ORIGINAL ARTICLE

# Seasonal variation of Pacific Northern Fulmar bycatch: Implications for age and sex-specific mortality

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## Abstract

Characterizing demography of fisheries bycatch is essential to understanding impacts on populations of long-lived, low-fecundity species. Northern Fulmars (*Fulmarus glacialis rogersii*) represent >50% of seabird bycatch in U.S. groundfish and halibut fisheries in the North Pacific. Using specimens collected by federal observer programs, we document the sex, age class, and body condition of 1,089 fulmars collected between 2004 and 2014. Using regional fulmar breeding phenology, we assess seasonal variation in the relative composition of a given sex or age class. Strong biases in bycatch toward adults and males were documented, with a slight increase in the proportion of males to females during the non-breeding period. High proportions of adults were observed year-round. Sex and age biases could be related to behavioral differences, including potential segregation at sea, and reflect similar biases seen in seabird bycatch in other subpolar fisheries. Overall body condition increased as the year progressed from breeding to non-breeding seasons, possibly revealing the costs of reproduction on adults and recovery through the availability of fisheries offal and bait. Year-round, only 3% of examined fulmars were emaciated. Together, these results indicate a persistent removal of adult male fulmars in good body condition across a decade, and highlight the contrast of fisheries-caused mortality and potential assistance of fishery discards to post-breeding recovery.

**KEYWORDS**

Alaska, bycatch, demography, longline, mortality, Northern Fulmar, Seabird

## 1 | INTRODUCTION

Bycatch during fishing activities is one of the greatest threats to many seabird species across the global ocean (Anderson et al., 2011; Croxall et al., 2012; Lewison et al., 2014). While gear- and region-specific techniques can be used to reduce or mitigate seabird bycatch (e.g., Gilman, 2011; Løkkeborg, 2011; Melvin et al., 2014), it remains a significant issue for many seabird populations, especially due to their life history characteristics: long-lived, delayed maturity, and low fecundity. Beyond the impact of removing an individual from the population, disproportionate mortality of individuals of a particular age or sex can have complex and significant demographic impacts (Gianuca et al., 2017; Tuck et al., 2015). Therefore, characterizing the demographic composition of bycatch is essential to understanding its impacts.

Demographic biases in seabird bycatch have been observed globally, with regional patterns of sex and age class biases indicating frequent male adult bias in subpolar and temperate habitats, and female

immature biases in sub-tropical areas (Gianuca et al., 2017). The demographic impacts of age and sex biases in bycatch can involve multiple levels. In colonies with a female bias in bycatch, increased extra-pair copulations, instances of aggressive behavior resulting in egg loss, or the death of a chick have been observed (Anderson et al., 2007; Huyvaert et al., 2000; Taylor et al., 2001). Furthermore, an individual's breeding success can be reduced for multiple years after widowing (the loss of a partner), due to the time involved in finding and successfully breeding with a new mate (Hatch, 1987).

Of all U.S. fisheries managed by federal agencies, the North Pacific groundfish fisheries have the highest estimated total seabird bycatch (Benaka et al., 2019). North Pacific groundfish fisheries include demersal longline, pelagic and non-pelagic trawl, jig, and pot fisheries targeting a broad suite of fish species or species groups (https://www.npfmc.org/). North Pacific groundfish fisheries do not include state-managed fisheries for salmon, crab, and other species using various gear types such as gillnet, purse seine, crab pot, troll, and others. Seabird bycatch in the North Pacific groundfish fisheries is composed primarily of demersal longline bycatch and occurs despite early adoption of the use of streamers (aka tori lines) on many longline vessels in 2002 (prior to regulatory requirements in 2004), which dramatically reduced bycatch rates (Eich et al., 2016; Melvin et al., 2001). For the Pacific Northern Fulmar (*Fulmarus glacialis rogersii*, hereafter "fulmar"), average annual bycatch fell by 64% when comparing pre-streamer years (1993–2001; Fitzgerald et al., 2008) to recent years when streamers were required and new methods of bycatch estimation were implemented (2007–2014; Eich et al., 2016). Annual patterns of fulmar bycatch can be seen in Table S1 and Figure S1. The majority of fulmar bycatch (and subsequently of overall seabird bycatch) in the North Pacific groundfish fisheries occurs in the Pacific cod hook-and-line fishery (83% from 2007 to 2014; Table S1; Eich et al., 2016).

Fulmars are the most common seabirds observed around groundfish vessels in Alaska waters (AFSC, unpublished data; Melvin et al., 2006) and regularly take advantage of fishery-related food opportunities such as bait or offal (Zador & Fitzgerald, 2008). Birds generally aggregate around trawl vessels during hauling, versus constant attendance around longline catcher–processors that produce a stream of offal (McElderry et al., 2004). While seabird bycatch proportions vary across Alaska regions and seasons, the fulmar is consistently the most caught seabird species, making up approximately half of the annual estimated seabird bycatch in the North Pacific groundfish fisheries (Benaka et al., 2019; Eich et al., 2016).

Bycatch estimates averaged 3,920 (range = 811–7,758) fulmars killed annually between 2007 and 2014 in North Pacific groundfish fisheries, including the Pacific cod hook-and-line fishery, and 2013–2014 halibut fisheries (Eich et al., 2016). Previous work characterizing bycatch composition in longline fisheries in Alaska indicated seasonal variation in the incidental mortality of fulmars, with bycatch during the breeding season near the colonies, and the majority of annual mortalities occurring in October and November (during the non-breeding season), farther from the colonies (Dietrich et al., 2009). Due to their broad distribution and large global

population, fulmars have the status of Least Concern according to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species criteria (BirdLife International, 2018). However, as a long-lived late-maturing species, an increase in adult mortality, including through fisheries bycatch, could cause a population to decline (Croxall et al., 1990; Tuck et al., 2001; Weimerskirch & Jouventin, 1987). Moreover, given demographic implications of disproportionate bycatch across sex and age, a full characterization of the demographic biases in fulmar bycatch is warranted. Analyzing the seasonal patterns in bycatch composition could provide additional insights into fulmar interactions with fisheries and their potential population or colony-level impacts. This work may also inform mitigation practices to reduce impacts.

This study addresses two key aims. First, we give an up-to-date characterization of the demographics of fulmar bycatch using specimens retained in federal North Pacific groundfish fisheries managed by National Oceanic and Atmospheric Administration (NOAA) Fisheries between 2004 and 2014, and halibut fisheries during 2013 and 2014. Second, we provide an ecological context for seasonal variation in bycatch based on regional fulmar phenology. These insights into the composition of fulmar bycatch contribute an improved understanding of seasonal interactions with these fisheries.

## 2 | METHODS

### 2.1 | Ethics statement

Fulmars examined in this study were collected under U.S. Fish and Wildlife Service Federal Fish and Wildlife Salvage Permit MB035470-0 to the NOAA Alaska Fisheries Science Center. All examined fulmars were killed incidental to normal fishing operations and were collected by NOAA Fisheries North Pacific Observer Program (Observer Program). The permittee had no part in the killing of the seabirds, and no live animals were used in this study. Necropsy protocols were adapted from protocols recommended by the European OSPAR Commission and jointly approved by NOAA Fisheries Alaska Fisheries Science Center and Oikonos Ecosystem Knowledge.

### 2.2 | Fishery management and observer coverage

The focal region is defined by the NOAA Fisheries North Pacific groundfish fisheries reporting areas associated with the Bering Sea, Aleutian Islands, and the Gulf of Alaska (Figure 1), and International Pacific Halibut Commission regulation areas. These fishing regions are jointly managed by the NOAA Fisheries Alaska Region and the North Pacific Fishery Management Council (NPFMC). Important targeted groundfish for longline gear include Pacific cod (*Gadus macrocephalus*), sablefish (*Anoplopoma fimbria*), and Greenland turbot (*Reinhardtius hippoglossoides*), while trawl fisheries target Pacific cod, walleye Pollock (*Gadus chalcogrammus*), Atka mackeral

**FIGURE 1** Location and relative size of major fulmar colonies within NOAA fisheries reporting areas associated with the Bering Sea/Aleutian Islands and Gulf of Alaska. Light-gray polygons indicate reporting areas within NOAA Fisheries North Pacific groundfish and halibut fisheries (NOAA, 2017). The relative size of each colony by the number of individuals is indicated by the radius of the circle (Mallory et al., 2020)
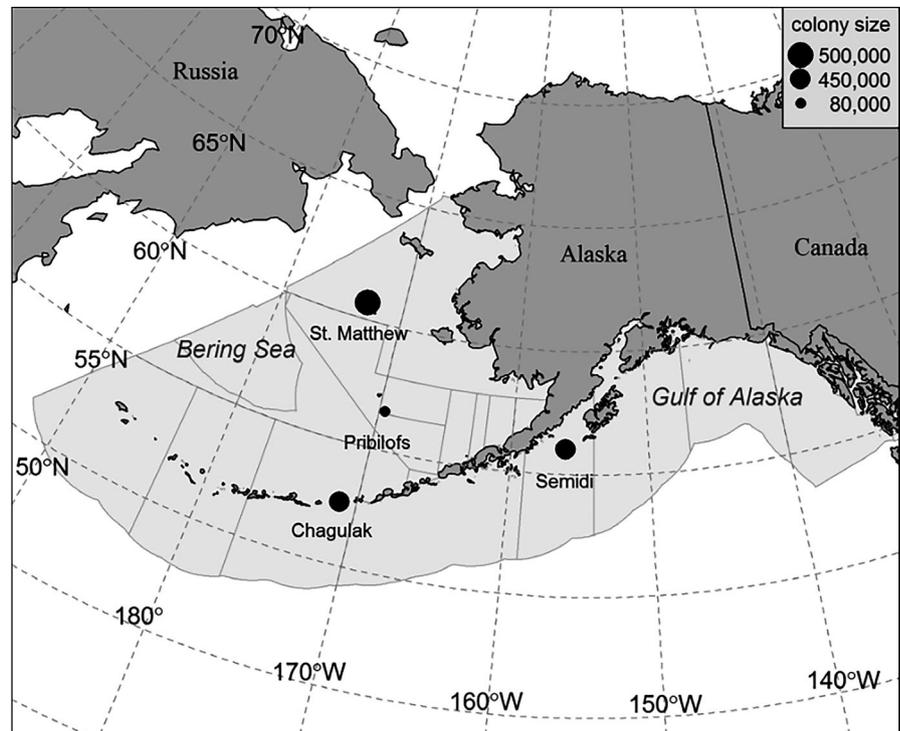


(*Pleurogrammus monopterygius*), and a broad suite of other species including many flatfish (Eich et al., 2016). Little seabird bycatch is documented in Pacific cod and sablefish fisheries using pot gear. In addition to groundfish, a demersal longline Pacific halibut (*Hippoglossus stenolepis*) fishery is co-managed by the International Pacific Halibut Commission and the NPFMC.

Initially, collection of fulmars through the Observer Program was opportunistic as observers were encouraged to focus on collecting species listed under the U.S. Endangered Species Act (AFSC, 2007). During the primary years of this study (2007–2014), observers were asked to collect as many fulmars as they could, within reason and within the confines of other duties. Observers were verbally notified that the target collection of fulmars was about 3–5 per cruise. With cruises being initiated throughout the year, and many cruises not having any seabird bycatch, this sampling approach would provide a representative sample of the temporal and spatial extent of the fishery.

Observer coverage requirements for the fleet changed throughout the study period and are thoroughly described in products from the NOAA Fisheries Alaska Fisheries Science Center (e.g., Faunce et al., 2017). In 2013, the Observer Program was restructured to include vessels ≤60 feet and halibut fixed gear fisheries, which were previously not covered (NOAA, 2018). In the restructured program, observer coverage (full or partial monitoring of fishing trips) is determined by operation type (catcher vessel, catcher/processor, or processor), fishery participation, and participation in limited access privilege program. Full coverage is required for most catcher–processor vessels, inshore processors when receiving or processing pollock, and some catcher vessels in certain limited access privilege programs (NOAA, 2018). Vessels in partial observer coverage categories included vessels exempted from the full coverage category,

catcher vessels with sablefish and halibut individual fishing quotas, and small catcher–processors (NOAA, 2018). In addition, some fulmars were collected from third wire strikes on trawl vessels, which were not included in observer sample data. While methods to estimate the magnitude of third wire mortality are under investigation, third wire mortality is not included in current and historical seabird bycatch estimates in these fisheries. Extrapolated estimates of the total seabird bycatch within North Pacific groundfish and halibut fisheries are published elsewhere (Eich *et al.*, 2016). To characterize the relative composition of the bycatch, we focus on the proportion as opposed to the number of individual fulmars examined in our sample.

## 2.3 | Fulmar ecology

Fulmars are generalist surface foragers that breed in large colonies on steep rocky cliffs in the subpolar regions of the Northern Hemisphere. Approximately 99% of the fulmar breeding in Alaska occurs at four colonies (Mallory et al., 2020). Chagulak Island is the largest and has an estimated 500,000 individuals. St. Matthew and Hall Islands have approximately 450,000 individuals, Semidi Islands have 440,000 individuals, and Pribilof Islands have approximately 80,000 individuals (Figure 1). While the Alaska-wide fulmar population is considered relatively stable, population trends for all breeding sites are not available year-to-year and often have wide margins of error (Dragoo et al., 2017). Fulmars initiate breeding activity in May, and the majority of chicks are fledged by the end of September. The age at first breeding is between 8 and 10 years (Mallory et al., 2020), and individuals can live to > 43 years (European longevity record; Fransson et al., 2017).

## 2.4 | Specimen processing

During 2004–2014, fulmar specimens collected by the Observer Program were sent to Oikonos Ecosystem Knowledge for examination. Specimens were necropsied to obtain morphometric, injury, molt, and demographic data, including sex, age class, and body condition following protocols in van Franeker (2004). We determined sexual maturity, inferred as an indicator of "adulthood" by assessing the presence of the Bursa of Fabricius, which is thought to atrophy with age and sexual development, being present in immature or visually absent in mature birds (Broughton, 1994). While we quantified gonad metrics, they did not improve age classification primarily due to little distinction between testes size and color in immatures and adults during non-breeding months. We used muscle and fat condition as metrics of body condition following van Franeker (2004). The *pectoralis-supracoracoideus* muscle complex was scored from 0—severely emaciated (muscle significantly below keel-line) to 3—excellent body condition (muscle at or above keel-line). We scored subcutaneous fat and internal fat from 0—no fat to 3—obese. To describe the overall condition of specimens, we calculated body condition by summing the scores from the *pectoralis-supracoracoideus* muscle complex and subcutaneous fat with a maximum score of 6. While internal fat surrounding the intestines can also be used to define the condition index (Donnelly-Greenan et al., 2014; van Franeker, 2004; Nevins et al., 2018), this would require omitting a large number of samples from the early portion of our study, notably 2006, which we sought to retain.

## 2.5 | Seasonal variation in bycatch

To assess the potential for a bycatch bias by sex (male or female) or age class (adult or immature), we compared the observed bycatch proportions to the expected proportion in the population: 1:2 (male) for sex and 7:10 (adult) for age class (Hatch, 1987) using a chi-square test (Zar, 1999). While the expected proportion of adult versus immature birds susceptible to fisheries bycatch (i.e., at sea) could differ from the observed proportion at a given colony, we proceeded with this assumption as we currently lack additional demographic information.

To provide an ecological context for patterns in bycatch, we categorized month of collection into three seasons based on fulmar breeding phenology, breeding (May through August), fledging (September), and non-breeding (October through April; Mallory et al., 2020). Although phenology can differ slightly by colony location, these periods capture the core phenological trends across the Alaska breeding region. To investigate the variation in bycatch between seasons, we calculated the proportion of males to females and adults to the sample population for each year. These relationships were assessed with a Kruskal–Wallis test.

When assessing sex and age class bias, all specimens with the relevant information were assessed. Data retained to investigate seasonal variation were further reduced from those above by excluding specimens without collection month information.

## 2.6 | Sex, age, and season relate to body condition

We used an ordered logistic regression to characterize how sex, age, and season relate to body condition. This approach uses odds ratios, as opposed to probabilities, to describe the potential for a given outcome and is suited for categorical response and predictor variables (Zurr et al., 2009). The odds ratios in logistic regressions are assumed to be proportional, meaning that the slope of a given predictor is constant across all categories.

We implemented the following model:

*Condition index = sex + age + season*

using the logistic method. Explanatory variables with 2 categories are modeled linearly: sex, age, and season with three categories. Since season has 3 categories, it is modeled with a linear and with a quadratic functional form. The quadratic equation indicates if the difference between consecutive categories is greater (or lesser) with increasing rank. Condition index is ordered from 0 to 6, with 0 and 6 being the lowest and highest categories, respectively. Sex is ordered from female (0) to male (1), age is ordered from immature (0) to adult (1), and season is ordered from breeding (1) to fledging (2) and non-breeding (3). Interactions between variables and categories were not directly assessed for simplicity.

To quantify the model's ability to correctly assign condition index, we split our observations into training (60%, $n = 459$) and testing (40%, $n = 304$) datasets. The condition index predicted by the model using the testing data was compared to the actual values, with statistics and results summarized in Tables S3 and S4.

The *polr()* and *poTest()* functions in the R MASS package were used to develop the model and test the proportional odds assumption, respectively (Venables and Ripley, 2002). All analyses were carried out in R 3.6.0 (R Core Team, 2019).

## 3 | RESULTS

Out of the original 1,089 specimens, some information was unavailable as a result of injuries or underwater scavenging by amphipods. Specifically, 39 were of unknown sex, 77 were of unknown age, and body condition was undetermined for 90 specimens. Removing these specimens resulted in 1,050 specimens of known sex, 1,012 of known age class, and 981 of known sex, age class, and body condition. For the seasonal analysis, 216 specimens were excluded due to lack of collection month information, leaving 765 specimens. Year and season-specific summaries of the number of specimens collected by sex and age class can be seen in Table S2. Despite notable seasonal variation in fishing effort, specimens were collected in every month, with more than 25 specimens available for all months but April ($n = 16$) and December ($n = 12$: Figure 2). The majority (90%: 124 of 138) of birds of known sex, age class, and bycatch
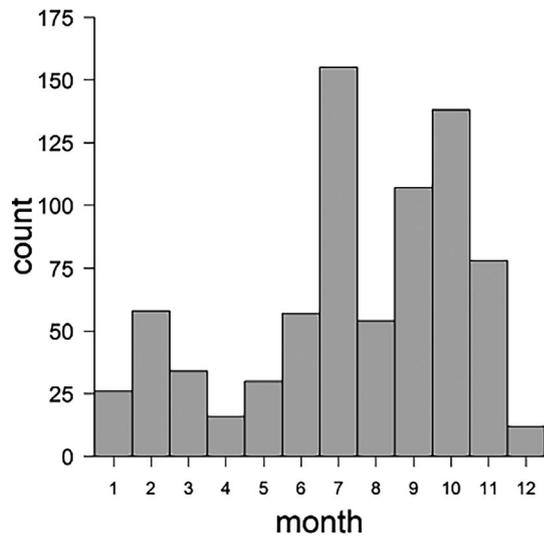
**FIGURE 2** Frequency of fulmar specimens of known collection season, sex, and age class caught in North Pacific groundfish (2004–2014) and halibut (2013–2014) fisheries ($n = 765$) managed by NOAA
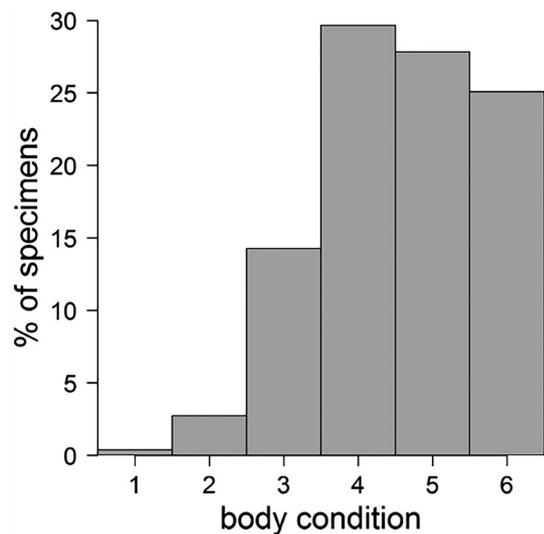


**FIGURE 3** Frequency of body condition scores of known sex and known age class fulmars caught in North Pacific groundfish (2004–2014) and halibut (2013–2014) fisheries ($n = 981$) managed by NOAA. Maximum body condition score is 6

location were collected in the Bering Sea along the continental shelf, where most fulmar bycatch in North Pacific groundfish and halibut fisheries occur (Eich et al., 2016). Therefore, we assumed that specimens we assessed represent regional bycatch patterns.

When assuming a proportion of 1:2 (males) for sex in the fulmar population, specimens collected by observers had a significant sex bias toward males, being 66% of all birds collected, 696 males, 354 females ($X^2$ [2, $n = 1050$] = 111.39, $p < .01$, $df = 1$). There was also an age class bias toward adults when assuming a proportion of 7:10 (adults), with 89% adults, 903 adults and 109 immatures ($X^2$ [2, $n = 1012$] = 178.19, $p < .01$, $df = 1$). The majority of specimens had

moderate (44%, score 3–4) to good (53% score 5–6) body condition, with only 3% emaciated (score < 3; Figure 3).

### 3.1 | Seasonal variation in bycatch

The bias (number of males/ number of individuals) toward males did not differ significantly among seasons, although the bias during the non-breeding season (median = 0.699, interquartile range 0.682–0.786) was slightly higher than during the breeding season (median = 0.64, interquartile range 0.620–0.647) and non-significantly lower than the bias during the fledging period (median = 0.714, interquartile range 0.657–1.00; Kruskal–Wallis $X^2$ [2, $n = 27$] = 3.7693, $p = .15$, $df = 2$ [Figure 4a]). The bias toward adults (number of adults/ number of individuals) did not statistically differ by season (Kruskal–Wallis $X^2$ [2, $n = 27$] = 2.3221, $p = .31$, $df = 2$ [Figure 4b]). Though non-significant, the adult bias was highest during the fledging period (median = 0.923, interquartile range 0.875–1.00), and very similar between the non-breeding period (median = 0.836, interquartile range 0.796–0.882) and the breeding period (median = 0.838, interquartile range 0.778–0.909).

### 3.2 | Sex, age, and season relate to body condition

In our ordered logistic regression, both linear and quadratic seasonal odds ratios indicated that body condition increased as the breeding season progressed to the non-breeding season, with the linear relationship with season being statistically significant ($p = .003$, Table 1). Specifically, the linear season odds ratio indicated that moving from one season to the next increased the odds of having a higher body condition by 1.48 times, holding constant all other variables. Our quadratic seasonal analysis indicated that the increase in body condition between consecutive seasons is greater as the year continues. For example, the increase in body condition from breeding and fledging season was less than the increase in body condition from the fledging and non-breeding season.

For sex, the odds of males having a higher body condition were 1.25 times that of females, holding constant all other variables. For age, the odds of juveniles having a higher body condition were 1.21 times [i.e., 1/0.827] that of adults, holding constant all other variables (Table 1). Neither of these results were significant. An assessment of the predictive performance of our model can be found in Table S3.

## 4 | DISCUSSION

We identified a strong bias toward adult male bycatch of Northern Fulmars across all seasons. These results confirm similar patterns reported in other studies within the Alaska region (Phillips et al., 2010; Winker, 2007). These biases suggest that males and females, as well as adults and immatures, differ in their relative susceptibility
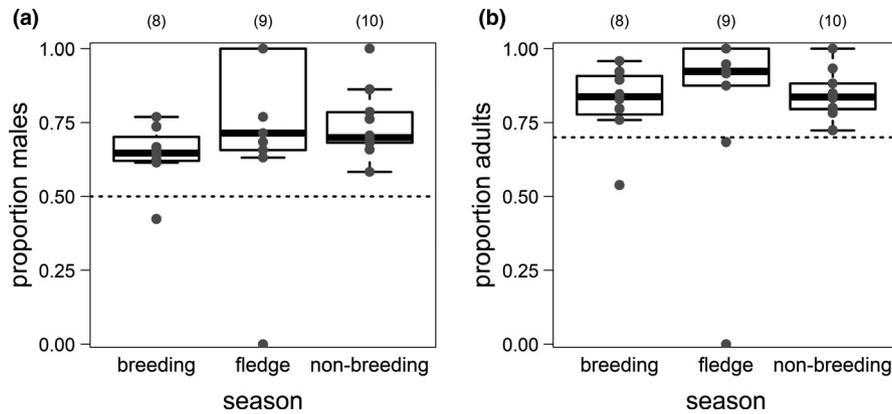
**FIGURE 4** Seasonal demographic composition of fulmars caught in North Pacific groundfish (2004–2014) and halibut (2013–2014) fisheries managed by NOAA. Box plots of (a) male/number of individuals bycatch proportions and (b) adult/number of individuals bycatch proportions by season, (x-axis of all plots) where breeding = May through August, fledge = September, and non-breeding = October through April (Mallory et al., 2020). The number of fulmar specimens represented in both plots is 765 (Table S2). The thick solid line indicates median of annual values, extent of the box spans from 25th to 75th quantile, and extent of the whiskers spans 95th percentile. All data points are shown as gray dots. Dashed line represents (a) 0.50 and (b) 0.70 expected proportions under the null hypothesis. Numbers in parentheses are the number of years with bycatch ratios for each season. No statistical differences were indicated according to the Kruskal–Wallis $X^2$; (A) Kruskal–Wallis [2, $n = 27$] = 3.7693 $p = .15$, $df = 2$, (B) Kruskal–Wallis [2, $n = 27$] = 2.3221 $p = .31$, $df = 2$

**TABLE 1** Summary of an ordered logistic regression of season, sex, and age on the body condition index of fulmars caught in North Pacific groundfish (2004–2014) and halibut (2013–2014) fisheries, using the training dataset ($n = 459$, residual deviance: 1,310.079)

| Variable | Category | Order | Logistic Coefficient | Standard Error | p-value | Odds ratio | 95% Conf. Intervals |
|---|---|---|---|---|---|---|---|
| Season *Linear* | Breeding | 1 | 0.394 | 0.132 | **.003** | **1.483** | 1.15–1.92 |
| | Fledging | 2 | | | | | |
| | Non-breeding | 3 | | | | | |
| Season *Quadratic* | Breeding | 1 | 0.369 | 0.198 | .063 | 1.446 | 0.980–2.14 |
| | Fledging | 2 | | | | | |
| | Non-breeding | 3 | | | | | |
| Sex | Female | 0 | 0.226 | 0.125 | .072 | 1.253 | 0.980–1.60 |
| | Male | 1 | | | | | |
| Age | Juvenile | 0 | −0.190 | 0.213 | .372 | 0.827 | 0.543–1.25 |
| | Adult | 1 | | | | | |

*Note:* Order refers to a category's variable-specific rank. Body condition was quantified by combining scores for pectoral muscle (scored 0–3) and subcutaneous fat (scored 0–3).
Bold values denote statistical significance.

to bycatch, possibly driven by non-mutually exclusive differences in competitive behavior and their exposure to fisheries through differing habitat use.

Fluctuations in fulmar bycatch rates in the North Pacific groundfish and halibut fisheries peak during the late fall and winter months (October–December; Dietrich et al., 2009), coinciding with the fulmar non-breeding season. Hatch et al. (2010) suggested that the high levels of bycatch observed in October and November in the Bering Sea were consistent with a large influx of fledgling birds. During these months, the primary operating fishery was the Pacific cod hook-and-line fishery along the Bering Shelf, which has the highest rates of fulmar bycatch of any fishery within the groundfish fisheries. Eich et al. (2016) postulate that higher incidental mortality rates in this fleet may result from fulmars' freedom from central place foraging

constraints during the breeding season, combined with fewer vessels in the region providing access to food subsidies through offal and bait. While our data hint at a slightly more pronounced male bias during the fledging season, the consistency in the adult bias suggests that similar demographic groups of birds are overlapping with fisheries year-round and that fledglings are not inflating bycatch rates during the peak months of October–December.

Previous studies have looked at the effect of specific vessels on seabird bycatch in these fisheries (although prior to the years of this study) and found a small subset of catcher–processor vessels made up a disproportionately high percentage of seabird bycatch. At least a few of these vessels had increased seabird bycatch due to discharging offal while retrieving longline gear (Dietrich & Fitzgerald, 2010). Although there are no available data on current vessel-specific

bycatch rates, this raises the possibility that poor compliance with seabird bycatch reduction measures on a few vessels may also contribute to increased fulmar bycatch. This would compound the effects of a contraction of available fisheries offal and a release from fulmar breeding constraints on fulmar bycatch rates during the late fall.

For fulmar body condition, we found that as the year progresses, body condition increases so that individuals caught in the non-breeding season are more likely to be in better condition than in either the breeding or fledging seasons. Males and juveniles also were more likely to have a better body condition, but sex and age had less of an effect than season. The increased body condition of birds caught during the non-breeding period likely reflects the energetic costs of reproduction and does not support the idea that birds caught in the non-breeding months in winter are in poorer condition in our study region (Dietrich et al., 2009). These results demonstrate the non-homogenous nature of bycatch in this region and identify opportunities to enhance our understanding of fulmar behavior.

## 4.1 | Seasonal variation in bycatch

There are two possible drivers of sex-biased bycatch assuming a 1:2 proportion of males in the population. Sexual dimorphisms in size and/or behavior could result in differential access and susceptibility to interaction with fishing gear (e.g., Tuck et al., 2015). Differences in at-sea distribution could also affect the sex proportion of birds around the boats, and therefore the exposure to bycatch (Bugoni et al., 2011). If behaviorally driven, the observed sex and age composition could indicate that adults, especially males, are more likely to dominate feeding on offal and on the bait used by these fisheries. This competitive dominance could result in different age classes "specializing" in different sources of food, such as post-processing offal (low risk of bycatch) or bait pieces associated with the auto-baiting process (higher risk of bycatch). Recent research suggests that neither size nor behavior alone are likely to drive this potential bias, as the species compositions of flocks aggregating around vessels can alter access to bait or offal. For example, Jiménez et al. (2012) found that the presence of diving seabirds increased the bycatch susceptibility of surface-feeding albatrosses, as the divers brought bait up to the surface where they were outcompeted by albatrosses. However, an explicit assessment of fulmar behavior and interaction rates relative to known sex or age class (or presence of other species) has not been performed. The experimental design for such an assessment would be extremely challenging. It would require observations of the interactions between known sex and age class birds in a foraging scenario, where hundreds of birds are gathered around a vessel. As a result, the relative competitive ability of different sexes and age classes remains poorly understood.

Regarding known fulmar habitat use patterns, known sex birds have been tracked during the breeding season within the Alaska region. However, low sample size prevents a robust analysis of sex-specific habitat use (Hatch et al., 2010). In north Atlantic

fulmars, sex-specific foraging has been observed in pre-breeding, breeding, and wintering birds. Although samples sizes are small, females (in comparison with males) were observed making longer trips in the pre-breeding period (Edwards et al., 2016); shorter, more frequent trips during the breeding season (Weimerskirch et al., 2001); and more pelagic trips in the non-breeding season (Quinn, 2014). Changes in foraging behavior throughout the reproductive season likely reflect increased energy investment from females during egg-laying and differences in chick provisioning responsibilities (Weimerskirch et al., 2001). The tendency of male fulmars to have larger wingspans and more mass than females (Mallory et al., 2020) could also drive differences in energetics, and foraging length and behavior. However, further information on sex and age class-specific habitat use is needed for Pacific fulmars. The mechanism(s) driving the persistence of male bias in bycatch across seasons in our study region remains unknown, but could be elucidated through behavioral trials and tracking of known sex birds.

Though not statistically significant, the slightly elevated proportion of males during the fledging season suggests a potential for seasonal interactions. The small increase in adult bycatch during fledging could relate to adults spending more time foraging near fishing vessels than newly fledged birds, to recover from the energetic costs of breeding. Or, it could reflect a tendency for adults to dominate feeding off of vessels in a manner that increases capture risk (i.e., the set). In southern hemisphere fisheries, increased capture of adults in multiple procellariid species may be linked with the dispersal of immature birds to northern waters (Gianuca et al., 2017). While the behavior of young fulmars at sea is not well described, fall and winter beach strandings of fulmars in British Columbia and the U.S. West Coast show high ratios of immatures to adults (Avery-Gomm et al., 2012; Donnelly-Greenan et al., 2014) indicating the possibility of a migration of immatures toward warmer regions similar to southern hemisphere species, although many other factors including foraging naivety may also explain stranding patterns. Similar to the suggestions regarding sex bias drivers, studies incorporating known age class birds, or at least adult versus immature, could clarify the mechanism for these age biases in fulmar bycatch from North Pacific groundfish and halibut fisheries.

With respect to body condition, breeding is a period of high energetic expenditure by adults, who balance their own body condition and that of their chick (Weimerskirch, 1998; Weimerskirch & Cherel, 1998). The lower body condition of adult specimens from breeding and fledging periods likely reflects parental investment as opposed to poorer foraging conditions, especially as the eastern Bering Sea can experience productive phytoplankton blooms in both the spring and the fall (Sigler et al., 2014). The possibility that males experience an increase in susceptibility to bycatch as a result of behavioral changes due to poor body condition is not supported by our data, but is possible for adult females given their lower body condition (Figure 4c). The relatively high body conditions observed during the non-breeding period suggests that the increase in the proportion of males collected as bycatch is not driven by an influx of individuals with poor body

condition. Overall, as most (97%) birds were of moderate or good body condition, the discards provided by this fishery may be an important food source, similarly to what has been documented in other populations (Bugoni et al., 2010; Garthe et al., 1996; Phillips et al., 1999). While diet data from non-fishery sources are lacking for the Alaska region, studies in the Atlantic have shown that fulmars' reliance on fisheries discards versus natural prey varies by latitude (Phillips et al., 1999) and possibly by season.

## 4.2 | Understanding bycatch impacts

Given possible differences in at-sea distributions of fulmars from different colonies during the non-breeding period, the impacts of bycatch may differ greatly among colonies (Hatch et al., 2010; Quinn, 2014). Fulmars from the Pribilof Islands, as the smallest of the major colonies (79,700 individuals) and with the pattern of remaining within 100s of km of the colony, may be heavily impacted by late fall fisheries occurring in the central region of the Bering Shelf during the non-breeding period (Eich et al., 2016; Hatch et al., 2010; Phillips et al., 2010). Pribilof Islands fulmars' exposure to fisheries during this period may contrast with the exposure of fulmars from Chagulak Island (500,000 individuals) and Hall of St. Matthew Islands (450,000 individuals), which may be less exposed to the fisheries around the Bering Sea Shelf if they spend more time foraging along the Aleutian Islands. Semidi Island (440,000 individuals) fulmars in the Gulf of Alaska presumably have relatively less exposure to these fisheries as indicated by tagging data (Hatch et al., 2010).

Confirming the colony of origin for bycaught fulmars would help to assess bycatch impacts and guide any potential mitigation. Colony-specific coloration and morphology has been described, but there is regional overlap and mixing (Hatch, 1991; Mallory et al., 2020). Genetic testing could also characterize the degree of genetic separation between colonies within Alaska waters, augmenting the understanding of region-wide fulmar population dynamics. As mentioned previously, deployment of additional tracking devices would greatly refine our understanding of the habitat use patterns between colonies, sexes, and age classes.

The population-level implications of our results hinge on a deeper understanding of the breeding status of fulmars caught as bycatch, and what removal of their reproductive contributions would mean. While it is not possible for us to determine reproductive status for individuals in the breeding season (with the exception of females with very mature gonads), we postulate that energetics of reproduction may be an underlying mechanisms to the patterns we observed. However, we must also consider that not all adults reproduce during the breeding season, especially since young but reproductively mature fulmars may go years before their first breeding attempt. Thus, our patterns during may also reflect the influence of a floating population of adult non-breeders that do not experience the energetic consequences of reproduction and are less tied to colonies.

It is important to note that the overall trajectory for these populations is shaped by additional factors, including bycatch in other regional fisheries (i.e., in Russia; Artukhin et al., 2010) and larger climatic conditions. Within the Alaska region, a multi-decadal analysis identified a possible decline in the abundance of fulmars at sea, implicating both fisheries behavior and broad-scale climate shifts in the North Pacific as drivers (Renner et al., 2013). From Alaska to California, large wrecks of fulmars in the non-breeding period have been linked to starvation, and may be increasing in magnitude and frequency (Donnelly-Greenan et al., 2014; Hatch et al., 2010; Nevins et al., 2011). Although fulmars breeding in the North Pacific are impacted by factors beyond the focal region and fisheries, understanding their interactions with the North Pacific groundfish and halibut fisheries provides valuable information to wildlife managers seeking to minimize the impacts of bycatch to this species.

## 4.3 | Conclusions

Our characterization of seasonal bycatch composition, involving over 1,000 fulmars sampled over a decade, highlights the susceptibility of adult male fulmars to regional fishing effort, and provides an opportunity to understand the demographic implications of fishery interactions in this region. Given that strong biases in incidental mortality can have population-level impacts (reviewed in Gianuca et al., 2017), the demographic patterns identified should be incorporated into population models that estimate population trajectories and the relative impact of bycatch. This work also identifies key research opportunities to enhance our understanding of Alaska fulmar behavior and population dynamics through behavioral trials, tracking the habitat use of birds of known sex and age classes, and investigating provenance of the injured birds, potentially through genetic analysis. Future opportunities to develop our understanding of bycatch dynamics, population connectivity, and the impacts of fisheries interactions on population trajectories require considering information from multiple sources of information and continued collaboration with fishers, observer programs, management organizations, and non-governmental organizations.

# AUTHOR CONTRIBUTIONS

J.B., H.M.N., S.M.F., and M.H. conceived the ideas. H.M.N. and J.B. designed the methodology. H.M.N., J.B., E.M.P., C.Y., C.G., and E.D.-G. oversaw data collection. J.B., E.M.P., C.Y., and C.G. collated or processed data. P.E.M. analyzed the data. S.M.F. led field collection, project administration, and funding acquisition. J.B., P.E.M., and M.H. led the writing of the manuscript. All authors provided intellectual input and gave the final approval for publication.

# DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request. A subset of the data is available in the online supporting information Appendix S1.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.