Eastern Pacific Ocean." *Fishery Bulletin* 94, no. 1: 98–112.

Schaefer, K. M., and D. W. Fuller. 2009. *Horizontal Movements of Bigeye Tuna (Thunnus obesus) in the Eastern Pacific Ocean, as Determined From Conventional and Archival Tagging Experiments Initiated During 2000–2005*. Inter-American Tuna Commission.

Schaefer, K. M., and D. W. Fuller. 2010. "Vertical Movements, Behavior, and Habitat of Bigeye Tuna (*Thunnus obesus*) in the Equatorial Eastern Pacific Ocean, Ascertained From Archival Tag Data." *Marine Biology* 157: 2625–2642.

Schaefer, K. M., and D. W. Fuller. 2022. "Horizontal Movements, Utilization Distributions, and Mixing Rates of Yellowfin Tuna (*Thunnus albacares*) Tagged and Released With Archival Tags in Six Discrete Areas of the Eastern and Central Pacific Ocean." *Fisheries Oceanography* 31, no. 1: 84–107. https://doi.org/10.1111/fog.12564.

Schaefer, K. M., D. W. Fuller, and G. Aldana. 2014. "Movements, Behavior, and Habitat Utilization of Yellowfin Tuna (*Thunnus albacares*) in Waters Surrounding the Revillagigedo Islands Archipelago Biosphere Reserve, Mexico." *Fisheries Oceanography* 23, no. 1: 65–82. https://doi.org/10.1111/fog.12047.

Schaefer, K. M., D. W. Fuller, and B. A. Block. 2007. "Movements, Behavior, and Habitat Utilization of Yellowfin Tuna (*Thunnus albacares*) in the Northeastern Pacific Ocean, Ascertained Through Archival Tag Data." *Marine Biology* 152, no. 3: 503–525. https://doi.org/10.1007/s00227-007-0689-x.

Schaefer, K. M., D. W. Fuller, and B. A. Block. 2009. "Vertical Movements and Habitat Utilization of Skipjack (*Katsuwonus pelamis*), Yellowfin (*Thunnus albacares*), and Bigeye (*Thunnus obesus*) Tunas in the Equatorial Eastern Pacific Ocean, Ascertained Through Archival Tag Data." In *Tagging and Tracking of Marine Animals With Electronic Devices*, edited by J. L. Nielsen, H. Arrizabalaga, N. Fragoso, A. Hobday, M. Lutcavage, and J. Sibert, 121–144. Springer Netherlands. https://doi.org/10.1007/978-1-4020-9640-2_8.

Selwyn, J. D., J. D. Hogan, A. M. Downey-Wall, L. M. Gurski, D. S. Portnoy, and D. D. Heath. 2016. "Kin-Aggregations Explain Chaotic Genetic Patchiness, a Commonly Observed Genetic Pattern, in a Marine Fish." *PLoS One* 11, no. 4: e0153381. https://doi.org/10.1371/journal.pone.0153381.

Senina, I., P. Lehodey, B. Calmettes, et al. 2018. "Impact of Climate Change on Tropical Pacific Tuna and Their Fisheries in Pacific Islands Waters and High Seas Areas." 14th Regular Session of the Scientific Committee of the Western and Central Pacific Fisheries Commission, WCPFC-SC14.

Shropshire, T. A., S. L. Morey, E. P. Chassignet, et al. 2022. "Trade-Offs Between Risks of Predation and Starvation in Larvae Make the Shelf Break an Optimal Spawning Location for Atlantic Bluefin Tuna." *Journal of Plankton Research* 44, no. 5: 782–798. https://doi.org/10.1093/plankt/fbab041.

Sibert, J., and J. Hampton. 2003. "Mobility of Tropical Tunas and the Implications for Fisheries Management." *Marine Policy* 27, no. 1: 87–95. https://doi.org/10.1016/S0308-597X(02)00057-X.

Sibert, J. R., M. K. Musyl, and R. W. Brill. 2003. "Horizontal Movements of Bigeye Tuna (*Thunnus obesus*) Near Hawaii Determined by Kalman Filter Analysis of Archival Tagging Data." *Fisheries Oceanography* 12, no. 3: 141–151. https://doi.org/10.1046/j.1365-2419.2003.00228.x.

Skotte, L., T. S. Korneliussen, and A. Albrechtsen. 2013. "Estimating Individual Admixture Proportions From Next Generation Sequencing Data." *Genetics* 195, no. 3: 693–702. https://doi.org/10.1534/genetics.113.154138.

Sun, C. L., S. Z. Yeh, Y. J. Chang, H. Y. Chang, and S. L. Chu. 2013. "Reproductive Biology of Female Bigeye Tuna *Thunnus obesus* in the Western Pacific Ocean." *Journal of Fish Biology* 83, no. 2: 250–271. https://doi.org/10.1111/jfb.12161.

Tajima, F. 1989. "Statistical Method for Testing the Neutral Mutation Hypothesis by DNA Polymorphism." *Genetics* 123, no. 3: 585–595. https://doi.org/10.1093/genetics/123.3.585.

Teears, T., N. Davies, P. Hamer, et al. 2025. "Stock Assessment of Skipjack Tuna in the Western and Central Pacific Ocean: 2025." Technical Report WCPFC-SC21-2025/SA-WP-01(REV3).

Thygesen, U. H., L. Sommer, K. Evans, and T. A. Patterson. 2016. "Dynamic Optimal Foraging Theory Explains Vertical Migrations of Bigeye Tuna." *Ecology* 97, no. 7: 1852–1861. https://doi.org/10.1890/15-1130.1.

Tseng, C. T., C. L. Sun, S. Z. Yeh, S. C. Chen, and W. C. Su. 2010. "Spatio-Temporal Distributions of Tuna Species and Potential Habitats in the Western and Central Pacific Ocean Derived From Multi-Satellite Data." *International Journal of Remote Sensing* 31, no. 17–18: 4543–4558. https://doi.org/10.1080/01431161.2010.485220.

United Nations. 1982. "United Nations Convention on the Law of the Sea: Annex I."

Veliz, D., P. Duchesne, E. Bourget, and L. Bernatchez. 2006. "Genetic Evidence for Kin Aggregation in the Intertidal Acorn Barnacle (*Semibalanus balanoides*)." *Molecular Ecology* 15, no. 13: 4193–4202. https://doi.org/10.1111/j.1365-294X.2006.03078.x.

Walker, M. M., J. L. Kirschvink, S. B. R. Chang, and A. E. Dizon. 1984. "A Candidate Magnetic Sense Organ in the Yellowfin Tuna, *Thunnus albacares*." *Science* 224, no. 4650: 751–753. https://doi.org/10.1126/science.224.4650.751.

Wang, S., E. Meyer, J. K. McKay, and M. V. Matz. 2012. "2b-RAD: A Simple and Flexible Method for Genome-Wide Genotyping." *Nature Methods* 9, no. 8: 808–810. https://doi.org/10.1038/nmeth.2023.

Waples, R. S., P. M. Grewe, M. W. Bravington, R. Hillary, and P. Feutry. 2018. "Robust Estimates of a High ne/N Ratio in a Top Marine Predator, Southern Bluefin Tuna." *Science Advances* 4, no. 7: eaar7759. https://doi.org/10.1126/sciadv.aar7759.

Ward, R. D., N. G. Elliott, P. M. Grewe, and A. J. Smolenski. 1994. "Allozyme and Mitochondrial DNA Variation in Yellowfin Tuna (*Thunnus albacares*) From the Pacific Ocean." *Marine Biology* 118, no. 4: 531–539. https://doi.org/10.1007/BF00347499.

Weist, P., H. Kusche, O. Tørresen, et al. 2024. "Genomic Differentiation and Interoceanic Population Structure of Two Large Pelagic Scombrid Species." *Global Ecology and Conservation* 54: e03117. https://doi.org/10.1016/j.gecco.2024.e03117.

Wiebe, P. H., D. Allison, M. Kennedy, and G. Moncoiffé. 2015. "A Vocabulary for the Configuration of Net Tows for Collecting Plankton and Micronekton." *Journal of PlanktonResearch* 37, no. 1: 21–27. https://doi.org/10.1093/plankt/fbu101.

Willing, E.-M., C. Dreyer, and C. van Oosterhout. 2012. "Estimates of Genetic Differentiation Measured by FST Do Not Necessarily Require Large Sample Sizes When Using Many SNP Markers." *PLoS One* 7, no. 8: e42649. https://doi.org/10.1371/journal.pone.0042649.

Wright, S. R., D. Righton, J. Naulaerts, et al. 2021. "Fidelity of Yellowfin Tuna to Seamount and Island Foraging Grounds in the Central South Atlantic Ocean." *Deep Sea Research Part I: Oceanographic Research Papers* 172: 103513. https://doi.org/10.1016/j.dsr.2021.103513.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Preserved larval *Thunnus* and larval *Katsuwonus pelamis*. **Table S1:** Summary of SNPs retained for each analysis. **Table S2:** Summary of larval and adult sampling. **Table S3:** Summary of geographic origin of larval and adult tuna samples. **Figure S2:** Dendrogram of all samples including technical replicates. **Figure S3:** Dendrogram of all samples excluding technical replicates and F_{ST}. **Figure S4:** ADMIXTURE likelihood values for analysis of all samples. **Figure S5:** Linkage disequilibrium decay plots. **Figure S6:** Frequency histogram of pairwise relatedness and kinship. **Figure S7:** Average expected heterozygosity by year for each species. **Figure S8:** Average least cross validation error for each species group. **Figure S9:** Sampling locations of the divergent population of yellowfin. **Table S4:** Sample collection metadata. **Table S5:** Depth of sequencing coverage statistics. **Table S6:** DNA fragment length distribution. **Table S7:** Proportion of sites with depth of coverage > 5× by sample.