DEMOGRAPHICS OF LAYSAN *PHOEBASTRIA IMMUTABILIS* AND BLACK-FOOTED *P. NIGRIPES* ALBTROSS CAUGHT AS BYCATCH IN ALASKAN GROUNDFISH AND HAWAIIAN LONGLINE FISHERIES

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ABSTRACT

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In fisheries, incidental bycatch of non-target species, including seabirds, is the result of complex interactions between species and fishing effort. While understanding the magnitude of bycatch is essential to understanding its impact on incidentally caught species, a full characterization requires describing the demographic composition of bycatch and formulating effective mitigation responses. We characterized the body condition, sex, and reproductive maturity of Laysan Albatross *Phoebastria immutabilis* and Black-footed Albatross *P. nigripes* collected by fishery observers in the US Alaskan groundfish and halibut fisheries (n = 129: 83 Laysan, 46 Black-footed; 2006–2014) and the US Hawaiian longline fisheries (n = 529: 206 Laysan, 323 Black-footed; 2010–2016). Across species and regions, there was a highly significant bias toward bycatch of sexually mature birds, and most birds were in good body condition. Whereas bycatch in the Alaska region was significantly male-biased for both species, bycatch in the Hawai'i region was slightly male-biased for Laysan Albatross and moderately female-biased for Black-footed Albatross. Overall, assessment of bycatch demographics across species, regions, and seasons provides valuable information for managers and modelers who assess the impacts of bycatch on wildlife populations.

En la pesca, la captura incidental (o bycatch) de especies no objetivo, incluidas aves marinas, es el resultado de interacciones complejas entre las especies y el esfuerzo pesquero. Si bien la comprensión de la magnitud de la captura incidental es esencial para comprender su impacto en las especies capturadas incidentalmente, una caracterización completa requiere describir la composición demográfica de la captura incidental y formular respuestas efectivas de mitigación. Caracterizamos la composición corporal, el sexo y la madurez reproductiva del Albatros de Laysan *Phoebastria immutabilis* y el Albatros de Patas negras *P. nigripes* recolectados por observadores científicos en dos pesquerías de EE.UU: las pesquerías de peces de fondo y Halibut de Alaska (n = 129: 83 Laysan, 46 Patas negras; 2006–2014) y las pesquerías de palangre en Hawái (n = 529: 206 Laysan, 323 Patas negras; 2010–2016). Para las dos especies y regiones estudiadas, se verifico un sesgo altamente significativo por la captura de aves sexualmente maduras, y en buenas condiciones corporales. A pesar que el bycatch en la región de Alaska evidenció un elevado sesgo hacia machos en ambas especies, las de Hawái fueron ligeramente sesgadas hacia hembras en los de Patas negras. En general, la evaluación de la demografía de la captura incidental a través de especies, regiones y estaciones proporciona información valiosa para los administradores de pesquerías y los modeladores que evalúan los impactos de la captura incidental en las poblaciones de vida silvestre.

Key words: albatross, bycatch, demographics, fisheries, North Pacific, Phoebastria

INTRODUCTION

Of the 22 albatross species worldwide, 15 are classified as Threatened and 13 have decreasing populations (IUCN 2017). Most species face many threats, including invasive species, disease, contaminants, ingestion of plastics, climate change, and fisheries bycatch (Phillips *et al.* 2016). Albatross life history traits include delayed maturity, long life-spans, and low fecundity, all of which make albatross populations especially vulnerable to threats that result in impacts such as the disproportionate removal of adults (Weimerskirch & Jouventin 1987, Tuck *et al.* 2001). Though incidental capture of protected species occurs in both Northern and Southern hemispheres, studies characterizing bycatch composition in Northern Hemisphere fisheries are comparatively rare (Gianuca *et al.* 2017).

Two species of albatross that commonly occur in the North Pacific are the Laysan *Phoebastria immutabilis* and the Black-footed *P. nigripes*; both are protected under various national and international laws, such as the Agreement on the Conservation of Albatross and Petrels. Both species are susceptible to multiple threats, and incidental bycatch during fishing activities is a notable source of mortality (Arata *et al.* 2009; Birdlife International 2017a, b). During the 1980s and 1990s, international high-seas driftnet and longline fleets on the high seas had substantial bycatch of both Laysan and Black-footed albatrosses (Johnson et al. 1993, Cousins et al. 2000). Addressing these threats through international actions, such as the 1992 ban on high-seas driftnets and coordinated observer monitoring programs, increased interest in seabird bycatch in the US, which in turn led to improved monitoring in US fisheries (e.g., Alaska and Hawai'i) and the implementation of first-generation seabird-bycatch mitigation measures. The adoption of bycatch mitigation measures in the Alaska and Hawai'i longline fisheries between 2001 and 2006 (Melvin et al. 2001, Eich et al. 2016, PIRO 2017) dramatically reduced bycatch in these areas. In turn, these results supported the creation of a National Seabird Program and the adoption of the US National Plan of Action for Reducing the Incidental Catch of Seabirds in Longline Fisheries (NMFS 2001). Since 2002, the cumulative bycatch of Laysan and Black-footed albatrosses is in the hundreds per year, down from thousands per year prior to the implementation of the driftnet ban and the bycatch mitigation measures (Eich et al. 2016, PIRO 2017).

While Laysan and Black-footed albatrosses overlap with many fisheries across the Pacific (Hyrenbach & Dotson 2003, Žyedlis et al. 2011), two US fisheries incurring bycatch of these species are the North Pacific groundfish fishery based in Alaska and the longline fisheries based in Hawai'i. For our purposes, "Alaska" refers to demersal longline and, to a much lesser degree, trawl groundfish fisheries in that region; "Hawai'i" refers to shallowand deep-set longline fisheries based in that state. Though there is inter-annual variability in bycatch numbers in both regions, the total estimated bycatch of Laysan versus Black-footed Albatross is comparable between regions (see values in Eich et al. 2016, PIRO 2017). Although the Alaska and Hawai'i fisheries differ in gear, target species, distribution, and fleet size, they interact with the birds during similar periods in their breeding cycles (Eich et al. 2016, PIRO 2017). Therefore bycatch in one region may compound population-level impacts of bycatch in another region.

In Alaska, the National Marine Fisheries Service (NMFS) North Pacific Observer Program provides observer coverage for both longline and trawl gear types in North Pacific groundfish fisheries. The longline Pacific halibut fleet was added to the program in 2013 (Eich et al. 2016). The same observer program also covers pot fisheries in the region, which have an albatross bycatch rate of zero (reported for 2007-2013; NMFS 2014) and thus are not included here. Groundfish longlines in Alaska are set in the demersal zone, and they include both the freezer (catcher-processor) fleet for Pacific cod Gadus macrocephalus and Greenland turbot Reinhardtius hippolglossoides and the catcher fleet for sablefish Anoplopoma fimbria and Pacific halibut Hippoglossus stenolepis. Alaska trawl fisheries include a broad suite of target species using both pelagic and non-pelagic gear (NMFS 2011). Of these fisheries, the sablefish longline fishery has the greatest total estimated albatross bycatch (Eich et al. 2016). Depending on the gear, target species, and vessel characteristics, seabird bycatch mitigation measures in the longline fisheries include single or paired streamers, strategic discard of offal, and optional deployment of hooks underwater (NOAA 1996, Eich et al. 2016). These Alaska fisheries occur in waters of the US Exclusive Economic Zone (EEZ) in the Gulf of Alaska (between 170°00'W and 132°40'W), and in the Aleutian Islands and Bering Sea (west of 170°W to the US-Russian Convention Line of 1867) (Eich et al. 2016).

The Hawai'i fisheries target bigeye tuna *Thunnus obesus* using deepset longlines; swordfish *Xiphias gladius* are targeted using shallowset longlines, which use fewer hooks and a smaller number of vessels (PIRO 2017). In Hawai'i, the NMFS Pacific Islands Regional Office (PIRO) runs the Fisheries Observer Program, which monitors both fisheries. The deep-set fishery sets lines during the day, and it tends to be clustered around the main Hawaiian Islands and to the north and east, generally spanning from 0°N to slightly above 30°N (PIRO 2017). The shallow-set fishery sets lines at night, is generally active between 20°N and 40°N, and extends farther west than the deep-set effort. Hawai'i longline fisheries adopted additional mitigation requirements in 2006, including a side-setting option in lieu of sternsetting, and require the use of strategic offal discards when setting lines from the stern in shallow-sets (anywhere) or deep-sets (north of 23°N) (NOAA 2005, PIRO 2017).

Understanding the demographic composition of seabird bycatch helps managers and researchers assess the impacts of fisheries-seabird interactions. Specifically, information on body condition, age, sex, and maturity of birds caught in these fisheries is crucial for informing population risk assessments and status models, because they provide observed demographic parameters in place of model assumptions. Significantly skewed ratios, or biases, in bycatch mortality that relate to sex or maturity could have population-level impacts (Bugoni et al. 2011, Lewison et al. 2012), as they directly affect survival and can indirectly affect fecundity (i.e., difficulty in finding a new mate, fewer birds of high reproductive value). Interestingly, research also indicates that juvenile survival can significantly affect population trajectories (Finkelstein et al. 2010). Sex-related differences in susceptibility to fisheries bycatch could differ by season, foraging conditions, reproductive status, behavior, or other factors. For example, female Laysan Albatross make trips of longer distance and duration than males during the chick-brooding season (Conners et al. 2015a). Sex-specific differences in the foraging range of Blackfooted Albatross in the eastern (male) and western (female) North Pacific could also result in differential overlap with fisheries, and thus differential susceptibility to bycatch (Hyrenbach et al. 2002). In addition to sex-related factors, age or maturity differences in bycatch can relate to a range of factors including experience and reproductive constraints, which can contribute to differential overlap with fishing effort (Gianuca et al. 2017).

Our objective was to determine demographic patterns in Laysan and Black-footed Albatross bycatch based on the examination of specimens collected by observers in the Alaska and Hawai'i fisheries described above. Specifically, we characterized the proportion of males versus females, and sexually mature versus immature individuals killed in each fishery region by reproductive season. We also evaluated the body condition of all specimens and the age distributions of banded birds. In Hawai'i, we investigated the bycatch composition of specimens caught in the shallow-set and deep-set longline fisheries separately.

METHODS

Albatross examined by fishery

Between 2008 and 2017, we examined Laysan and Black-footed Albatross specimens collected by the NMFS's North Pacific Observer Program in Alaska and by the PIRO Fisheries Observer Program in Hawai'i. Specimens were collected primarily by observers during specific fishing activities (e.g., monitoring of the haulback). Other seabird species caught in these fisheries are discussed in NMFS bycatch reports (e.g., NMFS 2011, NMFS 2016, PIRO 2017) and are not assessed here. In total, we assessed the sex, maturity, and body condition of 658 albatrosses for which collection month and year were known.

Source of samples: Alaska

Alaska albatross specimens were collected by observers deployed on commercial groundfish and halibut fisheries and by researchers in the field. Science charters included the International Pacific Halibut Commission longline survey, the Alaska Fishery Science Center (AFSC) demersal longline survey, and the AFSC pelagic and non-pelagic trawl survey.

On-board observers in the North Pacific Observer Program primarily collected dead albatross during sampling periods that occurred during gear retrieval operations. The number of these sampling periods varied depending on sampling protocol and observer capacity (see North Pacific Observer Program observer sampling manuals). Additional birds were collected during gear retrieval when the observer was not actively sampling or were provided to the observer by vessel crew. Except for a few specimens that observers were unable to collect (or unable to retain due to vessel restrictions), we received and necropsied a high proportion of the total observed albatross bycatch.

Observer coverage rates in the North Pacific Observer Program have changed over time and are documented through AFSC products (e.g., Faunce *et al.* 2017). The program is designed to meet the complex needs of fisheries management in Alaska, and



Fig. 1. The percentage of Laysan (LAAL, large grey circles) and Black-footed (BFAL, small black circles) albatross carcasses examined out of the total number of fishery interactions observed by the NMFS PIRO Fisheries Observer Program in Hawai'i (2010– 2015, shallow- and deep-set combined). Black-footed Albatross circles are shifted slightly to reduce overlap. Numbers above the plot indicate sample sizes by species (colors correspond to legend). Analysis included only carcasses that matched Observer Program interaction records (sample size slightly smaller than total necropsied).

it was restructured in 2013 to include the fixed-gear halibut and sablefish fleets (NOAA 2012). In the current deployment scheme, vessels are divided into two categories: (1) full observer coverage, including most catcher and catcher–processer vessels participating in certain limited-access privilege programs; and (2) partial observer coverage, which includes catcher vessels that are not in the full coverage category and small catcher–processors (Eich *et al.* 2016, AFSC 2017, Faunce *et al.* 2017). Information on observer deployment rates, sampling methods, and bycatch estimations can be found in North Pacific Observer Program annual reports.

It is difficult to quantify the degree to which the necropsied specimens are representative of the total bycatch estimates in the Alaska fisheries. The albatross specimens examined were predominantly caught by catcher-processer vessels and by smaller catcher vessels. Catcher-processers have 100%-200% observer coverage (by fishing day; AFSC 2017), meaning there is a higher likelihood of observing and collecting these specimens. That component of the fishery is well-represented with our sample. Complicating attempts of representation is the 2013 restructuring of observer coverage on catcher vessels. Before 2013, only vessels > 60 ft long (~20 m) and no halibut fishery vessels had observer coverage. Since then, most catcher vessels > 40 ft (\sim 12 m) have been included in a random selection scheme. Additionally, some birds were collected from third-wire strikes on trawl vessels, which are not included in observer sample data. Though methods to estimate the magnitude of third-wire mortality are under investigation (e.g., the US West Coast and Alaska Trawl Fisheries Seabird Cable Strike Mitigation Workshop 2017), this type of mortality is not included in historical albatross bycatch estimates for these fisheries.

Source of samples: Hawai'i

Specimens from the NMFS PIRO Fisheries Observer Program were collected in either the deep-set or the shallow-set longline fisheries. Observers in both fisheries collected all of the dead albatrosses in their observed sets. Specimens that could not be linked specifically to either fishery in observer databases were noted as coming from an "unknown" fishery. Some but not all of the specimens from 2017 were assessed at the time of analysis; thus, we conservatively describe the data as spanning 2010–2016. Shallow-set fisheries had observers present on 100% of trips, whereas the annual average observer coverage for the deep-set fisheries was 20% of trips (PIRO 2017).

Due to differences in total bycatch numbers (shallow-set) and total bycatch estimates (deep-set), we compared the bycatch sample examined in this study to the number of observed bycatch interactions by species and year (combined shallow-set and deep-set; PIRO 2017). We excluded samples categorized as "unknown" from analysis of how representative examined samples were of observed fishery interactions. Of birds with known fishery information, necropsy examinations represent 38.3% of all Laysan and 53.4% of all Black-footed albatross observed interactions in Hawai'i fisheries (deep-set and shallow-set combined) from 2010 to 2015, with notable inter-annual variation (Fig. 1). Fishery interaction information for 2016 was not available.

Regional differences in bycatch estimation

Calculated seabird bycatch estimates differ considerably between Alaska and Hawai'i in terms of observer coverage and catch per unit effort (i.e., total catch of target species in Alaska, total number of hooks by fishery in Hawai'i). Therefore, we did not attempt to directly compare estimates between Hawai'i and Alaska.

Seasonality of specimens

To understand the phenology of bycatch, we categorized our samples by breeding stage and compared the number of birds from Alaska to the number of birds from Hawai'i, both overall and by deep- and shallow-set fisheries. Stages for both species were defined as: incubation (November to January), chick-brood (February to April; when at least one parent continually attends the small chick at the nest), post chick-brood (May to July; when both parents are at sea foraging and attending the chick sporadically), and post-breeding (August to October) (Arata *et al.* 2009).

Geographic reference of regional bycatch

To provide a geographic reference for the relative distribution of bycatch events, we characterized the relative distribution of bycatch samples by region and species by creating a convex hull around all known bycatch locations (Fig. 2). Confidential fishing location data are obscured in these plots by adding a small random number (negative or positive) to longitude and latitude values for each bycatch event.



Fig. 2. Approximate areas encompassing the location of Laysan (grey) and Black-footed (black) albatross bycatch specimens obtained through the NMFS North Pacific Observer Program (2006–2014) and PIRO Fisheries Observer Program (2010–2016). Light-grey polygons represent Bering Sea and Aleutian Islands (BSAI) NMFS fishery management areas.

TABLE 1 Sample size, sex ratio, and maturity of Laysan Albatross and Black-footed Albatross incidentally killed in US Alaska and Hawai'i fisheries by breeding season

Fishery ^a Sample Years	Season ^b	n (birds)	% Male	1:1 Sex Ratio <i>P</i> -value ^c	% Mature ^d
LAYSAN ALBATROSS					
Alaska 2006–2014	Incubation	3	100%	-	100%
	Chick-brood	52	96%	< 0.001	98%
	Post chick-brood	24	96%	< 0.001	92%
	Post-breeding	4	75%	-	100%
Hawaiʻi 2010–2016	Incubation	24	58%	0.414	83%
	Chick-brood	123	59%	0.038	98%
	Post chick-brood	59	64%	0.027	100%
	Post-breeding	0	n/a	n/a	n/a
BLACK-FOOTED ALBATROS	8				
Alaska 2006–2014	Incubation	1	100%	-	100%
	Chick-brood	3	67%	-	100%
	Post chick-brood	30	70%	0.028	100%
	Post-breeding	12	75%	0.083	92%
Hawaiʻi 2010–2016	Incubation	65	31%	0.002	83%
	Chick-brood	121	36%	0.001	94%
	Post chick-brood	125	41%	0.040	81%
	Post-breeding	12	50%	1.000	92%

^a The Alaska fishery sample is composed of carcasses collected from commercial groundfish and halibut fleets. The Hawai'i fishery sample is composed of carcasses collected from deep- and shallow-set longline fleets.

^b Seasons are defined as: incubation (November to January), chick-brood (February to April), post chick-brood (May to July), and post-breeding (August to October).

^c Bold represents significance at P < 0.05; "-" indicates no P-value shown due to low sample size.

^d Mature is defined as "reproductive maturity" determined first by the presence of the bursa of Fabricius and secondarily by teste width or oviduct development.

Internal examinations of albatross

During necropsies, albatross specimens were identified by species, and data were collected on body condition, sex, and reproductive maturity according to van Franeker (2004).

Age and maturity of specimens

If a banded bird was recovered, banding data were provided by observer programs or submitted to the USGS Bird Banding Lab. Minimum ages (for birds banded as an adult) and known ages (for birds banded as a chick) are hereafter referred to as "known age."

We assessed the distribution of known-age birds by species. Additionally, we evaluated the distribution of body condition for each species and region for birds of known sex, maturity, collection year, and collection season. To assess the accuracy of anatomically based maturity categorizations of unbanded specimens, we pooled data for both species and calculated the percentage of known-age birds whose maturity was accurately categorized without prior knowledge of age (adult was defined as > 4 years; immature was defined as \leq 4 years).

Body condition characterization

Body condition was quantified by assessing muscle development and fat reserves. Using van Franeker's (2004) scoring system, the pectoralis–supracoracoideus muscle complex was scored from zero (severely emaciated, muscle significantly below keel-line) to three (excellent body condition, muscle at or above keel-line). Likewise, subcutaneous and adipose fat stores were each scored from zero (no fat) to three (very fat). Body condition was defined by summing these scores for each bird, with 0–3 indicating poor condition, 4–6 indicating moderate condition, and 7–9 indicating good condition.

Demographic biases of bycatch specimens

Sex was determined by internal observation of testes or ovaries. Reproductive maturity (hereafter "maturity") was assessed primarily by the presence of the bursa of Fabricius, which is assumed to atrophy with the onset of sexual maturity: present (immature, \leq 4 years old) or absent (adult, > 4 years old) (Broughton 1994). While the presence or absence of the bursa predicted reproductive maturity in the majority of banded, known-age birds, the maturity level of a small number of known-age birds did not correspond with their bursal status. To reduce the possibility of such outliers in birds without a known age, we assessed maturity secondarily by development of the brood patch and the gonads (i.e., teste width and oviduct development). Based on banded birds, maturity was best predicted by bursa presence, with gonads secondarily considered. Brood patch development was a poor predictor of maturity, and thus was removed from our categorization methods.

Hawai'i Fishery	Season ^a	n (birds)	% Male	1:1 sex ratio <i>P</i> -value ^b	% Mature ^c
LAYSAN ALBATROSS					
Shallow-set	Incubation	0	n/a	n/a	n/a
	Chick-brood	19	68%	0.108	100%
	Post chick-brood	16	69%	0.134	100%
	Post-breeding	0	n/a	n/a	n/a
Deep-set	Incubation	22	59%	0.394	86%
	Chick-brood	101	57%	0.136	98%
	Post chick-brood	42	64%	0.064	100%
	Post-breeding	0	n/a	n/a	n/a
BLACK-FOOTED ALBATRO	SS				
Shallow-set	Incubation	1	100%	-	100%
	Chick-brood	37	51%	0.869	97%
	Post chick-brood	15	40%	0.439	100%
	Post-breeding	0	n/a	n/a	n/a
Deep-set	Incubation	58	31%	0.004	81%
	Chick-brood	78	29%	< 0.001	94%
	Post chick-brood	109	40%	0.044	79%
	Post-breeding	11	45%	0.763	91%

 TABLE 2

 Sample size, sex ratios, and maturity of Laysan Albatross and Black-footed Albatross caught in deep and shallow-set Hawai'i longline fisheries by breeding season

^a Seasons are defined as: incubation (November to January), chick-brood (February to April), post chick-brood (May to July), and post-breeding (August to October).

^b Bolded represents significance at P < 0.05; "-" indicates no *P*-value shown due to low sample size.

^c Mature is defined as "reproductive maturity," as determined first by the presence of the bursa of Fabricius and second by teste width and oviduct development.

We tested the significance of potential sex-biases by testing the observed ratios by species, region, and season of males to females by an expected ratio of 1:1 using a chi-squared test with a Yates' continuity correction (Zar 1999). We also compared proportions of mature to immature individuals by species, region, and season (Table 1 and 2). We did not test these statistically, as the expected proportion of mature to immature birds within the populations of these species is uncertain. *P*-values < 0.05 were considered significant.

RESULTS

Albatross examined by fishery

We examined 129 Laysan (n = 83) and Black-footed (n = 46) Albatross specimens from Alaska. From Hawai'i, we examined 529 albatross (n = 206 Laysan, n = 323 Black-footed). Most specimens were from Hawai'i fisheries: 71% (206/289) of all Laysan specimens and 88% (323/369) of all Black-footed specimens (Table 1a, b). We examined 421 individuals from the deep-set fishery (n = 165Laysan, n = 256 Black-footed) and 88 from the shallow-set fishery (n = 35 Laysan, n = 53 Black-footed; Table 2a, b). We examined 20 specimens from "unknown" fisheries (n = 6 Laysan, n = 14 Blackfooted).

Seasonality of specimens

The number of specimens collected for both regions and both species tended to peak around chick-brood and post chick-brood. While fishing effort in both regions changes through the seasons and affects the number of birds collected, this peak in number of specimens collected by observers corresponded to an associated peak in bycatch rates in Hawai'i and Alaska during chick-provisioning periods (Melvin *et al.* 2015, Gilman *et al.* 2016, PIRO 2017). An exception to this pattern was Black-footed Albatross from Alaska, where the number of specimens was lower during chick-brood and greater during post chick-brood and post-breeding (Table 1b).

Geographic reference of regional bycatch

In Alaska, bycatch of both species overlapped in the Bering Sea and Aleutian Islands west of Samalga Pass, but only Black-footed Albatross were caught east of the Pass and in the Gulf of Alaska



Fig. 3. Distribution of (minimum) known age for (A) Laysan (n = 46) and (B) Black-footed (n = 63) albatross bycatch in Alaska groundfish 2006–2014 (n = 12) and Hawai'i longline 2010–2016 (n = 97) fisheries with anatomical maturity categorizations.



Fig. 4. Body condition of Laysan (n = 285) and Black-footed (n = 368) albatross bycatch in Alaska groundfish 2006–2014 (n = 126) and Hawai'i longline 2010–2016 (n = 527) fisheries.

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(Fig. 2). The segregation in the spatial distribution of bycatch in Alaska is likely a result of species-specific habitat use, as opposed to an artifact of bycatch. Samalga Pass is a described transition zone in many seabird distributions and assemblages (Hunt & Stabeno 2005, Jahncke *et al.* 2005), including albatross (Fischer *et al.* 2009, Conners *et al.* 2015b). In Hawai'i, there were no distinct differences in the extent of bycatch locations among albatross species (Fig. 2). Tracking studies have found distributional differences between species, seasons, and colonies (e.g., Hyrenbach *et al.* 2002, Fischer *et al.* 2009, Kappes *et al.* 2010). However, these patterns did not create a discrepancy in occurrence in the fishery sampling area when seasons and years were combined.

Internal Examinations

Age and maturity of specimens

Of 109 banded birds from both regions, representing 17% of the 658 birds assessed, 46 were Laysan and 63 were Black-footed Albatross (Fig. 3). Banded birds were more often encountered in Hawai'i (n = 97 over seven years) versus Alaska (n = 12 over nine years). All the banded birds except three had confirmed minimum known ages. The sample of known-age birds banded as chicks ranged from 2 to 29 years of age for Laysan and from 1 to 23 years for Black-footed Albatross. Birds of 5–14 years were more common than younger or older birds in both species, composing 70% of Laysan and 71% of Black-footed known-age specimens.

Proportions of mature birds were similar for both species, with 97% of Laysan (280/289) and 88% of Black-footed (325/369) albatross being mature. Of the banded specimens (n = 109), female maturity was correctly predicted from bursa and gonadal information in 97% (n = 63) of cases. Male maturity was correctly predicted in 86% (n = 44) of cases. Within males, maturity assessment was incorrectly categorized in 80% (n = 5) of the small sample of immature specimens, thus reducing our overall accuracy for this sex and this age class.

Body condition characterization

Most specimens with sufficient information of both species had body condition scores of either moderate or good (Fig. 4). Specifically, 49% and 46% of Laysan and 44% and 47% of Black-footed specimens were in moderate and good condition, respectively; 5% of Laysan and 9% of Black-footed specimens were in poor condition. Although there were differences in sample sizes, the proportion of birds in good body condition was similar across species and maturity status: 50% (4/8, immature) and 45% (126/277, mature) for Laysan specimens, and 50% (22/44, immature) and 47% (152/324, mature) for Black-footed specimens.

Demographic biases of bycatch specimens

For biases in sex distribution, although 54% (357/658) of all specimens were male, the bias in the sex of individuals caught as bycatch varied by species and region. Laysan bycatch was 95% (79/83) male in Alaska and 61% (125/206) male in Hawai'i. Seasonally, Laysan Albatross bycatch was strongly male-biased in Alaska across all breeding seasons, with a highly significant male bias during chick-brood and post chick-brood (Table 1a, Fig. S1a). Incubation and post-breeding samples were rare in Alaska but were similarly male-biased (Table 1a, Fig. S1a). In Hawai'i, the

bias towards males was weaker than in Alaska, yet still significant during the chick rearing (chick-brood and post chick-brood) season (Table 1a, Fig. S1a). There were no post-breeding Laysan Albatross represented in this Hawai'i sample.

Overall Black-footed Albatross bycatch was 72% (33/46) male in Alaska but female-biased in Hawai'i fisheries, with only 37% (120/323) of samples male. The bias towards male bycatch in our samples of Black-footed Albatross in Alaska was significant in the post chick-brood and post-breeding season, but generally weaker than that of Laysan in the same region (Table 1b, Fig. S1b). In Hawai'i, a significant female bias occurred during incubation, chick-brood, and post chick-brood. No sex bias was observed in post-breeding Black-footed Albatross in Hawai'i.

There was a strong bias towards the bycatch of mature individuals: 92% (605/658) of all albatross specimens, 97% (125/129) of Alaska samples, and 91% (480/529) of Hawai'i samples. Laysan Albatross bycatch was 96% (80/83) mature in Alaska and 97% (200/206) mature in Hawai'i. The percent of mature birds was consistently > 90% in Alaska during chick-brooding and post chick-brooding (Table 1a, Fig. S1c, d). In the Hawai'i fisheries, the bias towards mature birds was strong during incubation, chick-brood, and postbrood seasons. Black-footed Albatross bycatch was 98% (45/46) mature in Alaska and 87% (280/323) mature in Hawai'i. The bias towards sexually mature birds persisted across seasons for both species and regions, with a slightly weaker bias in Hawai'i (Table 1a, b, Fig. S1c, d).

In Hawai'i longline fisheries, the majority (80%: 421/529) of specimens came from the deep-set as opposed to the shallow-set (17%: 88/529) fishery. This is not surprising, as the deep-set fleet is larger than the shallow-set fleet (47.4 million hooks set versus 1.3 million, respectively) (see PIRO 2017 for further details). Additionally, most albatrosses caught in the deep-set fishery are found dead, while the majority of albatrosses caught in the shallow-set fishery are not and are thus not sampled. Most of the shallow-set vessels are also active in the deep-set fishery (PIRO 2017). Approximately 4% (20/529) of samples were from an unspecified fishery and were not assessed in a gear-specific context.

For both species, shallow-set fishery samples were 57% (50/88) male while deep-set samples were slightly female-biased (45% male: 188/421) (Table 2). For Laysan Albatross, samples were 69% (24/35) and 59% (98/165) male for shallow-set and deep-set fisheries, respectively (Table 2). Black-footed specimens indicated a weaker male-bias than Laysan in the shallow-set fishery: 49% (26/53) of specimens were male, whereas only 35% (90/256) of specimens were male in the deep-set fishery (Table 2).

Regarding seasonal patterns, there was a strong bias towards males across seasons for Laysan Albatross in both fisheries, with a stronger bias in the shallow-set fisheries (Table 2a). However, these biases were not significant in either fishery for this species. The sex-bias in the deep-set fishery (57%–64% male) was similar to the combined Hawai'i fisheries (58%–64% male) (Table 1a, 2a). Black-footed Albatross specimens were slightly female-biased in the shallow-set fishery during the post chick-brooding stage (40% male, 6/15) but had a significant female bias in the deep-set fishery across the three breeding seasons (31%–40% male; Table 2b).

Similar to region-wide patterns, the majority of specimens (99%: 87/88 and 89%: 376/421) were mature for shallow-set and deep-set

fisheries. Laysan Albatross were 100% (35/35) and 97% (160/165) mature for the shallow-set and deep-set fisheries, respectively. Black-footed Albatross were 98% (52/53) mature in the shallow-set fishery and 84% (216/256) mature in the deep-set fishery. In both species and in each gear setting, there was a strong bias towards mature specimens across seasons in Hawai'i (Table 2a, b).

DISCUSSION

When examining the composition of albatross bycatch, the consistency of the bias towards mature birds in our study contrasts with the variation in sex-bias across regions and species. Our results are in general agreement with other studies investigating bycatch biases both globally and within these fishery regions, with a tendency towards adult male bycatch in subpolar Alaska and a female bias in the subtropical Hawai'i region for Black-footed Albatross (Phillips et al. 2010, Gianuca et al. 2017). However, differences in the magnitude of sex biases in Hawai'i shallow-set and deep-set fisheries demonstrate important deviations from these general trends. Furthermore, the moderate to good body condition of mature and immature individuals of both species indicates that birds in poor body condition are not more susceptible to bycatch, and could reflect the positive impact on body condition of repeated foraging on fisheries offal (e.g., Hüppop & Wurm 2000). Potential drivers of the observed trends are non-exclusive and are discussed below. The population-level impacts of these biases on each species may be compounded or reduced, depending on the magnitude of bycatch, as well as by season, if individuals caught as bycatch are actively breeding. Studies characterizing the demographic composition of bycatch across species, regions, and time provide unique and valuable information for managers and modelers assessing the impacts of bycatch on wildlife populations.

Observed biases

While the age distributions of these species are unknown, it is estimated that 70% of a healthy albatross population is likely to be mature (Bakker et al. 2018). As a result, the extreme bias towards bycatch of mature birds observed in this study indicates differential exposure or susceptibility to bycatch. Jiménez et al. (2017) suggest that segregation among sexes at sea may lead to unequal overlap with fisheries, resulting in sex-biased bycatch. Differential exposure to bycatch could relate to differences in morphology or behavior resulting in differential exposure to fishing gear, different foraging preferences, or differential habitat use, with none of these factors being mutually exclusive (Gianuca et al. 2017). Although a small portion of the total birds assessed in this study were banded, the age distribution of known-age birds examined in this study indicates that birds near the age of first breeding (8 years for Laysan Albatross [VanderWerf & Young 2016] and 7 years for Black-footed [Viggiano 2001]) were frequently caught (Fig. 3). Behavior and habitat-use patterns of young age-classes are an emerging research topic, with differences between immature and mature individuals observed in several procellariid species (de Grissac et al. 2016). This is true of Black-footed Albatross, where newly fledged birds tended to remain in the central North Pacific, overlapping less with fisheries in the Alaska region than adults (Gutowsky et al. 2014). No such description for immature Laysan Albatross is currently available. As more information on the behavior of different age-classes emerges, a better understanding of the mechanisms underlying the observed bias towards mature birds can be assessed at regional and sub-regional levels.

The bias towards mature Black-footed Albatross in the deep-set longline fishery was weakest during the post chick-brood period, a pattern supported by high sample size in 2015 and to a lesser extent in 2013 (Table S1b). Newly fledged Black-footed Albatross have been observed to spend more time in the North Pacific Transition Zone (NPTZ) and in the subtropical gyre, whereas post-breeding adults spend more time along productive continental shelf regions (Gutowsky *et al.* 2014). Therefore, any increase in or shift of deepset longline effort to the NPTZ and the subtropical gyre could increase proportional bycatch of immature versus adult birds. A better understanding of age-class-specific temporal variation in albatross habitat use, paired with increased knowledge of fishing effort distribution relative to oceanographic conditions, could help identify the factors driving variation in bycatch demographics in both time and space.

The variability in bycatch sex bias is noteworthy when considered in the context of the broad habitat use of both species. Both species use subtropical, temperate, and subpolar habitats. The strong male bias in both species in Alaska supports global sex-bias patterns regarding subpolar regions, but a bias towards females is more common in the subtropics (Gianuca et al. 2017). The female bias in Black-footed Albatross bycatch in the Hawai'i region may relate to the greater use of warmer waters by both sexes during the breeding season than by Laysan Albatross (Hyrenbach et al. 2002, Kappes et al. 2010) and to possible differential distribution by sex within the species (Conners et al. 2015b). As indicated by the different sexbiases observed in the shallow-set and deep-set longline fisheries in Hawai'i, subregional variation in bycatch composition cautions against over-generalization and demonstrates the need for a better understanding of bycatch composition drivers, including the range and intensity of fishery effort over time. As with maturity, a better understanding of sex-specific albatross behavior and habitat use, along with the distribution and intensity of fishing effort over time, could help researchers to interpret these patterns in a more complete context. In addition, further investigation is needed to enhance the accuracy of anatomical ageing of immature males in these species, in order to improve the confidence of analyses that include distributions of different maturity groups.

CONCLUSION

For bycatch of Laysan and Black-footed Albatross, our results highlight biases towards adults in good body condition in Hawai'i and Alaska fisheries, and regional differences in male and female composition. Knowledge of these biases could help inform population models, facilitate targeted actions to minimize bycatch impacts on albatrosses, and help elucidate at-sea patterns in body condition and distribution of demographic groups. Patterns in the demographic composition of bycatch can emerge through sampling methods, the interactions of species-specific behavior, interspecific competition (not discussed here), environmental variation (not discussed here), sex and age- or maturity-related variation, and seasonal demands. Expanding our knowledge of inter- and intraspecific variations in behavior, as well as habitat use among age groups and sexes, is needed to thoroughly understand bycatch patterns. Another critical component of understanding bycatch patterns is the composition, distribution, and behavior of fisheries. Communication and collaboration with fisheries has helped in efforts to reduce bycatch (NMFS 2011). Continued collaborative work with fisheries, observer programs, and necropsy programs can create more opportunities to better understand fisheries interactions.

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