Biological Conservation 303 (2025) 110965

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Quantifying impacts of seabird bycatch using genetic assignment: A case study of black-footed albatross in U.S. fisheries

Jessie N. Beck[a,b,*,1,2], Diana S. Baetscher[c,1], Claire Tobin[c,3], Scott V. Edwards[d,e], Simon Yung Wa Sin[f], Shannon Fitzgerald[a,4], Vanessa J. Tuttle[g], John Peschon[h], Wesley A. Larson[c]

[a] *NOAA Fisheries, Alaska Fisheries Science Center, Seattle, WA, USA*
[b] *University of California Santa Cruz, Santa Cruz, CA, USA*
[c] *NOAA Fisheries, Alaska Fisheries Science Center, Auke Bay Laboratories, Juneau, AK, USA*
[d] *Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA*
[e] *Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA*
[f] *School of Biological Sciences, The University of Hong Kong, Hong Kong, China*
[g] *NOAA Fisheries, Northwest Fisheries Science Center, Seattle, WA, USA*
[h] *NOAA Fisheries, Pacific Islands Regional Office, Fisheries Observer Program, Honolulu, HI, USA*

1. Introduction

Migratory species encounter multiple threats as they move through and occupy distinct habitats (Bairlein, 2016). Assessing the severity of interacting threats complicates quantifying the cumulative impact, yet is critical for management and conservation (Mahon et al., 2019). Managing threats to migratory animals can become even more complex in species with metapopulation structure (Schnell et al., 2013) when discrete populations share similar environments during some parts of their lifecycle but not others (e.g., specific links between breeding and foraging areas). In these cases, holistic management requires understanding how individuals from discrete populations experience threats across habitats (Rushing et al., 2016).

Quantifying the impact of distinct and cumulative threats is a major challenge in marine systems, especially for species that return to specific breeding grounds, but range widely while foraging. Seabirds are a classic example: many seabirds encounter invasive species, sea-level rise, and disease on breeding islands, yet they also face fisheries bycatch, marine heat waves, and plastic pollution at sea where they forage (Dias et al., 2019). In addition, seabirds often have metapopulation structures, with populations made up of individuals returning to specific colonies to breed (Kersten et al., 2021). Long-lived seabirds, who are slow to reproduce and have low reproductive output, are particularly sensitive to anthropogenic impacts (Tuck et al., 2015).

Evaluating at-sea threats for seabirds, particularly at the subpopulation level, is a challenge for resource managers due to the widespread and diffuse foraging strategies. Mark-recapture banding studies have linked a small number of at-sea mortalities back to subpopulations (Nevins et al., 2009), and satellite or GPS tagging studies can illustrate how different foraging grounds result in differential exposure to at-sea threats (Corbeau et al., 2021). However, neither method measures direct impacts of at-sea threats to different populations.

Genetic stock identification (GSI) is one approach to study the movement of populations (e.g., Ruegg et al., 2021). Frequently used in management of Pacific salmon, GSI has also been applied to other commercially targeted and bycatch fish species (Hasselman et al., 2016), but is rarely used in studies of seabird conservation (but see Abbott et al., 2006; Baetscher et al., 2022; Walsh and Edwards, 2005). GSI was previously considered a tool primarily for populations with substantial genetic structure, but multiple studies over the last decade have demonstrated that high-resolution markers identified with genomic techniques can substantially improve assignment accuracy (McKinney et al., 2020). With these advances, GSI should be considered a valuable conservation tool for linking threats across habitats to specific subpopulations in taxa such as seabirds.

---

* Corresponding author.
E-mail address: jessica.beck@noaa.gov (J.N. Beck).

[1] J.N. Beck and D.S. Baetscher contributed equally to this publication, and share first authorship.

[2] Previous affiliation: Oikonos Ecosystem-Knowledge, Kailua, HI, USA

[3] Current affiliation: University of Utah, Salt Lake City, UT, USA

[4] Retired.

https://doi.org/10.1016/j.biocon.2025.110965
Received 29 April 2024; Received in revised form 23 December 2024; Accepted 2 January 2025

We demonstrate the utility of GSI for connecting at-sea threats to specific colonies in a seabird species of conservation concern, the black-footed albatross (BFAL, *Phoebastria nigripes*). BFAL are slow-reproducing, long-lived seabirds that forage throughout the North Pacific and breed on nine low-lying islands in the Northwestern Hawaiian Islands and on three islands in Japan (Arata et al., 2009). Breeding colonies are separated by large distances, corresponding to meta-population structure, with individuals typically returning to breed on the same colony with their long-term mates (Rice and Kenyon, 1962). Several studies identified genetic differentiation between Hawaiian and Japanese colonies (Walsh and Edwards, 2005; Dierickx et al., 2015), but little genetic differentiation among Hawaiian colonies, which make up 97% of the breeding population, has been documented (but see recent whole-genome data from Huynh et al., 2023).

BFAL bycatch has been documented in U.S. fisheries since the 1970s, with the highest rates in the 1990s (Arata et al., 2009) followed by reduced catch in the 2000s after seabird mitigation was required, including tori-lines in longline fleets north of 23°N, which reduced BFAL bycatch by an order of magnitude (Eich et al., 2016; Gilman et al., 2008). However, monitoring and enforcement of seabird mitigation in regional fishery management organizations and international fleets is minimal. Bycatch is the largest source of mortality for the species (Arata et al., 2009), and has likely limited population growth of the species for decades (Bakker et al., 2018).

In this study, we conduct GSI with high resolution markers identified from low-coverage whole genome sequencing (lcWGS) to link BFAL caught and collected as bycatch in U.S. federally-managed fisheries to six breeding colonies in Japan and the Northwestern Hawaiian Islands. These six breeding colonies comprise 82% of the total breeding population. We also use the lcWGS data to examine population structure and genetic differentiation across the colonies. GSI allows us to directly connect at-sea mortalities to colonies. Through this approach, we investigate whether specific colonies are disproportionately impacted by bycatch relative to population size, and how spatially-explicit bycatch interactions may differ by colony. Based on these results, we recommend specific conservation actions that incorporate connectivity of BFAL populations across their habitats.

2. Methods

2.1. Genetic baseline collection and sequencing data

Samples from 6 BFAL breeding colonies in the Northwestern Hawaiian Islands and Japan were prepared for lcWGS to identify fine-scale population genetic structure and targeted genetic markers for population assignment (Fig. 1). For baseline representation from each colony, we obtained a total of 137 samples with the following numbers of samples per colony: Kure (*Hōlanikū*, 23), Midway (*Kuaihelani*, 23), Laysan (*Kamole*, 8), Tern (30) and Whale-Skate (3) in the French Frigate Shoals (FFS, *Lalo*), Lehua (2), and Torishima (48). Samples consisted of either blood preserved in Queen's lysis buffer, blood on filter paper, or tissue samples from birds of known provenance from existing collections and from birds banded at their breeding colony and later sampled as fisheries bycatch (SI Table S1).

Information on DNA extraction, whole genome library preparation, and analysis of whole genome data to generate genotype likelihoods can be found in SI. These data were used to identify genetic differentiation among breeding colonies using the fixation index (F_{ST}), which ranges from 0–1, from no genetic differentiation ($F_{ST} = 0$) to highly differentiated populations that share no genetic diversity ($F_{ST} = 1$).

2.2. Fisheries sample collection

BFAL bycatch in this study were collected by observers in the National Oceanic and Atmospheric Administration (NOAA) North Pacific, Pacific Islands Region, and At-Sea Hake Observer Programs between 2005 and 2022 (SI Fig. S1). The North Pacific Observer Program monitors groundfish and halibut fisheries operating in the Alaska Exclusive Economic Zone (EEZ). These fisheries use multiple gear types (longline, pot, trawl, and jig). Observer coverage varies by vessel and participation, and limited access programs (SI Table S2). The Pacific Islands Region Observer Program monitors deep- and shallow-set longline fisheries operating in U.S. and international waters around the Hawaiian Islands. The At-Sea Hake Observer Program (A-SHOP) monitors the at-sea Pacific hake (*Merluccius productus*) trawl fishery operating off of the U.S. west coast (with most effort occurring from 42-48°N). These fisheries represent three of the four NOAA observer programs that regularly interact with BFAL (the West Coast Groundfish Observer Program is not included in this study). From 2005-2022, observers on

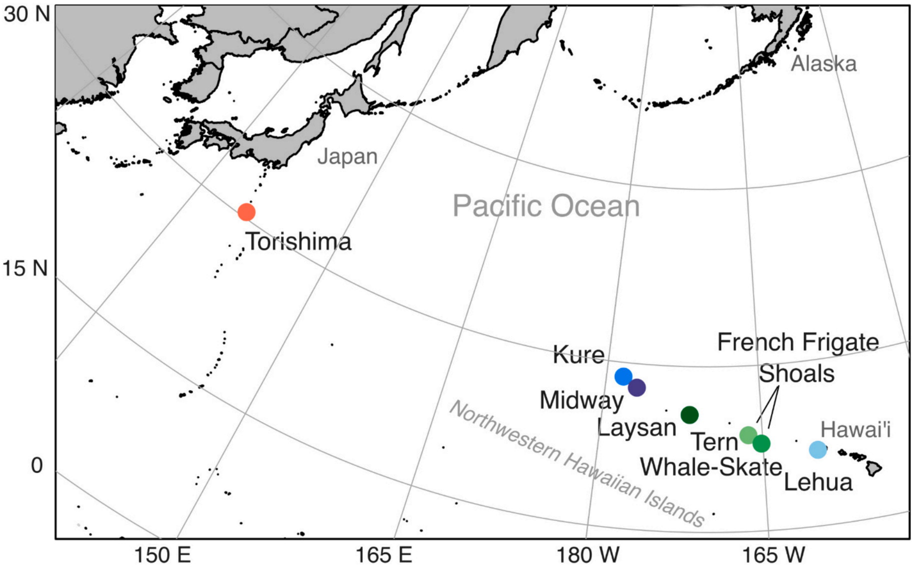

Fig. 1. Location of seven breeding colonies from which samples were obtained for lcWGS: Torishima (Japan), and Kure, Midway, Laysan, Tern, Whale-Skate, and Lehua in the Northwestern Hawaiian Islands. Tern and Whale-Skate Islands are part of the FFS.

vessels collected between 1–127 BFAL each year for necropsy (SI Table S4). North Pacific Groundfish and A-SHOP observers were asked to collect all dead BFAL. Hawaiʻi longline observers were requested to collect all banded BFAL and the first dead unbanded BFAL of each cruise.

During necropsies, we sampled 1 mL of pectoral muscle and stored samples at -20 °C. Collection data for BFAL was provided by researchers from the NOAA Observer Programs and Science Centers.

We sampled 855 BFAL for this study (151 banded birds and 704 without bands; SI Table S4). The majority of birds came from the Hawaiʻi deep-set fishery. Together with birds from the shallow-set longline fishery and unknown set-type, Hawaiʻi was the source for 79% of our samples. North Pacific Groundfish fisheries in Alaska made up almost 18% of BFAL samples and 3% of the birds came from the At-Sea Hake Trawl Fishery on the west coast. Bycatch estimates for this fishery are typically lumped with other West Coast Groundfish fisheries. Due to logistical difficulty of retrieving and storing BFAL specimens at sea, observers from all regions were unable to collect 100% of observed bycatch. For fisheries with <100% observer coverage, fishery managers use observed bycatch rates to calculate estimated bycatch across observed and unobserved vessels (see SI Table S2 and S4).

2.3. GSI marker design and genotyping

To assign bycatch samples to breeding colonies, we designed a set of genetic markers to identify samples from the baseline colonies using an amplicon-sequencing protocol (GT-seq; Campbell et al., 2015; full details in SI). From the lcWGS data, we selected and designed primers to target 344 genomic regions containing single nucleotide polymorphisms (SNPs) with elevated allele frequency differences between pairs of colonies. We tested the primer sets in a single multiplex PCR reaction and retained 168 for genotyping (details in SI). For GSI, we combined samples for Whale-Skate and Tern Islands into a single genetic group for the FFS based on the lack of genetic differentiation and geographic proximity of these two colonies. We removed Lehua due to a small sample size (only two individuals).

Using these 168 targeted genetic markers, we generated genotypes for baseline (breeding colony) and bycatch samples. We sequenced all samples across three lanes of a MiSeq instrument (Illumina) with 384 samples per lane. We analyzed sequencing data using the workflow described in Baetscher et al. (2018, 2022), including calling microhaplotype alleles using the R package 'microhaplot' (Ng and Anderson, 2019) and then filtering for minimum read depth (10), minimum allele balance (0.4), and missing data (<25%; details in SI).

Following initial genotype quality filters, we analyzed baseline genotypes using the R package 'rubias' to evaluate the statistical power of the 168 genetic markers for accurately identifying samples from each population (Moran and Anderson, 2019; methods in SI). This evaluation provides information about the confidence level for assignment accuracy of bycatch in this study and whether mis-assignments are more likely to occur between a particular set of colonies.

2.4. GSI of individuals caught in fisheries and spatially-explicit interactions

For GSI of bycatch, we analyzed genotypes from samples collected by observers from 2010–2022, and assigned them to five genetic baseline groups: FFS, Midway, Laysan, Kure, and Torishima. We constrained the years to 2010–2022 to focus on years where observer coverage and collection protocols were standardized within each fishery region. We used the R package 'rubias' to perform assignment of unknown samples to one or more baseline groups with the *infer_mixture* function using the MCMC method, 2000 cycles, and 100 burn-in. We retained high probability genetic assignments with posterior values >0.9 and z-statistics within 3.5 standard deviations in order to exclude bycatch that would have originated at colonies not sampled as part of the baseline.

In addition to assigning samples through GSI, we also received 151 bycatch samples from banded birds. Banding data allowed us to link the birds back to the colonies where they were banded as chicks.

Following genetic assignment of bycatch, we assessed whether a disproportionate amount of bycatch originated from any one of the colonies in this study. We compared the proportion of bycatch per colony to the proportion that each colony comprises of the total metapopulation for the colonies comprising the five genetic groups included in genetic marker development, plus the populations of the unrepresented colonies (Table 1, Fig. 2). We excluded all 124 banded bycatch from Hawaiʻi fisheries from this analysis due to non-random retention of banded bycatch (whereas Alaska and west coast fisheries retain all BFAL bycatch). Generating population estimates for seabird colonies on islands in the Pacific is notoriously difficult due to the remote and inaccessible nature of many of the colonies. Because of this limitation, we used population estimates spanning 1994–2005 (Arata et al., 2009).

Based on the assumption that the proportion of bycatch per colony per fishery should be equivalent to the proportion of the total population, we used goodness-of-fit tests (G^2) to evaluate whether the observed proportions of bycatch by colony differed from the expected proportion based on colony size. For Alaska and A-SHOP comparisons, we combined birds with colony assignments from both GSI and banding data since observers were instructed to collect all albatross. In the Hawaiʻi fisheries, observers were instructed to collect all banded birds, plus the first unbanded individual of each species caught. Since this collection protocol could skew proportions towards colonies with high numbers of banded individuals (FFS in particular), we excluded banded birds from the Hawaiʻi fisheries comparison and only included birds assigned with GSI.

To evaluate which areas of the Pacific and Bering Sea had the highest probability of bycatch on a per-colony basis, we linked colony assignment and fisheries collection data for BFAL bycatch interactions. Because the number of bycatch samples from the west coast of the U.S. was small ($n = 24$), spatial analyses included just data from the Hawaiʻi and Alaska regions. For individuals with GSI or band assignments and available spatial data, we calculated 50% and 90% utilization distributions (UDs) using the adehabitatHR package in R (Calenge, 2006), and mapped the UDs by colony. UDs are probability density distributions that define the spatial occupancy of an animal (Worton, 1989). Although typically used with tracking data, our application uses the point locations of bycatch birds to generate UDs for each breeding colony based on GSI and band assignments. This spatial analysis allowed us to link at-sea threats back to colonies and inform resource managers about how the distribution of fishing effort differentially impacts discrete colonies.

3. Results

3.1. Genetic baseline collection and sequencing data

From the lcWGS, 4.7 billion sequences were generated for the 137 albatross samples. Sequencing coverage ranged from 0.58-5.2x (mean: 2.6, sd: 1.07). Samples with <1x coverage were removed from analyses, which eliminated seven samples across three colonies: Kure (5), Torishima (1), and Midway (1). From the remaining 130 samples, we were able to identify a total of nearly 2.3 million SNPs with a minor allele frequency > 0.05 and present in a minimum of 85 samples across the 3397 scaffolds in the reference genome assembly.

Both F_{ST} values and a principal components analysis (PCA) showed clear population differentiation between Torishima and the Hawaiian colonies (SI Table S3, SI Fig. S2). Across the Northwestern Hawaiian colonies, genetic differentiation was very low, with F_{ST} values ranging from 0.006-0.013 (SI Table S3).

3.2. GSI marker design and genotyping

We genotyped 855 fisheries samples (bycatch, including banded birds) and an additional 92 reference samples with the targeted genetic

Table 1
The estimated breeding population sizes by colony (Arata et al., 2009) compared to the bycatch for birds caught between 2010-2022, and assigned using GSI and band data to each colony (Alaska and A-SHOP), or via GSI alone (Hawai'i). Goodness-of-fit (G^2) tests compare bycatch percentages against expected population percentages (except for A-SHOP data due to small sample sizes). Significant p-values are in bold.

Colony	Pop. Est.	% Total Pop.	All fisheries		Alaska				Hawai'i (GSI only)				A-SHOP	
			n assigned	% bycatch	n assigned	% bycatch	$G^2(1)$	p-value	n assigned	% bycatch	$G^2(1)$	p-value	n assigned	% bycatch
Kure Atoll	4040	3	39	6	18	13	25.8183	**<0.0001**	21	4	1.5755	0.2094	0	0
Midway Atoll	43,658	35	56	8	8	6	70.6842	**<0.0001**	46	9	199.4658	**<0.0001**	2	8
Laysan Island	42,012	34	0	0	0	0	116.5615	**<0.0001**	0	0	438.7843	**<0.0001**	0	0
French Frigate Shoals	8518	7	420	61	87	61	281.1138	**<0.0001**	315	60	783.3777	**<0.0001**	18	75
Torishima (Izu Shoto)	3120	3	1	0	0	0	8.6504	**0.0033**	1	0	24.5808	**<0.0001**	0	0
Other Colonies (Japan and U.S.)	22,014	18	–	–	–	–	–	–	–	–	–	–	–	–
Unassigned by GSI	–	–	178	26	29	20	0.5461	0.4599	145	27	750.3683	**<0.0001**	4	17
Total	***123,362***		694		142				528				24	

markers for GSI. This dataset included 437 alleles across 168 loci. Of 947 genotyped samples, 40 bycatch and eight reference samples had >25% missing data and were removed from further analyses. The reference evaluation included the remaining 126 samples. Excluded from the GSI baseline were two Lehua samples, which by themselves constituted too small of a sample size for a GSI baseline, and one Laysan Island individual, which was removed because of an ambiguous genotype that suggested it might have hybrid ancestry with Laysan Albatross. The remaining 126 baseline samples were used for generating allele frequency estimates per-population. Baseline populations included 7–46 samples per group (SI Table S1).

Results from the leave-one-out baseline assessment showed that the genetic markers were effective for assigning simulated genotypes to the correct population. Using a 90% likelihood threshold, for all reporting units, correct assignments were >88% for all populations, with specific accuracy as follows: Torishima (100%), FFS (99.9%), Midway (99%), Laysan (98.9%), and Kure (88.7%). Misassignments included simulated Kure genotypes assigned to FFS (6.5%) or Midway (4.8%) instead, and 1% of simulated genotypes misassigned between Midway and Kure, and Laysan and Midway (SI Fig. S3).

3.3. *GSI of individuals caught in fisheries and spatially-explicit interactions*

The GSI analysis included 771 bycatch samples (banded birds that were part of the reference baseline were excluded from GSI). Of these, 590 could be assigned to a single colony with >90% likelihood. Samples that did not attain this threshold were assigned at lower probabilities to FFS (93 samples), Kure (40 samples), and Midway (31 samples; SI Table S5). Nine samples in the GSI analysis were > 3.5 standard deviations away from the mean allele frequencies for their assignment group (z-score outliers), indicating that they are most likely from colonies not included as part of the baseline. One of these outliers was a banded bird from Laysan Island, while the others were not banded and removed from further analyses.

In addition to samples assigned through GSI, 151 bycatch samples were from banded birds (see methods). After filtering for incomplete banding data and redundancy between GSI and band assignments, we had a total of 666 samples assigned through either GSI or bands across all years included in the study. For estimating population- and colony-level impacts of fisheries bycatch, we limited samples to collections from 2010-2022 and removed banded birds from Hawai'i (see methods), which resulted in 516 samples (Table 1, Fig. 2). We were unable to assign 178 birds collected from 2010-2022 (Table 1). For spatial analyses and UDs, we used this same dataset, further reduced to the 495 bycatch samples for which we had geographic collection information available (Fig. 3).

Three breeding colonies had sufficient bycatch sample sizes for spatial analyses. Utilization distributions for FFS, Kure, and Midway depicted primary areas of bycatch north/northwest of the Hawaiian Islands and along the shelf break in the Gulf of Alaska (Fig. 3). Kure includes the largest proportion of its 90% UD in the central and eastern Gulf of Alaska, whereas the FFS 90% UD in the Gulf is farther west. For FFS and Midway colonies, the 90% UD extends below 20° N. Bycatch from Kure extends farthest to the west, and both FFS and Midway encounter small hotspots of bycatch that include both 50% and 90% UD along the west coast north of 40° N.

4. Discussion

Genetic stock identification of black-footed albatross bycatch in U.S. fisheries revealed a disproportionate amount of bycatch from the FFS relative to its population size, while Midway Atoll and Laysan Island experienced relatively low levels of bycatch relative to their population sizes. Although utilization distributions from bycatch locations indicate that BFAL are caught across similar geographic areas within fishing

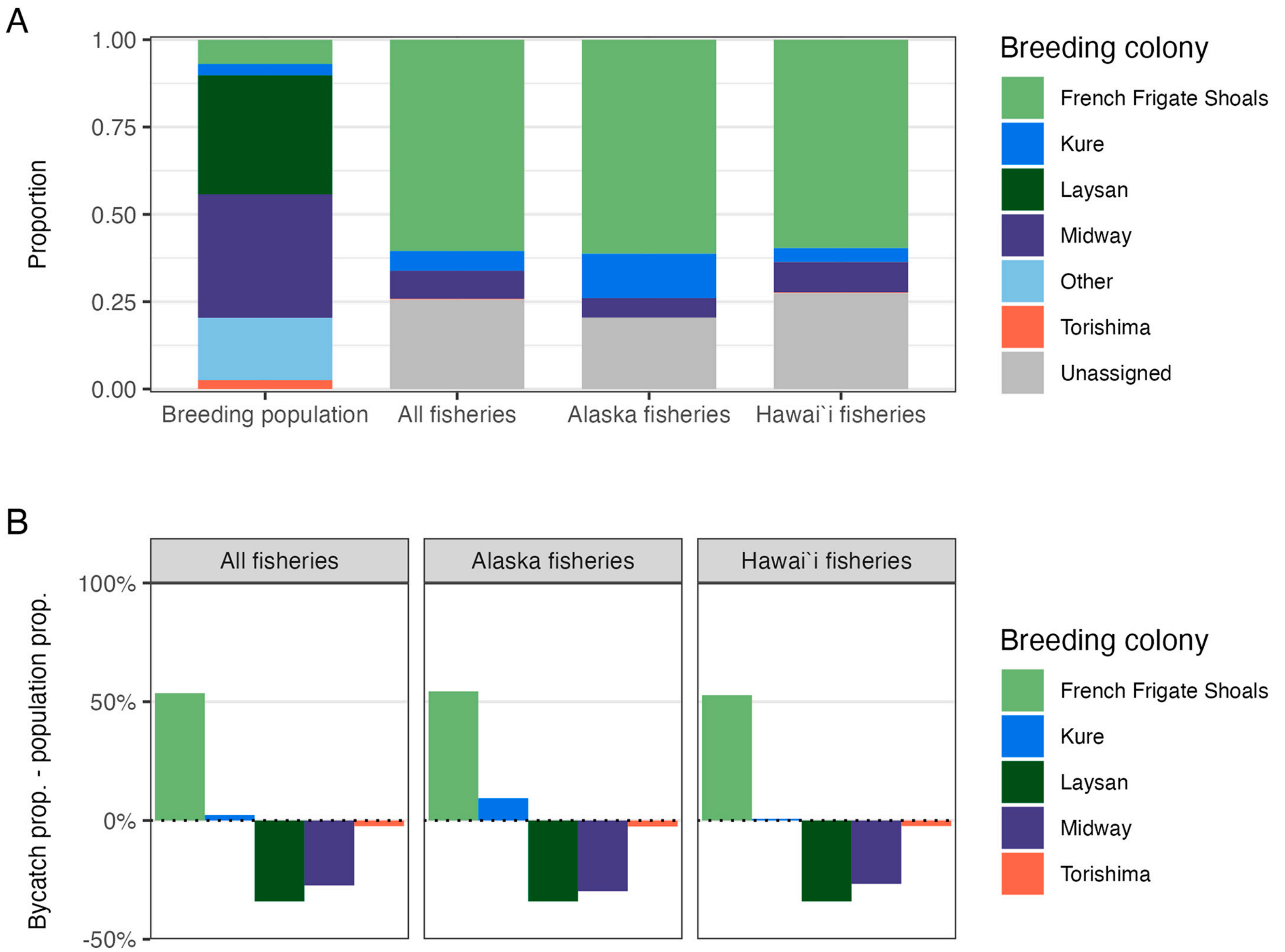

Fig. 2. Proportion of BFAL by colony in the total metapopulation compared to bycatch assigned to each colony by fishery area (A). Percent difference between the proportion of bycatch per breeding colony and the proportion of the total estimated metapopulation of BFAL at that colony (B). Colonies with negative percentages are underrepresented in bycatch. These data represent 694 bycatch samples across all fisheries: 528 from Hawai'i and 142 from Alaska. Unassigned birds are potentially from breeding colonies not included in the reference baseline and so the "Other" colonies are not represented in panel B. See Table 1 for percentages and G^2 tests.

areas, the disparity between bycatch and population size suggest that BFAL from the large, western colonies (Kure and Midway Atolls, and Laysan Island) may forage more heavily outside U.S. fishing areas. These results indicate that albatross from one of the smaller BFAL breeding colonies is more heavily impacted by U.S. fisheries and that coordinated management of bycatch across fishery regions might be necessary to protect the FFS population. More broadly, this study demonstrates the ability to use marker-based GSI for populations with very low levels of genetic differentiation, making this a viable and cost-effective conservation tool for marine species regularly caught in fisheries.

4.1. *Disproportionate bycatch in U.S. fisheries*

Overall, we found disproportionate bycatch from specific colonies across all fishery regions (Table 1, Fig. 2). The FFS made up 61–75% of BFAL bycatch in both Alaska and Hawai'i fisheries, despite being only 7% of the total metapopulation (Fig. 2). BFAL from Kure Atoll were also overrepresented in Alaska fisheries. Bycatch from Midway and Laysan Islands was underrepresented across all fishery regions, making up <10% of bycatch while comprising almost 70% of the global population (Table 1, Fig. 2). Meanwhile, bycatch originating from Torishima was underrepresented compared to colony size, although this pattern is potentially unsurprising given the location of Torishima in the Western Pacific, far from U.S.-based fisheries.

The prevalence of FFS BFAL is particularly concerning given that the island complex is predicted to lose 12% of terrestrial habitat to sea level rise by 2100 (Reynolds et al., 2016). BFAL colonies on two islands in the FFS complex, East and Whale-Skate Islands, were lost in the last 20 years due to erosion and over-topping by storm swells. The largest island in the complex and the primary source of bycatch in this study, Tern Island, was enlarged by the U.S. Navy but is eroding due to lack of infrastructure maintenance after a damaging microburst storm in 2018 (Baker et al., 2020).

4.2. *Spatial bycatch trends and colonies*

Albatross rely on wind currents to access foraging areas thousands of kilometers from their breeding colonies (Thorne et al., 2016) in productive regions, such as the California Current and the Transition Zone Chlorophyll Front in the North Pacific (Hyrenbach et al., 2021). Bycatch UDs from this study show how BFAL foraging ecology intersects with U.S. fishing fleets, and suggests that the proximity of individual breeding

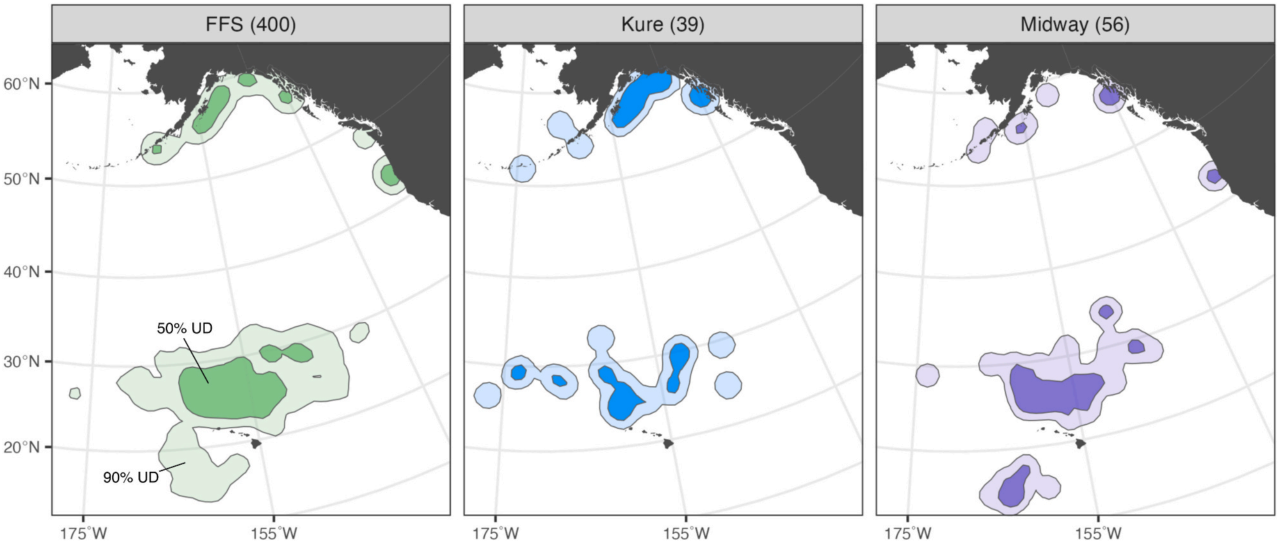

Fig. 3. Utilization distributions (UD) for fisheries bycatch from three of the BFAL colonies based on genetic stock identification and location information from banded birds. Samples sizes are as follows: FFS (400), Kure (39), Midway (56). Data are from 495 BFAL bycatch collected between 2010-2022 from fisheries in Alaska, Hawaiʻi, and the west coast. The 90% and 50% UD represent the probability density distribution for bycatch from the colony indicated.

colonies to different wind currents (and thus to foraging grounds) may influence the amount of bycatch from specific colonies.

The distribution of FFS bycatch matches tracking studies that show consistent use of areas north of the main Hawaiian Islands by BFAL from Tern Island. The core FFS bycatch area (50% UD) at 20–31°N overlaps with this tracking data (Gutowsky et al., 2015; Fig. 3) and includes an area south of 23°N where no seabird bycatch mitigation is required (NOAA, 2023; IATTC, 2023). Additionally, tracking data show FFS BFAL using winds in the California Current to access the Pacific Northwest during July and August (overlapping with A-SHOP) and Gulf of Alaska mid-October to mid-December (Gutowsky et al., 2015). These spatial patterns are evident in the FFS bycatch UDs in our dataset (Fig. 3). Whereas the Alaska and U.S. west coast core bycatch areas are within the U.S. EEZ, the 50% UD north of Hawaiʻi is partly located in international waters, and overlaps with Vanuatu and Taiwanese longline fleets (GFW, 2023). International fleets represent a source of uncertainty for BFAL bycatch since no samples from non-U.S. fisheries were obtained for this study and observer coverage and/or reporting is often low.

North Pacific Groundfish fisheries in Alaska had a disproportionately high number of BFAL originating from Kure Atoll, one of the westernmost colonies (Table 1; Fig. 2). Our spatial data are the first evidence that Kure BFAL use waters around the Aleutians, Gulf of Alaska, and areas north of the main Hawaiian Islands (Fig. 3). Tracking studies from Midway Atoll, ~50 miles east of Kure, show BFAL use the Western Pacific with hotspots around the Aleutian Islands and Bering Sea (Fischer et al., 2009). BFAL from Midway use the Kuroshio Current to access the North Pacific Current below the Aleutian Islands and presumably Kure Atoll BFAL would use similar migration routes, although the low numbers of Midway BFAL in our Alaska fisheries samples might indicate differences in foraging distributions among birds from these two colonies.

4.3. Non-U.S. sources of bycatch

Tracking data for BFAL from Midway Atoll, Tern Island, and Kure Atoll show that these birds also frequently use waters not fished by U.S. fleets (Gutowsky et al., 2015; Thorne et al., 2016; Hyrenbach et al., 2021). International fleets (both regulated and IUU [illegal, unreported and/or unregulated]) present additional at-sea threats for BFAL from the colonies in this study. BFAL from colonies under-represented as bycatch in U.S. fisheries could be foraging more heavily in areas targeted by international vessels. For example, birds from all colonies likely interact with non-U.S. longline tuna fleets in the Western and Central Pacific Fisheries Commission convention area, which reports annual BFAL bycatch of 35–175 birds with an observer coverage rate of 1.7–3.8% (2013–2019, WCPFC, 2020). Western BFAL colonies, including Kure and Midway Atolls, and Torishima also likely encounter Japanese and Russian trawl fleets, which do not actively report and/or monitor seabird bycatch (Arata et al., 2009; Phillips et al., 2024).

Birds from BFAL colonies farther east in the Northwestern Hawaiian Islands, such as FFS, also likely experience mortality in non-U.S. fleets in the Eastern Pacific. BFAL bycatch has been reported by the Inter-American Tropical Tuna Commission (IATTC, 2023) and in Canadian longline fisheries in British Columbia (Fox et al., 2021). Thus, although international fleets might be impacting some of the colonies under-represented in U.S. fisheries bycatch, unreported bycatch is likely impacting all colonies to some extent. Moreover, the cumulative impact of bycatch on small eastern colonies, such as FFS, could lead to suppressed breeding populations and loss of adaptive and genetic diversity.

4.4. Genetic considerations

Whole-genome data for each of the breeding colonies indicated low genetic differentiation, with the largest F_{ST} values between the Northwest Hawaiian island colonies and Torishima, consistent with prior studies (SI Table S3; Ando et al., 2014; Dierickx et al., 2015; Walsh and Edwards, 2005). Among the Hawaiʻi colonies, very low population structure (pairwise $F_{ST} = 0.006–0.013$) suggests ongoing gene flow and/or relatively recent population divergence, consistent with the highly admixed mitochondrial genomes for the small number of individuals from Tern and Midway in Huynh et al. (2023). North Pacific albatrosses have experienced large fluctuations in population size, including expansion during the Last Glacial Period followed by population contraction as the climate changed, sea-level rose, and breeding habitat was reduced (Huynh et al., 2023). Additionally, feather hunting in the late-19th and early-20th century removed well-over one million birds from the Northwestern Hawaiian Islands, including >150,000 from Laysan Island in a single year and >1 million birds from Midway in 1910 (Spennemann, 1998). These population fluctuations coincide with a loss of genetic diversity in the species (Dierickx et al., 2015; Huynh et al., 2023), potentially reducing the evolutionary potential to adapt under changing conditions.

Despite low levels of differentiation, the targeted genetic markers in this study provided the first opportunity to assign BFAL bycatch from U. S. fisheries to individual breeding populations. We excluded lower confidence genetic assignments (~20% of samples; Table 1) to ensure that inferences about fisheries bycatch and spatial distributions used only those samples with high probability-of-assignment (>0.9). Notably, bycatch samples assigned to Laysan Island using GSI were outside the threshold for confident assignment. This was also true for one banded Laysan bird used for the baseline and evaluated by self-assignment. On Laysan Island, BFAL can hybridize with Laysan Albatross, generating offspring with intermediate plumage coloration (McKee and Pyle, 2002). Although hybrids are uncommon, hybridization could result in introgression of Laysan Albatross into the BFAL population, which might result in underestimating bycatch from Laysan Island. Yet even if Laysan bycatch were underestimated, only nine bycatch samples assigned to Laysan were later excluded, indicating that the total proportion of bycatch from Laysan is unlikely to be substantially higher than identified in this study and certainly not proportional to 34% of the total BFAL population.

4.5. Conservation implications

Consistently over-represented BFAL colonies (FFS) in bycatch across U.S. fisheries regions highlights the need for bycatch reduction and coordinated management. Although BFAL is listed as near threatened (IUCN, 2023), the species is not federally listed in the U.S. Bycatch is managed regionally through multiple NOAA offices, but cumulative bycatch across U.S. fisheries regions is not formally reported. Formal coordination among NOAA offices to manage BFAL across its marine distribution would allow for adaptive management of bycatch threats such as changes in gear types and vessel-specific bycatch analysis (Fitzgerald and Dolliver, 2023). While our genome-wide analysis suggests the potential for gene flow among colonies - at least over longer time scales - the regularity with which cross-colony emigration occurs is uncertain. Characterizing both demographic connectivity and the impact of international bycatch would allow for managers to evaluate sustainable levels of bycatch from U.S. fisheries. Further, bycatch management could be complemented by targeted conservation planning with terrestrial managers that addresses disproportionate bycatch impacts across habitats.

Our work highlights the use of GSI within well-monitored fisheries, but internationally, addressing the threat of bycatch is challenged by a lack of enforcement, difficulty implementing independent observer programs, and limited transparency in many fleets (Dias et al., 2019; Lewison et al., 2004; Phillips et al., 2016).

Our study shows the benefits of increasingly cost-effective and efficient genetic technology and analysis methods that allow for greater population-specific management of migratory species and more effective use of large genomic datasets to improve population assignment (e.g., DeSaix et al., 2023). Experts from a growing community of academics, practitioners, and government agencies are applying these approaches to a range of conservation scenarios. For migratory species, such as seabirds, genetic tools give us the ability to link threats to specific populations and create targeted and more effective conservation measures.

CRediT authorship contribution statement

Jessie N. Beck: Conceptualization, Data Curation, Analysis, Writing and Figures, Review and Editing, Funding Acquisition, Samples. **Diana S. Baetscher:** Conceptualization, Data Curation, Analysis, Writing and Figures, Review and Editing, Funding Acquisition. **Claire Tobin:** Review and Editing, Data curation. **Scott V. Edwards:** Review and Editing, Samples. **Simon Yung Wa Sin:** Review and Editing, Samples. **Shannon M. Fitzgerald:** Data Curation, Review and Editing, Funding Acquisition. **Vanessa J. Tuttle:** Data Curation, Review and Editing. **John Peschon:** Data Curation, Review and Editing. **Wesley A. Larson:** Review and Editing.

Ethics statement

All appropriate ethics and other approvals were obtained for the research. Samples were obtained from birds accidentally killed in fishery interactions and covered by USFWS salvage permits to NOAA observer programs. Samples were examined prior to author J. Beck's affiliation with the University of California Santa Cruz.

Declaration of competing interest

The authors declare they have no competing interests.

Acknowledgements

We thank K. Hayes and K. DeLeon from the Pacific Center for Molecular Biodiversity at the Bishop Museum, and N. Mejia and F. Termignoni Garcia of Harvard University for help locating and shipping samples. We also thank H. Nevins and the staff of the Marine Wildlife Veterinary Care and Research Center for supporting necropsies. Thanks to J. Felis for assistance with coordinate reference systems for maps. We thank D. Hanselman and two anonymous reviewers for providing helpful feedback on the manuscript. Thanks to the fishers of the Hawaiʻi longline, North Pacific Groundfish, and At-Sea Hake Trawl fisheries, the staff members who operate these programs, and to the NOAA observers that contributed to this study. Funding for this study was provided by the Revive and Restore Wild Genomes program grant #WGM 2021-027, with support for the necropsy program from NOAA's National Seabird Program.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.110965.

Data availability

Low-coverage whole genome sequencing data are available on the NCBI SRA under BioProject PRJNA1099630. Analyses are available at https://github.com/DianaBaetscher-NOAA/BFAL-GSI. Specific fisheries collection date and location data are confidential under the Magnuson Stevens Act.

References

Abbott, C.L., Double, M.C., Gales, R., Baker, G.B., Lashko, A., Robertson, C.J.R., Ryan, P. G., 2006. Molecular provenance analysis for shy and white-capped albatrosses killed by fisheries interactions in Australia, New Zealand, and South Africa. Conserv. Genet. 7, 531–542. https://doi.org/10.1007/s10592-005-9064-y.

Ando, H., Young, L., Naughton, M., Suzuki, H., Deguchi, T., Isagi, Y., 2014. Predominance of Unbalanced Gene Flow from Western to Central North Pacific Colonies of the Black-Footed Albatross (*Phoebastria nigripes*). Pacific Science 68 (3), 309–319. https://doi.org/10.2984/68.3.1.

Arata, J.A., Sievert, P.R., Naughton, M.B., 2009. Status Assessment of Laysan and Black-Footed Albatrosses, North Pacific Ocean, 1923–2005. US Geological Survey, Reston, Virginia, pp. 2009–5131.

Baetscher, D.S., Clemento, A.J., Ng, T.C., Anderson, E.C., Garza, J., 2018. Microhaplotypes provide increased power from short-read DNA sequences for relationship inference. Mol. Ecol. Resour. 18 (2), 296–305. https://doi.org/10.1111/1755-0998.12737.

Baetscher, D.S., Beck, J., Anderson, E.C., Ruegg, K., Ramey, A.M., Hatch, S., Nevins, H., Fitzgerald, S.M., Garza, J.C., 2022. Genetic assignment of fisheries bycatch reveals disproportionate mortality among Alaska northern fulmar breeding colonies. Evol. Appl. 15 (3), 447–458. https://doi.org/10.1111/eva.13357.

Bairlein, F., 2016. Migratory birds under threat. Science 354 (6312), 547–548.

Baker, J. D., Harting, A. L., Johanos, T. C., London, J. M., Barbieri, M. M., & Littnan, C. L. (2020). *Terrestrial habitat loss and the long-term viability of the French frigate shoals Hawaiian monk seal subpopulation*. NOAA technical memorandum NMFS-PIFSC-107. Doi:10.25923/76vx-ve75.

Bakker, V.J., Finkelstein, M.E., Doak, D.F., VanderWerf, E.A., Young, L.C., Arata, J.A., Vanderlip, C., 2018. The albatross of assessing and managing risk for long-lived pelagic seabirds. Biol. Conserv. 217, 83–95.

Calenge, C., 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Model. 197 (3–4), 516–519.

Campbell, N.R., Harmon, S.A., Narum, S.R., 2015. Genotyping-in-thousands by sequencing (GT-seq): a cost effective SNP genotyping method based on custom amplicon sequencing. Mol. Ecol. Resour. 15 (4), 855–867. https://doi.org/10.1111/1755-0998.12357.

Corbeau, A., Collet, J., Orgeret, F., Pistorius, P., Weimerskirch, H., 2021. Fine-scale interactions between boats and large albatrosses indicate variable susceptibility to bycatch risk according to species and populations. Anim. Conserv. 24 (4), 689–699.

DeSaix, M., Rodriguez, M., Ruegg, K., Anderson, E., 2023. Population Assignment from Genotype Likelihoods for Low-Coverage Whole-Genome Sequencing Data.

Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., Croxall, J.P., 2019. Threats to seabirds: a global assessment. Biol. Conserv. 237, 525–537.

Dierickx, E.G., Shultz, A.J., Sato, F., Hiraoka, T., Edwards, S.V., 2015. Morphological and genomic comparisons of Hawaiian and Japanese black-footed albatrosses (Phoebastria nigripes) using double digest RAD seq: implications for conservation. Evol. Appl. 8 (7), 662–678.

Eich, A. M., Mabry, K. R., Wright, S. K., & Fitzgerald, S. M. (2016). Seabird bycatch and mitigation efforts in Alaska fisheries summary report: 2007 through 2015. U.S. Dept. of Commerce, NOAA Tech. Memo. NMFS-F/AKR-12, 47p.

Fischer, K.N., Suryan, R.M., Roby, D.D., Balogh, G.R., 2009. Post-breeding season distribution of black-footed and Laysan albatrosses satellite-tagged in Alaska: inter-specific differences in spatial overlap with North Pacific fisheries. Biol. Conserv. 142 (4), 751–760.

Fitzgerald, S. M., & Dolliver, J. E. (2023). Alaska fisheries science center coordinated seabird studies strategic plan 2022-2026. U.S. Dept. of commerce, NOAA Tech. Memo. NMFSAFSC-460, 59p.

Fox, C.H., Robertson, C., Hara, P.O., Tadey, R., Morgan, K.H., 2021. Spatial assessment of albatrosses, commercial fisheries, and bycatch incidents on Canada's Pacific coast. Mar. Ecol. Prog. Ser. 672, 205–222.

Gilman, E., Kobayashi, D., Chaloupka, M., 2008. Reducing seabird bycatch in the Hawaii longline tuna fishery. Endanger. Species Res. 5 (2–3), 309–323.

Global Fishing Watch (GFW). (2023).www.globalfishingwatch.org. Accessed on 1/5/2024.

Gutowsky, S.E., Leonard, M.L., Conners, M.G., Shaffer, S.A., Jonsen, I.D., 2015. Individual-level variation and higher-level interpretations of space use in wide-ranging species: an albatross case study of sampling effects. Front. Mar. Sci. 2, 93.

Hasselman, D.J., Anderson, E.C., Argo, E.E., Bethoney, N.D., Gephard, S.R., Post, D.M., Palkovacs, E.P., 2016. Genetic stock composition of marine bycatch reveals disproportional impacts on depleted river herring genetic stocks. Can. J. Fish. Aquat. Sci. 73 (6), 951–963.

Huynh, S., Cloutier, A., Chen, G., Chan, D.T.C., Lam, D.K., Huyvaert, K.P., Sin, S.Y.W., 2023. Whole-genome analyses reveal past population fluctuations and low genetic diversities of the North Pacific albatrosses. Mol. Biol. Evol. https://doi.org/10.1093/molbev/msad155.

Hyrenbach, K. D., Ishizaki, A., Polovina, J., & Ellgen, S. (2021). The factors influencing albatross interactions in the Hawaii longline fishery: towards identifying drivers and quantifying impacts. U.S. Dept. of Commerce, NOAA Tech. Memo. NMFS-PIFSC-122. doi:10.25923/nb95-gs31.

Inter-American Tropical Tuna Commission (IATTC), 2023. Other Reports. https://www.iattc.org/en-US/Data/Other-reports. (Accessed 5 January 2024).

International Union for Conservation of Nature (IUCN). (2023). *The IUCN Red List of Threatened Species. Version 2023–1*. https://www.iucnredlist.org. Accessed on 1/10/2024.

Kersten, O., Star, B., Leigh, D.M., Anker-Nilssen, T., Strøm, H., Danielsen, J., Boessenkool, S., 2021. Complex population structure of the Atlantic puffin revealed by whole genome analyses. Commun. Biol. 4 (1), 922.

Lewison, R.L., Crowder, L.B., Read, A.J., Freeman, S.A., 2004. Understanding impacts of fisheries bycatch on marine megafauna. Trends Ecol. Evol. 19 (11), 598–604.

Mahon, C.L., Holloway, G.L., Bayne, E.M., Toms, J.D., 2019. Additive and interactive cumulative effects on boreal landbirds: winners and losers in a multi-stressor landscape. Ecol. Appl. 29 (5), e01895.

McKee, T., Pyle, P., 2002. Plumage variation and hybridization in black-footed and Laysan albatrosses. North American Birds 56, 131–138.

McKinney, G.J., Pascal, C.E., Templin, W.D., Gilk-Baumer, S.E., Dann, T.H., Seeb, L.W., Seeb, J.E., 2020. Dense SNP panels resolve closely related Chinook salmon populations. Can. J. Fish. Aquat. Sci. 77 (3), 451–461.

Moran, B.M., Anderson, E.C., 2019. Bayesian inference from the conditional genetic stock identification model. Can. J. Fish. Aquat. Sci. 76 (4), 551–560.

National Oceanic, Atmospheric Administration, NOAA, 2023. *Seabird Interactions and Mitigation Efforts in Hawaii Pelagic Longline Fisheries 2022 Annual Report*. National Marine Fisheries Service, Sustainable Fisheries Division, Honolulu, Hawai'i.

Nevins, H.M., Adams, J., Moller, H., Newman, J., Hester, M., Hyrenbach, K.D., 2009. International and cross-cultural management in conservation of migratory species. J. R. Soc. N. Z. 39 (4), 183–185. https://doi.org/10.1080/03014220909510576.

Ng, T.C., Anderson, E.C., 2019. Microhaplot: microhaplotype constructor and visualizer. R software package. https://CRAN.R-project.org/package=microhaplot.

Phillips, R.A., Gales, R., Baker, G.B., Double, M.C., Favero, M., Quintana, F., Wolfaardt, A., 2016. The conservation status and priorities for albatrosses and large petrels. Biol. Conserv. 201, 169–183.

Phillips, R.A., Fox, E., Crawford, R., Prince, S., Yates, O., 2024. Incidental mortality of seabirds in trawl fisheries: a global review. Biol. Conserv. 296, 110720.

Reynolds, M., Courtot, K., Krause, C., Seavy, N., Hartzell, P., Hatfield, J., 2016. Dynamics of Seabird Colonies Vulnerable to Sea-Level Rise at French Frigate Shoals, Hawai'i. Hawai'i Cooperative Studies Unit, Hilo, Hawai'i. Technical Report HCSU-037,.

Rice, D.W., Kenyon, K.W., 1962. Breeding distribution, history, and populations of North Pacific albatrosses. Auk 79 (3), 365–386.

Ruegg, K., Anderson, E.C., Somveille, M., Bay, R.A., Whitfield, M., Paxton, E.H., Smith, T.B., 2021. Linking climate niches across seasons to assess population vulnerability in a migratory bird. Glob. Chang. Biol. 27 (15), 3519–3531.

Rushing, C.S., Marra, P.P., Dudash, M.R., 2016. Winter habitat quality but not long-distance dispersal influences apparent reproductive success in a migratory bird. Ecology 97 (5), 1218–1227.

Schnell, J.K., Harris, G.M., Pimm, S.L., Russell, G.J., 2013. Estimating extinction risk with metapopulation models of large-scale fragmentation. Conserv. Biol. 27 (3), 520–530.

Spennemann, D.H., 1998. Excessive exploitation of Central Pacific seabird populations at the turn of the 20th century. Mar. Ornithol. 26, 49–57.

Thorne, L.H., Conners, M.G., Hazen, E.L., Bograd, S.J., Antolos, M., Costa, D.P., Shaffer, S.A., 2016. Effects of El Niño-driven changes in wind patterns on North Pacific albatrosses. J. R. Soc. Interface 13 (119), 20160196.

Tuck, G.N., Thomson, R.B., Barbraud, C., Delord, K., Louzao, M., Herrera, M., Weimerskirch, H., 2015. An integrated assessment model of seabird population dynamics: can individual heterogeneity in susceptibility to fishing explain abundance trends in Crozet wandering albatross? J. Appl. Ecol. 52 (4), 950–959. https://doi.org/10.1111/1365-2664.12462.

Walsh, H.E., Edwards, S.V., 2005. Conservation genetics and Pacific fisheries bycatch: mitochondrial differentiation and population assignment in black-footed albatrosses (*Phoebastria nigripes*). Conserv. Genet. 6, 289–295.

Western and Central Pacific Fisheries Commission (WCPFC). (2020). Bycatch data Excel file (BDEP). https://www.wcpfc.int/doc/bycatch-data-file-bdep. Accessed 1/5/24.

Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70 (1), 164–168.