Exxon Valdez Oil Spill
Long-Term Monitoring Program (Gulf Watch Alaska) Final Report

Long-term Monitoring of Marine Bird Abundance and Habitat Associations during Fall and Winter in Prince William Sound

Exxon Valdez Oil Spill Trustee Council Project 21120114-E
Final Report

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June 2023

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*With contributions by: Elaine Gallenberg, Mayumi Arimitsu, and Richard Thorne†.

† Deceased

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Study History: This project is a continuation of a long-term fall and winter marine bird monitoring data set initiated in 2007 under the direction of co-principal investigators Bishop and Kuletz. In 2012, the methodology and results from that (project 090814) and a subsequent project (project 10100132-H) were used to develop the long-term fall and winter marine bird monitoring project under the umbrella of the Pelagic Component of the Gulf Watch Alaska long-term monitoring program (project 16120114-C and this current project). In 2017, the project was improved by a collaboration with the Gulf Watch Alaska humpback whale and forage fish projects and further enhanced in 2019 by collaboration with the Gulf Watch Alaska monitoring ocean conditions in Prince William Sound project and in 2021 through a collaboration with the Prince William Sound Regional Citizens' Advisory Council. Publications related to this project include Zuur et al. 2012, Bishop et al. 2015, Dawson et al. 2015, Stocking et al. 2018, Schaefer et al. 2020, Arimitsu et al. 2021, and Suryan et al. 2021.

Abstract: Management activities, including response to perturbations, damage assessments, and permitting for development, should consider the seasonal variation in abundance and distribution of marine birds in Prince William Sound, as well as the importance of forage fish availability and quality to marine birds during fall and winter. We identified seasonal patterns in all (11) focal species groups when characterizing marine bird distribution over 15 nonbreeding seasons (2007/08 – 2021/22). Our results emphasize the importance of Prince William Sound as a refuge from the harsher conditions of the Gulf of Alaska. While wintering in the Sound, marine birds were more likely to be distributed in areas that were closer to shore, shallower, and protected from wave exposure. Finally, our results underscore the complexity of predator-prey relationships during the nonbreeding season. Whereas only 20% of fish schools in surveyed bays were associated with birds, flocks were twice as likely to be observed within 150 m of a fish school. When examining upper-trophic level foraging dynamics, we observed humpback whales using forage flocks of seabirds as cues to locate scattered prey resources when whale, seabird, and forage fish abundances were suppressed following a heatwave event. Further research is needed to understand how predators respond to variation in prey quantity and quality during the non-breeding season and to understand top-down forcing on prey communities as marine habitats continue to change and experience perturbations.

Key words: foraging dynamics, forage fish, habitat associations, long-term monitoring, marine birds, nonbreeding season, predator-prey relationships, Prince William Sound, spatial correlation, seasonality, upper-trophic level

Project Data:

Description of data: Data on the at-sea distribution and abundance of marine birds were collected following US Fish and Wildlife Service standardized protocols in Prince William Sound, Alaska during various cruises conducted during fall and winter months from September through March beginning in March 2007 and ending in March 2022.

Format: All at-sea marine bird survey data since March 2007 are available as comma-delimited text files.

Bishop, M. A., A. Schaefer, K. Kuletz, M. McCammon, and K. Hoffman. 2017. Fall and winter seabird abundance data, Prince William Sound, 2007 – 2017, Gulf Watch Alaska pelagic component. Research Workspace. 10.24431/rw1k1w.

Bishop, M. A., and A. Schaefer. 2022. Fall and winter seabird abundance data, Prince William Sound, 2007-2022, Gulf Watch Alaska pelagic component. Gulf of Alaska Data Portal. https://gulf-of-alaska.portal.aoos.org/#metadata/771492cd-94b6-47ab-952a-02b152a535cf/project/folder_metadata/1766253

Drew, G. S., S. K. Schoen, M. D. Hood, M. L. Arimitsu, and J. Piatt. 2023. PWS fall and winter 2007-2021 seabird observations. Bishop, M. A. and A. Schaefer contribution to North Pacific Pelagic Seabird Database (NPPSD) v. 4.0, January 2023: U.S. Geological Survey data release.

The data custodian is Carol Janzen, Director of Operations and Development, Alaska Ocean Observing System, 1007 W. 3rd Ave. #100, Anchorage, AK 99501, 907-644-6703. janzen@aoos.org.in

Data are archived by Axiom Data Science, a Tetra Tech Company, 1016 W. 6th Ave., Anchorage, AK 99501.

Individuals interested in using these data are expected to follow standard, collegial guidelines such as those outlined by the US LTER Network's Data Access Policy, Requirements, and Use Agreement: http://www.lternet.edu/policies/data-access. In particular, we highlight the following from the US LTER Network data policy: The consumer of these data ("Data User" herein) has an ethical obligation to cite it appropriately in any publication that results from its use. The Data User should realize that these data may be actively used by others for ongoing research and that coordination may be necessary to prevent duplicate publication. The Data User is urged to contact the authors of these data if any questions about methodology or results occur. Where appropriate, the Data User is encouraged to consider collaboration or coauthorship with the authors. The Data User should realize that misinterpretation of data may occur if used out of context of the original study. It is strongly recommended that careful attention be paid to the contents of the metadata file associated with these data to evaluate dataset limitations or intended use.

Citation:

Schaefer, A. L., and M. A Bishop. 2023. Long-term monitoring of marine bird abundance and habitat associations during fall and winter in Prince William Sound. *Exxon Valdez* Oil Spill Long-term Monitoring Program (Gulf Watch Alaska) Final Report (*Exxon Valdez* Oil Spill Trustee Council Project 21120114-E), *Exxon Valdez* Oil Spill Trustee Council Project, Anchorage, Alaska.

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EXECUTIVE SUMMARY

Of the marine birds that overwinter in Prince William Sound (PWS), nine species were initially injured by the *Exxon Valdez* oil spill (EVOS), three of which have either not yet recovered (marbled murrelet *Brachyramphus marmoratus* and pigeon guillemot *Cepphus columba*) or have unknown recovery status (Kittlitz's murrelet *B. brevirostris;* EVOS 2014). Most marine bird monitoring in areas affected by EVOS has occurred during the breeding season, a time when food is generally at its most plentiful. Fall and winter are critical periods for survival as food tends to be relatively scarce, light levels and day length reduced, and water temperatures colder (Daunt et al. 2006). Long-term monitoring of marine birds in PWS during fall and winter is needed to understand how post-spill ecosystem recovery and changing physical and biological factors are affecting marine bird abundance, distribution, community composition, and habitat use. Further, understanding the challenges presented during the nonbreeding season will provide information necessary to successfully conserve and manage marine bird populations.

Systematic fall and winter marine bird surveys were conducted during the nonbreeding season (September through March) in PWS from February 2017 through November 2021 as part of the Gulf Watch Alaska (GWA) program. This project was a continuation of three previous and consecutive marine bird monitoring studies in PWS: Project 090814 (conducted March 2007 to March 2009), Project 10100132-H (conducted November 2009 through March 2012), and Project 16120114-C (conducted October 2012 through November 2016). Over the course of the study, this project shifted from reliance on ships of opportunity to dedicated marine bird survey platforms. Beginning in 2017 as part of the second, five-year cycle of GWA, the project was expanded through a collaboration with the GWA humpback whale (principal investigators Moran and Straley, project 21120114-O) and forage fish (principal investigators Arimitsu and Piatt, project 21120114-C) projects. The project was further enhanced in 2019 by partnering with the GWA monitoring ocean conditions in PWS project (principal investigator Campbell, project 21120114-G) and in 2021 through a collaboration with the PWS Regional Citizens' Advisory Council.

The objectives of this study were to:

1. Characterize the spatial and temporal distribution of marine birds in Prince William Sound during fall and winter (Chapter 1).
2. Estimate marine bird abundance and distribution in areas with known seasonally predictable aggregations of predators and prey.

  a. Relate marine bird presence to prey fields identified during concurrent hydroacoustic surveys (Chapters 2 & 3, Appendix A).
  b. Characterize marine bird-humpback whale foraging dynamics (Chapter 4).
3. Model species abundance in relation to physical and biological variables across time and space (Chapter 1).

We identified seasonal distribution patterns in all (11) focal marine bird species groups over 15 nonbreeding seasons (2007/08 – 2021/22). Movements into and out of PWS over the course of the nonbreeding season demonstrate that the nonbreeding season cannot be characterized as a single time period when describing "winter" marine bird distribution (Chapter 1 of this report). For example, kittiwakes were more likely to be observed during fall, while loons, large gulls, and small gulls were most likely to be present in PWS in mid-winter, and scoters were most likely to be present during late-winter. Grebes, cormorants, mergansers, murrelets, and murres were all observed throughout the mid- and late-winter period.

Water depth, distance from shore, and habitat type were identified as key environmental covariates for most species groups. When significant, species groups were generally more likely to be present and in greater numbers closer to shore and in shallower water. Grebes, murrelets, mergansers, and small gulls were less likely to be present in open water habitats. In contrast, cormorants were more likely to be present in mouths of bays and passages and open water habitats, scoters were more likely to be found in mouths of bays and passages and murres were more likely to occur in open water habitats compared to bays.

We characterized the factors influencing piscivorous marine bird response to forage fish during early (November) and late (March) winter at two spatial scales within juvenile Pacific herring nursery bays in PWS (Schaefer et al. 2020, Chapter 2 and Appendix A of this report). More than 40% of observed marine birds were associated with a fish school (within 150 m), while only 20% of fish schools were associated with birds. Seasonally, we recorded significantly more fish schools during November compared to March. At the school-level, marine birds were more likely to be associated with shallow fish schools within 500 m of shore and within smaller prey patches. At the bay-level, gull abundance was positively associated with the total number of fish schools recorded in the bay, while diving birds were more abundant when fish schools were higher in the water column, in shallower bottom depths, and in areas with more eel grass habitat. Targeting schools that are easier to access (e.g., shallower bottom depths, higher in water column) maximizes the potential energy return from the prey item by minimizing energy expenditure by the predator.

In pelagic regions of PWS that are consistently used by humpback whales as foraging areas, marine birds distribution and abundance was correlated more strongly with habitat variables indicative of protection from harsh oceanic conditions than hydroacoustic prey measures. Marine birds were more likely to be found in shallower water, closer to shore, and in more protected areas during the September post-breeding season (Chapter 3 of this report) and occurred in greater numbers with warmer sea surface temperatures (Chapter 3 of this report).

Finally, we found that humpback whales used forage flocks of seabirds as cues to locate scattered prey resources (Chapter 4 of this report). In all cases of observed humpback whale and forage flock interactions, humpback whales acted as flock disruptors (Haynes et al. 2011, Hoffman et al. 1981, Goodale et al. 2020) rather than facilitators (Pitman and Balance 1992, Obst and Hunt 1990, Degrati et al. 2014). All observations of interactions involved a single whale surfacing through an already established feeding aggregation, after which the aggregation would disperse.

Management activities, including response to natural (e.g., marine heatwave events) or anthropogenic (e.g., oil spills), damage assessments, and permitting for development activities (e.g., mariculture farming, oil and gas development), should take into account the seasonal variation in abundance and distribution of marine birds in PWS, as well as the importance of forage fish availability and quality to marine birds during fall and winter. Our results underscore the complexity of predator-prey relationships in PWS during the nonbreeding season. Temporal, habitat, and prey variables were all drivers of marine bird presence and abundance. Further quantitative measures of upper trophic-level densities and distribution relative to prey during the nonbreeding season will increase our understanding of how predators respond to variation in prey quantity and quality and inform our understanding of top-down forcing on prey communities as marine habitats continue to change and experience perturbations.

CHAPTER 1: SPATIO-TEMPORAL DISTRIBUTIONS OF PISCIVOROUS BIRDS IN A SUBARCTIC SOUND DURING THE NONBREEDING SEASON

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Abstract

Understanding bird distributions outside of the breeding season may help to identify important criteria for winter habitats. We surveyed marine birds in Prince William Sound, Alaska, USA over fifteen fall/winters from 2007/08 to 2021/22. Our objectives were twofold: to examine the seasonal patterns of marine bird species overwintering in Prince William Sound, and to explore the relationships between spatial covariates and bird distributions, accounting for inherent spatial structure. We used hurdle models to examine eleven species groups of marine seabirds: loons, grebes, cormorants, mergansers, inshore ducks, scoters, large gulls, small gulls, kittiwakes, *Brachyramphus* murrelets, and murres. All groups showed unique seasonal patterns. Models commonly identified water depth and distance from shore as key environmental covariates, while habitat type, wave exposure, and seafloor slope had less support. The environmental associations we documented are consistent with the available knowledge of marine bird and forage fish dynamics during the nonbreeding season. Our results support the assertion that birds are seeking refuge during winter, with Prince William Sound providing superior winter habitat relative to the harsher Gulf of Alaska.

Introduction

Understanding marine bird distribution outside of the breeding season is important, especially for birds overwintering at higher latitudes where short days and cold temperatures decrease foraging opportunities and increase energetic demands (Daunt et al. 2006, Fort et al. 2009). Marine bird distribution during the nonbreeding season may signal important criteria for winter refuge, which can increase individual survival and subsequent reproductive success, ultimately resulting in population-level impacts (Alves et al. 2013).

Following the *Exxon Valdez* oil spill in Prince William Sound (PWS), Alaska, annual marine bird surveys were implemented in March and July to represent the nonbreeding and breeding seasons, respectively (McKnight et al. 2008). However, work by Dawson et al. (2015), Stocking et al. (2018), and Schaefer et al. (2020) show that the nonbreeding season cannot be represented by a single interval when describing marine bird distribution in PWS.

In this study, we update the results of Stocking et al. (2018). We incorporated an additional six years of survey data to model marine bird distribution across fifteen fall/winter seasons (2007/08 – 2021/22). While Stocking examined nine species groups, for this analysis we had sufficient data that allowed us to analyze two additional species groups: inshore ducks and scoters. Our objectives were twofold: to examine the seasonal patterns of marine birds overwintering in PWS and to explore the relationships between spatial covariates and bird distributions.

Methods

Study Area

Encompassing ~ 5600 km of coastline, PWS is bounded to the east and north by the Chugach Mountains and to the west by the Kenai Peninsula. To the south, large, mountainous islands separate PWS from the Gulf of Alaska. Water depths in bays and fjords range from 50 to 400 m while depths of up to 700 m occur in the central portion of PWS. Surface water from the GOA flows into PWS pushed by the westward flowing Alaska Coastal Current. This flow, combined with abundant rain, snow and glacial runoff, results in a strong cyclonic circulation (Niebauer et al. 1994). Severe storms are common from October through March (Wilson and Overland 1986) and result in extensive mixing within the water column (Niebauer et al. 1994). By late winter, sea surface temperatures can be as low as 1 °C and some bays and fjords can be ice covered (Gay and Vaughan 2001).

Forage fish in PWS include several high-lipid species, such as Pacific herring (*Clupea pallasii*), Pacific sand lance (*Ammodytes hexapteru*s), and capelin (*Mallotus villosus*), that support upper-level predators of various taxa (Pearson et al. 2012). These three species of forage fish comprised 58% of the diet by weight of fourteen seabird species in PWS (Spies 2007). During winter, Pacific herring have been cited as the most abundant forage fish in PWS (Stokesbury et al. 2000). Adult herring in PWS overwinter in deeper waters of more protected areas, including close to their spring spawning grounds (Thomas and Thorne 2003, Thorne 2010), while juvenile herring overwinter in more shallow waters of bays and fjords (Norcross et al. 2001, Thorne 2010, Lewandoski and Bishop 2018).

Marine bird surveys and data preparation

Surveys were conducted between September and March over fifteen nonbreeding seasons (2007/08 – 2021/22, Table 1). We placed observers on vessels (15 – 18 m length) chartered to conduct multi-year herring, spot shrimp (*Pandalus platyceros*), and humpback whale (*Megaptera novaeangliae*) surveys, and an annual cruise to maintain hydroacoustic arrays in PWS. Additionally, beginning with a pilot season in 2014/15, we conducted annual marine bird surveys in September as part of the Gulf Watch Alaska Integrated Predator Prey surveys. With additional vessel-charter funding from the *Exxon Valdez* Oil Spill Trustee Council (EVOSTC) from 2019-2022, dedicated marine bird transects were surveyed in bay, open water, and nearshore areas in November and March.

Marine bird surveys were conducted while vessels were traveling on a direct course at a constant speed between 3 and 9 knots. Using the vessel's wheelhouse as an elevated viewing platform, an experienced observer using 10x binoculars continuously identified and recorded all marine birds sighted within a 180° arc extending 150 m forward and to either side of the vessel (for more detail on survey techniques, see Dawson et al. 2015). This radius was selected to minimize variance in detectability for smaller birds (Hyrenbach et al. 2007). To the same end, observations from times when wave height exceeded 1 m (Beaufort Sea State > 3) were not included. Flying individuals were recorded when first sighted and ignored thereafter to minimize effects of vessel attraction (Tasker et al. 1984). We assumed the probability of detection was close to or equal to 1 and that any biases that did occur would be consistent across cruises and locations (Dawson et al. 2015). Observations of marine bird and environmental conditions were recorded using dLOG software (R. G. Ford Consulting, Portland, Oregon). Location data (latitude, longitude) was automatically recorded every 15-20 s and with each observer entry.

An R shiny app developed by C. Swingley (ABR, Inc.) was used to divide each survey trackline into ~ 3 km segments and summarize observations by segment. Most segments (79.9%) were between 2.5 – 3.5 km long. The final segment in a trackline was the longest if even divisions around 3 km were not possible and 19.3% of segments were 3.51 – 6 km. GPS error caused some tracklines to be somewhat spotty resulting in 0.8% of segments that were 0.5 – 2.49 km long. Observations were aggregated within each segment and differences in segment size were accounted for during analysis. We grouped taxonomically similar species into eleven groups (Table 2).

Table 1. Temporal allocation of marine bird surveys in Prince William Sound, Alaska during the nonbreeding season, 2007 – 2022. Each survey is indicated by an "X". Two surveys were conducted in November 2007/08 and March 2008/09.

Winter	**Sep**	**Oct**	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**
2007/08			XX		X		X
2008/09	X	X	X		X		XX
2009/10			X				X
2010/11			X				X
2011/12		X	X	X		X	X
2012/13		X	X	X			X
2013/14		X	X	X		X	X
2014/15	X	X	X	X		X	
2015/16		X	X			X	
2016/17		X	X			X	
2017/18	X	X		X		X	X
2018/19	X	X					X
2019/20	X		X				X
2020/21			X				X
2021/22	X		X				X

Table 2. Percentage of segments each species was recorded on during marine bird surveys in Prince William Sound, Alaska during the nonbreeding season (September – March) from 2007/08 to 2021/22.

Species group	n	Common name	Scientific name	%
Loons	848 (17.9%)	Pacific	*Gavia pacifica*	56.6
		Common	*G. immer*	22.4
		Yellow-billed	*G. adamsii*	6.8
		Red-throated	*G. stellata*	5.4
		Unidentified	-	35.3
Grebes	308 (6.5%)	Horned	*Podiceps auritus*	53.2
		Red-necked	*P. grisegena*	37.7
		Unidentified	-	26.0
Cormorants	1136(24.0%)	Pelagic	*Phalacrocorax pelagicus*	86.4
		Double-crested	*P. auritus*	9.9
		Unidentified	-	15.1
Mergansers	307 (6.5%)	Common	*Mergus merganser*	48.5
		Red-breasted	*M. serrator*	33.9
		Unidentified	-	29.6
Inshore Ducks	416 (8.8%)	Harlequin Duck	*Histrionicus histrionicus*	55.3
		Barrow’s Goldeneye	*Bucephala islandica*	48.8
		Bufflehead	*B. albeola*	9.4
		Common Goldeneye	*B. clangula*	1.7
		Unidentified Goldeneye	-	14.7
Scoters	394 (8.3%)	Surf	*Melanitta perspicillata*	53.0
		White-winged	*M. deglandi*	47.2
		Black	*M. americana*	5.1
		Unidentified	-	12.9
Large Gulls	2140 (45.1%)	Glaucous-winged	*Larus glaucescens*	94.4
		Herring	*L. argentatus*	9.3
		Glaucous	*L. hyperboreus*	0.1
		Unidentified	-	4.3
Small Gulls	1067 (22.5%)	Short-billed	*L. brachyrhynchus*	95.2
		Bonaparte's	*L. philadelphia*	1.7
		Unidentified	-	7.6
Kittiwakes	1471 (31.0%)	Black-legged	*Rissa tridactyla*	100.0
Murrelets	1202 (25.4%)	Marbled	*Brachyramphus marmoratus*	85.1
		Kittlitz's	*B. brevirostris*	0.5
		Unidentified	-	35.4
Murres	1796 (37.9%)	Common	*Uria aalge*	99.7
		Unidentified	-	1.2

Covariate data

We related marine bird distribution to one temporal and six physical variables, including season, habitat type, wave exposure, distance from shore, bottom depth, slope of the seafloor, and sea surface temperature. The value for each covariate was assigned to the midpoint of each segment. Additionally, the area of the segment in km^2 was included to adjust for the higher likelihood of finding birds on larger segments.

For modeling purposes, a baseline level (indicated in parentheses) was defined for each of the categorical variables. Based on survey schedules, we divided the seven-month survey season into four seasonal categories: Sep–Oct (baseline), Nov–Dec, Jan–Feb, and Mar. We delineated four marine habitat types: bay (baseline), mouth (of bay or passage), passage, and open water. Bay refers to areas inside the mouth of an enclosed bay or fjord; mouth refers to the line between two headlands buffered by 1 km in either direction; passage refers only to narrower passes measured as <3 km wide; passages >3 km wide and all other waters were categorized as open. Wave exposure (exposure) represents the impact of Gulf of Alaska weather on the shoreline of PWS and was sourced from the National Oceanic and Atmospheric Administration ShoreZone coastal inventory and mapping project (NOAA 2010). We used the value of the nearest shoreline for each segment. Some exposure categories were uncommon, so we combined the six ShoreZone exposure categories into three categories: exposed (baseline), semi-protected (SP), and protected-very protected (P/VP).

Other habitat variables included distance from shore, depth and slope of the seafloor, and sea surface temperature (Table 3). However, sea surface temperature and the seasonal categories are correlated as sea surface temperatures generally decrease from September – March. The variance inflation factors for these terms were equal to 3.4. Therefore, sea surface temperature was dropped from consideration, which brought all variance inflation factor estimates below two (Johnston et al. 2018). Distance from shore (m) was calculated as the Euclidean distance from the midpoint of the segment to the nearest shoreline. Depth (m) at the segment midpoint was obtained from the Alaska Region Digital Elevation Model v.2.0 (Danielson et al. 2015) bathymetry grid, modeled to a horizontal resolution of 1 km. We reversed the sign of the values such that increasing depth is represented by larger (i.e., positive) values. Slope (angle of the seafloor) at the segment midpoint was calculated from the bathymetry layer (see Dawson et al. 2015). We standardized continuous variables (distance from shore and depth) to z-scores to improve model convergence.

Table 3. Mean, standard deviation (±1SD), and range of continuous environmental and geomorphic variables used in analysis of surveys of marine birds in Prince William Sound, Alaska, 2007–2022. Depth and distance from shore were standardized prior to analysis.

Variable	Mean	SD	Min	Max
Depth (m)	146	114	7	752
Slope (degrees)	1.4	1.4	0.0	13.2
Distance from shore (m)	2,023	2,167	0	17,430

Statistical analyses

After thorough exploratory data analysis, we did not identify any further concerns related to multicollinearity and did not find strong evidence of non-linear relationships between predictors and observations. Marine bird datasets are characterized by irregular distributions: few observations of large flocks, occasional observations of small flocks or single birds, and many zeros (Balderama et al. 2016). To accommodate these over-dispersed data, we used a Poisson hurdle model (Arab 2015), which is a mixture of two processes, one for zeros and the other a truncated Poisson that generates values larger than zero:

$$P(Yi \mid \theta) = p \times 1[Yi=0] + (1 - p) \times \text{Poisson}(Yi \mid Yi > 0).$$

Thus, the first process models the probability of observing zero birds, and the second process models the probability of the value of the observation (i.e., count, or flock size) conditional on a non-zero observation. A Poisson hurdle model for the set of n independent and identically distributed (iid) observations Yi's (for i = 1, …, n) is the mixture of a point mass at zero with probability p and a zero-truncated Poisson distribution with probability (1- p):

$$P(Yi = 0) = p, \qquad 0 \leq p \leq 1,$$

$$P(Yi = k) = (1 - p)\frac{\mu^k e^{-\mu}}{k!\,(1-e^{-\mu})}, \qquad k = 1, 2, \ldots, +\infty,\ \mu > 0,$$

where Y_i is the i-th response and μ is the mean of the untruncated Poisson distribution. This definition can be extended so that a log-linear regression model may be considered for observation-specific means, μ_i's, based on predictor variable(s) information. Similarly, a logistic regression may be considered for observation-specific probabilities, p_i's.

Here, we define a general hierarchical model for count observations Y_i's (for $i = 1, \ldots, n$) and predictor variables $X_1, \ldots X_p$. Note that the observations are not iid due to spatial correlation structure. In the first stage, the data model is defined, and the advantage of the hierarchical modeling framework is that it allows us to consider conditional independence of observations at this level (i.e., the dependence structure is defined at a different level of the hierarchical model).

Data model
The general hierarchical model can be described as follows:

$Yi \sim f\,(yi \mid \mu i, pi), \qquad i = 1, \ldots n,$

where $f\,(yi \mid \mu i, pi)$ is a Poisson hurdle distribution with intensities μi's and mixture probabilities pi's.

Process models
We define the following process models. The first process model is a log-linear model for the Poisson intensities:

$\log(\mu i) = \beta 0 + \beta 1X1i + \ldots + \beta pXpi + \gamma i, \qquad i = 1, \ldots, n,$

where βi's are the regression coefficients for predictor variables X1, …, Xp. Similarly, a logistic regression can be considered for the mixture probabilities:

$\mathrm{logit}(pi) = \log\left(\frac{p_i}{1-p_i}\right) = \alpha 0 + \alpha 1X1i + \ldots + \alpha qXqi + \eta i, \qquad i = 1, \ldots, n,$

where αi's are the regression coefficients for the predictor variables X1, …, Xq. Note that the predictor variables in these two models may or may not be the same.

To account for spatial autocorrelation inherent in most ecological observations (Hoeting 2009), we included spatially correlated error terms, represented by parameters γi in the Poisson process and ηi in the logistic process. Let $\gamma = (\gamma 1, \ldots, \gamma n)'$ be the vector of spatially correlated error such that

$\gamma \sim N(0, \Sigma\ ),$

where Σ is the covariance matrix which describes the spatial dependence of the data. In our case, for geostatistical data, the covariance matrix is defined as $\Sigma = \sigma\ 2R(\tau)$, where the spatial correlation is based on the Matérn covariance function (Cressie 1993, Cressie and Wikle 2011).

To account for the different levels of effort per segment due to the differences in size, the area in km^2 of segments was included in each model. It was included directly in the logistic regression portion of the model and the log of area was included as an offset term in the Poisson regression portion of the model.

Relatively non-informative prior distributions were used for unknown parameters (e.g., βi's, τ, and σ 2). The integrated nested Laplace approximation (INLA; Rue et al. 2009) approach is a numerically implemented analytical solution for approximating posterior marginals in hierarchical models with latent Gaussian processes. We adapted the hurdle model for use with INLA (see Arab 2015) and fit models using the R-INLA package (Lindgren and Rue 2015) in the program R (R Core Team 2021). In R-INLA, the Stochastic Partial Differential Equations (SPDE) approach was used to estimate spatial effects (Lindgren et al. 2011).

Models including all variables of interest (the full models) were fit for each group of marine birds (Figs. 1 and 2). Following the advice in Forstmeier and Schielzeth (2011), these full models are presented and discussed instead of reduced models found by employing backward variable selection, as was done in the Stocking et al. (2018) analysis. Using the full models allowed for better comparison between the Stocking et al. (2018) results and these updated results as estimates for all variables could be considered. Additionally, when comparing variables present in both the full model and model resulting from backward selection, coefficient point estimates and credible intervals were extremely similar suggesting overall conclusions about variables were generally the same using either procedure.

For each of the eleven groups, the Deviance Information Criterion (DIC) (Spiegelhalter et al. 2002) of the full model was compared to a version of the null model. Rather than true intercept only null models, our "null models" still included the covariate terms used to account for variation in segment length. In each case, the full model resulted in a significant reduction in DIC compared to the null model (between 77 - 907 units depending on the group), indicating a superior fit. In Figs. 1 and 2, only the estimates of the parameters of main interest are shown (i.e., the environmental covariates); the intercept, terms to correct for different sized segments, and parameters associated with the spatially correlated errors are not shown but were included in all models.

Results and Discussion

Observational data were collected over fifteen nonbreeding seasons from 55 surveys. The additional six years of survey data account for 43.5% of segments included in the analysis. After removing segments with Beaufort Sea States greater than three (wave height > 1 m), we analyzed 4,740 segments equivalent to 4,669 km^2 surveyed. Spatial coverage was greatest during Sep–Oct and the most limited during Jan–Feb (Fig. 3).

For the remainder of this report, we refer to "significant variables" as those whose 95% credible intervals did not include zero. For simplicity, results and discussion are focused on these significant variables. For each group, variables found to be significant in the logistic regression portion modeling presence/absence were not necessarily found to be significant in the Poisson regression portion modeling density and vice versa. In either case, we discuss the variable.

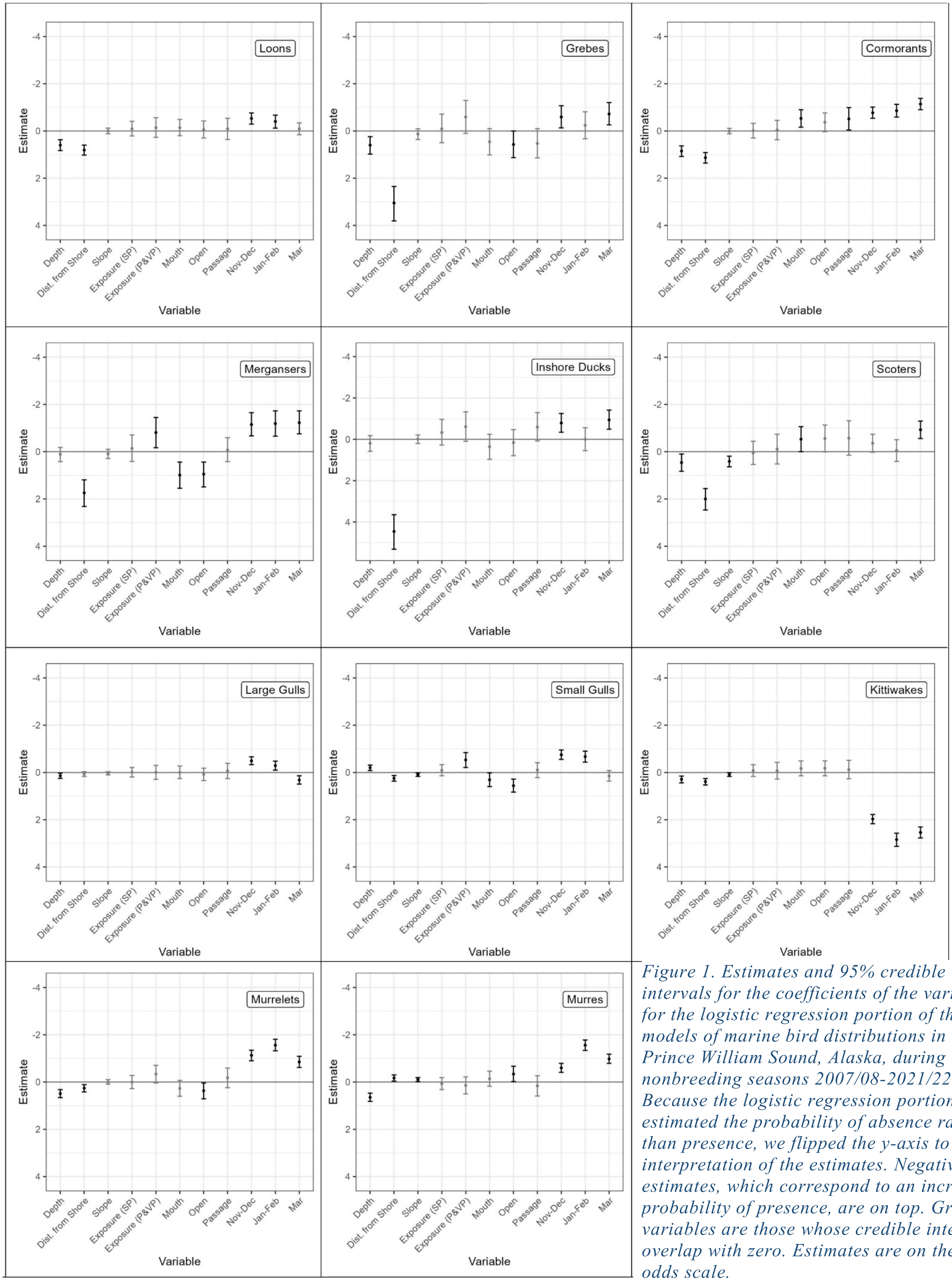

Figure 1. Estimates and 95% credible intervals for the coefficients of the variables for the logistic regression portion of the models of marine bird distributions in Prince William Sound, Alaska, during nonbreeding seasons 2007/08-2021/22. Because the logistic regression portion estimated the probability of absence rather than presence, we flipped the y-axis to aid interpretation of the estimates. Negative estimates, which correspond to an increased probability of presence, are on top. Gray variables are those whose credible intervals overlap with zero. Estimates are on the log odds scale.

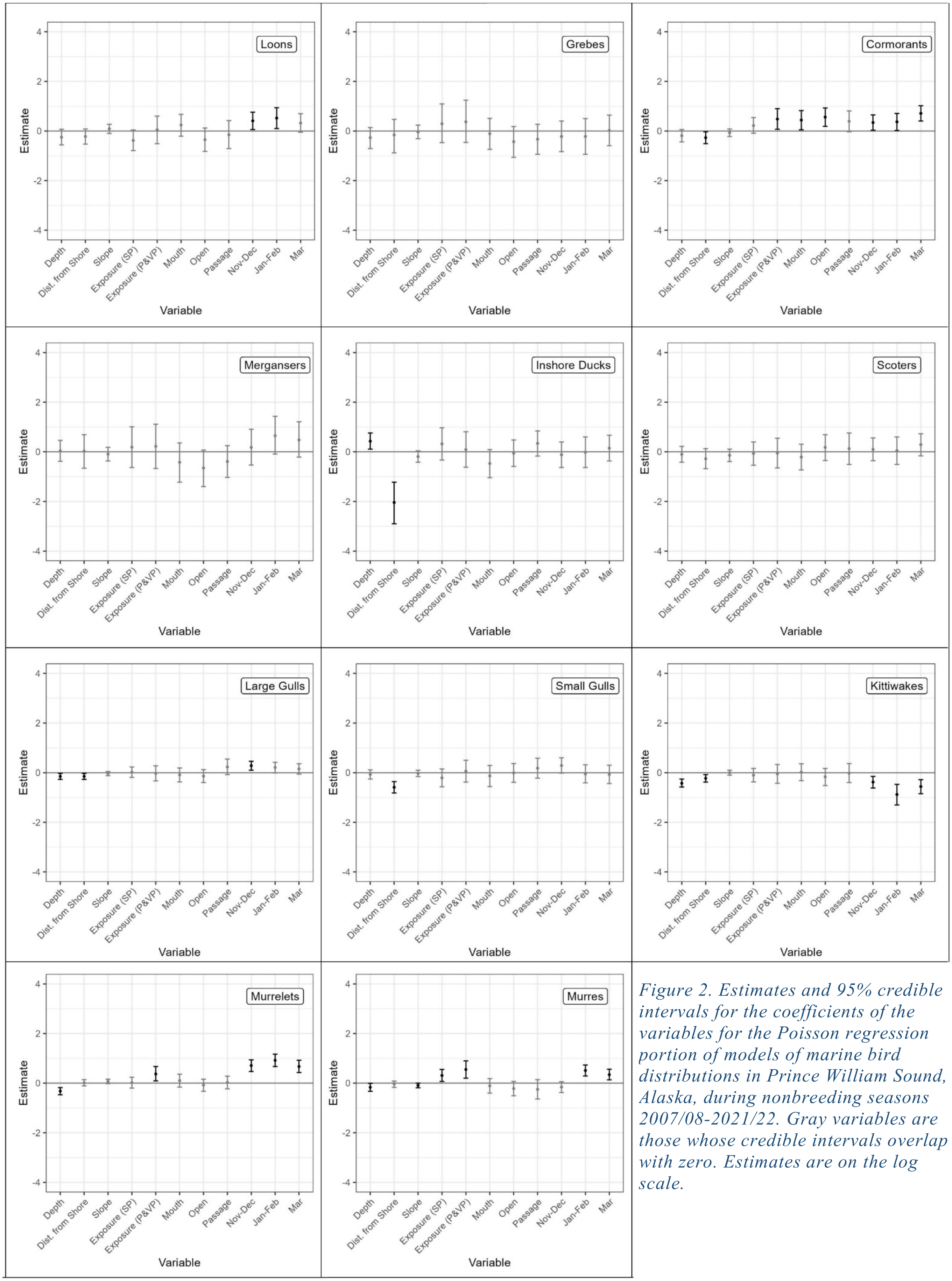

Figure 2. Estimates and 95% credible intervals for the coefficients of the variables for the Poisson regression portion of models of marine bird distributions in Prince William Sound, Alaska, during nonbreeding seasons 2007/08-2021/22. Gray variables are those whose credible intervals overlap with zero. Estimates are on the log scale.

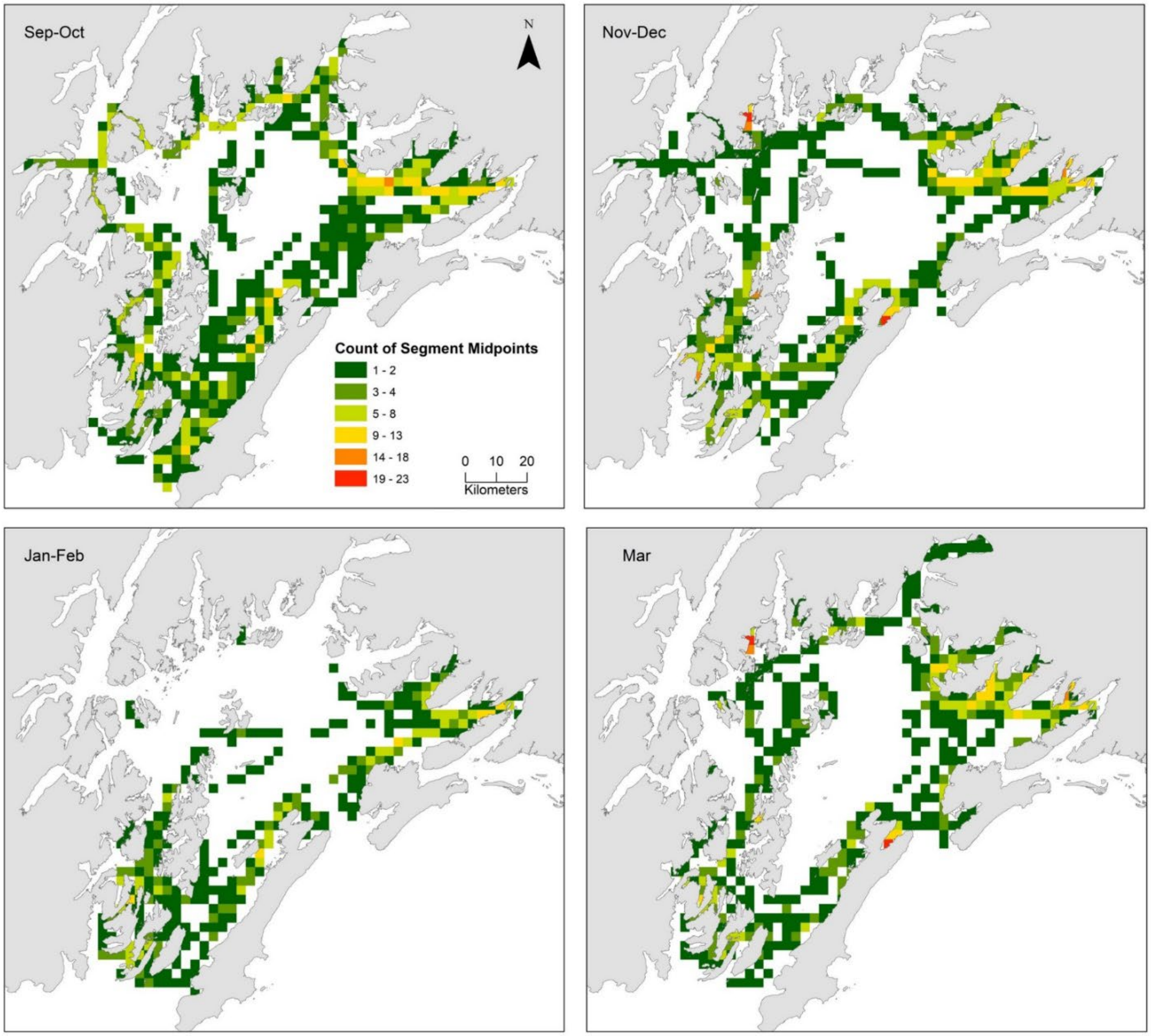

Figure 3. Spatial allocation of effort shown in a 3 km x 3 km grid for nonbreeding (September through March) marine bird surveys of Prince William Sound, Alaska, 2007-2022.

Seasonal patterns in marine bird distributions

All groups showed significant seasonal differences related to their presence and six of eleven groups (except grebes, mergansers, small gulls, inshore ducks, and scoters) also showed seasonal differences related to their density when present (Figs. 1 and 2), indicating movements into and out of PWS over the course of the nonbreeding season. Because the seasonal category Sep–Oct category to that baseline. The effect of the seasonal category varied depending on the species group. It was common for a season category to affect presence and density in a similar way (i.e., for each group, probability of presence and abundance are related) (Figs. 1 and 2).

Kittiwakes were more likely to be present in PWS during fall, while loons, large gulls, and small gulls were most likely to be present in PWS in early- to mid-winter, and scoters were most likely to be present during late-winter. Grebes, cormorants, mergansers, murrelets, and murres were all observed more likely to occur in PWS from early- through late-winter compared to fall. Kittiwake densities were highest in the fall. Densities of large gulls were highest in early winter, while, loon, murrelet, and murre densities were highest in mid-winter. Cormorant densities were highest in late winter.

Patterns of environmental correlates

There is ample precedent for environmental characteristics and conditions serving as proxies for prey availability in the studies of marine birds (Amorim et al. 2009, Ainley et al. 2012, Allyn et al. 2012). We selected relatively few variables and attempted to capture different spatial scales of possible predator-prey interactions. Previous studies of multiple scales seem to support a fine- to medium-scale association (i.e., 2–8 km) of marine birds to prey (Piatt 1990, Mehlum et al. 1999, Burger et al. 2004). We incorporated temporally static coarse-scale predictors, habitat category, and exposure. Ecological rationale for individual covariates is outlined in Dawson et al. (2015).

Depth was significant for nine of the eleven binomial models and five of the eleven Poisson models (Figs. 1 and 2). Species groups were more likely be present (except for small gulls) and in greater numbers (except for inshore ducks) in shallower water.

Distance from shore was estimated as significant in ten of the eleven presence/absence models (all except large gulls) and five of the eleven density models (Figs. 1 and 2). When significant, species groups were more likely to be present and more abundant closer to shore. This effect was found to be especially strong for the presence of grebes and for the presence and abundance of inshore ducks.

Slope of the seafloor was estimated as significant in four of the presence/absence models and one of the abundance models (Figs. 1 and 2). As slope increased, murres were slightly more likely to be present, but in fewer numbers. Other groups were more likely to be present as slope decreased. In all models, the effect was estimated to be relatively small.

Wave exposure was found to be significant in two of the presence models and three of the abundance models (Figs. 1 and 2). Mergansers and small gulls were more likely to be present in protected/very protected areas compared to exposed areas. Cormorants, and murrelets murres occurred in greater numbers in protected/very protected habitats while murre densities were higher in semi-protected and protected/very protected habitats.

Habitat type was estimated as significant in seven of the binomial models and one of the Poisson models (Figs. 1 and 2). The effect on presence varied by species group. Cormorants were found in greater numbers when present in mouth and open habitats compared to bays. Grebes, murrelets, mergansers, and small gulls were less likely to be present in open habitats, and mergansers and small gulls were also less likely to be present in mouth habitats compared to bays. Conversely, scoters were more likely to be present in mouth habitats and murres were more likely to be present in open habitat compared to bays.

Focal group distribution patterns

Pacific loon (*Gavia pacifica)* was the most common loon species observed (57%); however, an additional 35% of all loon observations were not identified to species (Table 2). Loons were more likely to be present and in greater numbers in Nov–Dec and Jan–Feb compared to Sep–Oct (Figs. 1 and 2). Loons were also more likely to be present in shallower water and closer to shore (Fig. 1).

Grebe observations were not dominated by a single species. Horned grebes (*Podiceps auritus*) were detected on about 53% of segments with grebes present, red-necked grebes (*P. grisegena*) were detected on about 38% of segments, and 26% had grebes not identified to species (Table 2). Grebes were more likely to occur during Nov–Dec and Mar compared to Sep–Oct. They were also more likely to be present in open waters that were shallower and closer to shore (Fig. 1). The effect of distance from shore was especially strong. No variables were found to significantly explain variation in grebe abundance.

Cormorant observations were dominated by pelagic cormorants (*Phalacrocorax pelagicus*) which were detected on 86% of the segments with cormorants present. Cormorants were more likely to be present and in larger numbers on surveys later in the winter (Nov–Dec, Jan–Feb, and Mar) compared to Sep–Oct (Figs. 1 and 2). Cormorants were more likely to occur in shallower water, closer to shore, and in mouth and passage habitats compared to bays (Fig. 1). Cormorants were found in greater numbers closer to shore, in protected/very protected areas, and in mouth and open, habitats compared to bays (Fig. 2).

Merganser observations were comprised of common mergansers (*Mergus merganser*; 49% of segments), red-breasted mergansers (*M. serrator*; 34% of segments), and unidentified mergansers (30% of segments; Table 2). Mergansers were more likely to be observed later in the winter (Nov–Dec, Jan–Feb, and Mar) as well as closer to shore, in protected/very protected areas, and in bays compared to mouth and open habitats (Fig. 1). No variables were found to significantly affect merganser abundance.

Harlequin ducks (*Histrionicus histrionicus*) were detected on 55% of segments with inshore duck observations and Barrow's goldeneyes (*Bucephala islandica*) were observed on 49% (Table 2). Inshore ducks were more likely to be present closer to shore and in Nov–Dec and Mar compared to Sep–Oct (Fig. 1). They were more abundant at deeper depths and closer to shore (Fig. 2). The effect of distance from shore was particularly strong for both presence and abundance.

Surf scoters (*Melanitta perspicillata*) were recorded on 53% of segments with scoter observations and white-winged scoters (*M. deglandi*) were detected on 47% (Table 2). Scoters were more likely to be present in Mar compared to Sep–Oct and in areas with shallower water, closer to shore, with shallower slopes, and in mouth habitats (Fig. 1). No variables explained variation in scoter abundance (Fig. 2).

Large gull observations were overwhelmingly glaucous-winged gulls (*Larus glaucescens*) which were detected on 94% of segments with large gulls present (Table 2). Large gulls were more likely to be present in Nov–Dec and Jan–Feb, and less likely in Mar (Fig. 1). When present, they were observed in greater numbers during Nov–Dec. Large gulls were slightly more likely to occur in shallower water. (Fig. 1). Large gulls were present in larger numbers in shallower water and closer to shore (Fig. 2).

Small gull observations were overwhelmingly short-billed gulls (*Larus brachyrhynchus*) which were detected on 95% of segments with small gulls present (Table 2). Small gulls were more likely in Nov–Dec and Jan–Feb compared to Sep–Oct (Fig. 1). They were also more likely to be present in deeper waters, closer to shore, at less severe slopes, in protected/very protected areas, and in bays compared to mouth and open habitats (Fig. 1). Small gulls occurred in greater numbers closer to shore (Fig. 2).

Kittiwake observations were all black-legged kittiwakes, which were much more likely to be present and in greater numbers during Sep–Oct compared to later in winter (Nov–Dec, Jan–Feb, and Mar; Figs. 1 and 2). Kittiwakes were also more likely to be present and more abundant in shallower water closer to shore and were more likely in areas with less severe slopes (Figs. 1 and 2).

Marbled murrelets (*Brachyramphus marmoratus*) comprised most murrelet observations; they were present on 85% of segments where murrelets were observed (Table 2). Murrelets were more likely to be present and occur in greater numbers in winter (Nov–Dec, Jan–Feb, and Mar) as well as in shallower water (Figs. 1 and 2). They were more likely to be present closer to shore and in bays, compared to open habitats and to be more abundant in protected/very protected areas (Figs. 1 and 2).

Murres were almost exclusively common murres (*Uria aalge*), which were present on over 99% of the segments where murres were observed (Table 2). Murres were more likely to be present in winter (Nov–Dec, Jan–Feb, and Mar) (Fig. 1) and were found in greater numbers during Jan–Feb and Mar compared to Sep–Oct (Fig. 2). They were also more likely in shallower water, farther from shore, at more severe slopes, and in open habitats compared to bays (Fig. 1). Murres were observed in greater numbers in shallower water, at less severe slopes, and in semi-protected and protected/very protected areas compared to exposed areas.

Comparison to Stocking et al. (2018)

In this analysis (hereafter the “updated analysis”), we identified distribution patterns for 11 marine bird species groups. In the original analysis of 9 species groups published by Stocking et al. (2018; hereafter the “original analysis”), seasonal patterns were not able to be determined for grebes, cormorants, or mergansers. By incorporating six additional years of data, we were able to uncover the temporal use of PWS for these species groups and examine distribution patterns of two additional species groups (scoters and inshore ducks).

Most patterns with environmental characteristics identified in the original analysis held in the updated analysis. Interestingly, Stocking et al. (2018) found that grebes were less likely to be present in open water habitat, while we identified a preference for open water habitat. As in the original analysis, cormorants were more likely to occur in open water habitat, but we also found they were more likely to be present in mouth habitats.

There were a few differences in the methods of the updated analysis compared to the original analysis. In the original analysis, using data from 2007/08 – 2015/16, a different method for the division and selection of tracklines was used; if the final portion of a trackline that had been divided into 3 km segments was less than 2.5 km, it was dropped. No adjustment term was used to account for the small differences in the size of sampling units (Stocking et al., 2018). In this updated analysis, with data from 2007/08 – 2021/22, a new method of trackline division resulted in segments with a wider range of lengths and no segments were dropped based on size alone (see "Marine bird surveys and data preparation" section of this chapter). Instead, a term to account for the varying levels of effort per segment was included in this updated analysis. Another difference between the original and updated analyses was that sea surface temperature was dropped in this updated analysis due to multicollinearity concerns. A final difference was in the definition of the mesh used in R-INLA to approximate the spatial relationship of the data. Following evidence from simulations by Righetto (2017), the mesh was redefined in this updated analysis to avoid a definition that was either too fine or too sparse.

These differences in methods did not result in concerning differences in estimates between the original and updated analysis. Comparing the variables with 95% credible intervals that did not overlap zero within species groups showed much agreement between the estimates from the original and updated analysis. Because many effects were estimated to be small and therefore close to zero, slight differences in the estimates between the original and updated analysis did sometimes result in differing conclusions when using the binary definition of significance. More important than differences due to the binary definition of significance was the agreement of the 95% credible intervals, which indicated consistency in the methods as well as the additional data. The six additional years of data resulted in more precise estimates (smaller credible intervals), especially for the species groups of grebes, mergansers, and loons which had relatively few observations in the original analysis. It also enabled estimates of inshore ducks and scoters for which there were too few observations to include in the original analysis.

Conclusions

We identified seasonal patterns in all 11 species groups when characterizing marine bird distribution over 15 nonbreeding seasons. These results clearly indicate movements into and out of PWS over the course of the nonbreeding season and demonstrate that the nonbreeding season cannot be characterized as a single time period when describing "winter" marine bird distribution. Overall, habitat use was fairly consistent across the two analyses. Water depth, distance from shore, and habitat type were identified as key environmental covariates for most species groups. When significant, species groups were generally more likely to be present and in greater numbers in areas that were closer to shore and in shallower water. The effect of habitat type varied by species group. Grebes, murrelets, mergansers, and small gulls were less likely to be present in open habitats and mergansers and small gulls were also less likely to occur in open habitats. In contrast, cormorants were more likely to be present in mouth and open habitats, scoters were more likely to be found in mouth habitats and murres more likely to occur in open habitats compared to bays. Our results support the assertion that birds are seeking refuge during winter, with PWS superior winter habitat relative to the harsher conditions in the Gulf of Alaska.

Acknowledgements

We are grateful to our observes including N. Dawson, K. Brenneman, A. Lang, T. Morgan, R. Kaler, and J. Stocking. We thank the following people and organizations for allowing us to share their vessel time: R. Thorne, M. Buckhorn, P. Rand, and R. Campbell (PWS Science Center), J. Moran and S. Rice (National Marine Fisheries Service), J. Straley (University of Alaska Sitka), M. Arimitsu and J. Piatt (U. S. Geological Survey), and M. Wessel and K. Goldman (Alaska Department of Fish and Game). We also thank our vessel captains D. Beam (*M/V Montague*), D. Janka (*M/V Auklet*), D. Anderson (*R/V Solstice*), K. Jones (*M/V Serenity*), A. Schroeder and T. Jones (*R/V Island C*), R. Campbell (*R/V New Wave*), and P. Tate (*R/V Alaskan Gyre*). We also thank the *Exxon Valdez* Oil Spill Trustee Council and the PWS Regional Citizens' Advisory Council for their support and funding of this study. This project is part of the Gulf Watch Alaska long-term monitoring program. These findings and conclusions presented by the author(s) are their own and do not necessarily reflect the views or position of the *Exxon Valdez* Oil Spill Trustee Council.

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CHAPTER 2: MARINE BIRD RESPONSE TO FORAGE FISH DURING WINTER IN SUBARCTIC BAYS

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Abstract

Despite the importance of understanding marine bird response to prey fish, few studies have examined this relationship during winter. Over a five-year period, we conducted synoptic marine bird and hydroacoustic forage fish surveys during early (November) and late (March) winter to characterize the factors influencing marine bird and forage fish dynamics at two spatial scales (fish school and bay) within subarctic bays of coastal Alaska, USA. Over 40% of observed marine birds were associated with a fish school (within 150 m of a fish school), although only 20% of fish schools were associated with birds. Seasonally, we recorded significantly more schools during early winter. The marine bird community also shifted from being comprised primarily of marbled murrelets (*Brachyramphus marmoratus*) and large gulls (*Larus* spp.) in early winter to common murres (*Uria aalge*) in late winter. At the school-level, marine birds were more likely to be associated with shallow fish schools within 500 m of shore and in smaller prey patches. At the bay-level, gull abundance was positively associated with the total number of fish schools recorded, while diving birds were more abundant when fish schools were higher in the water column, in shallower bottom depths, and in areas with more eel grass habitat. Our results indicate the importance of temporal, habitat, and fish school variables as drivers of marine bird presence and abundance, underscoring the complexity of predator-prey dynamics in the marine environment during winter.

Introduction

Most free-living animals inhabit environments with patchily distributed resources (Wiens, 1976, Johnson et al. 1992). This is especially true for birds foraging in the marine environment, where prey is highly mobile, elusive, and dispersed. At-sea distribution of marine birds is driven by the distribution and availability of prey (Birkhead and Furness 1985, Hunt et al. 1999, Becker and Beissinger 2003), which is contingent on a range of factors, such as light and nutrient availability, sea and surface air temperature, sea level pressure, surface winds, water depth, and upwelling strength (Behrenfeld et al. 2006, Brown et al. 2011). Strong associations between forage fish and marine birds have been documented at broad spatial scales (10s of km; Fauchald et al. 2000, Fauchald 2009). However, at finer spatial scales (10s of m), these relationships tend to break down, possibly due to incomplete information on prey densities by the predator or antipredator behavior of prey (Logerwell and Hargreaves 1996, Hunt et al. 1999, Fauchald et al. 2000, Fauchald 2009, Hentati-Sundberg et al. 2018).

Most research on marine bird and fish dynamics has focused on the effect of prey availability and quality on the productivity or foraging behavior of birds during the breeding season (e.g., Ostrand et al. 1998, Piatt 2002, Suryan et al. 2002, Kuletz 2005, Hentati-Sundberg et al. 2018) when birds must rely on prey resources and foraging locations within commuting distance of their nest. When prey is scarce or highly variable, the restricted foraging range of nesting birds can have cascading effects that impact foraging behavior, reproductive success, and abundance (Suryan et al. 2002).

Less emphasis has been placed on marine bird and forage fish dynamics during winter (although see Fauchald et al. 2000, Suryan et al. 2006, Amélineau et al. 2018) especially including measures of prey (Hunt et al. 1999). Understanding this relationship during winter is important because this is the time period during which marine birds face the greatest environmental and physiological pressures. Marine birds overwintering at higher latitudes experience colder temperatures, shorter days, and more extreme climate (Daunt et al. 2006), limiting foraging activities at a time when metabolic energy demands are higher (Fort et al. 2009). Additionally, for many animals the nonbreeding season is a time when breeding-capable individuals accumulate energy stores in preparation for future reproductive events (Sorensen et al. 2009). Poor conditions encountered during the winter may carry over into other parts of the year (Barbraud and Weimerskirch 2003, Daunt et al. 2006, Sorensen et al. 2009); therefore, the association between marine birds and prey during winter likely has important implications for subsequent survival and reproductive decisions.

In this study, we collected marine bird observations synoptic with hydroacoustic forage fish surveys to characterize the distribution and abundance of birds in relation to forage fish abundance and habitat characteristics in bays of PWS, Alaska during early and late winter. Prior research identified spatial and temporal patterns of marine birds in PWS throughout the nonbreeding season (Dawson et al. 2015, Stocking et al. 2018) but recognized the lack of direct prey information as a gap. To address this, we first used a two-step approach to understand how fish school and habitat characteristics influence bird presence and abundance at individual fish schools. We then took a larger-scale approach and evaluated predator-prey relationships at the bay level.

Methods

Study Area

Prince William Sound is a subarctic sound located along the southcentral coast of Alaska (primarily between 60° and 61° N) comprised of more than 70 bays and fjords. PWS is separated from the Gulf of Alaska by large, mountainous barrier islands and provides access to extensive and protected ice-free habitat for wintering populations of at least 18 species of piscivorous marine birds (McKnight et al. 2008, Bishop et al. 2015). During winter, marine birds occur primarily in semi-protected and protected nearshore habitats, preferring shallower, warmer waters (Stocking et al. 2018). Our surveys occurred in two fjords (hereafter referred to as bays: Eaglek and Whale Bays) and two bays (Simpson and Zaikof Bays) (Gay and Vaughn 2001; Fig. 4). The study bays vary in depth from 90 m (Simpson Bay) to 300 m (Whale Bay) and basin area from 25.7 km^2 (Whale Bay) to 50.0 km^2 (Eaglek Bay).

The primary forage fish species in PWS include Pacific herring (*Clupea pallasii*), walleye pollock (*Gadus chalcogrammus*), and capelin (*Mallotus villosus*) (Rand 2018), with Pacific herring the dominant species during winter (Stokesbury et al. 2000, Rand 2018, Lewandoski and Bishop 2018). Adult herring overwinter in deep protected waters near their spring spawning grounds (Thomas and Thorne 2003, Thorne 2010, Rand and Thorne 2018) and near entrances to the Gulf of Alaska (Bishop, PWS Science Center, unpubl. data), while juvenile herring prefer eelgrass beds and the shallow waters of fjords and bays (Norcross et al. 2001, Thorne 2010, Lewandoski and Bishop 2018).

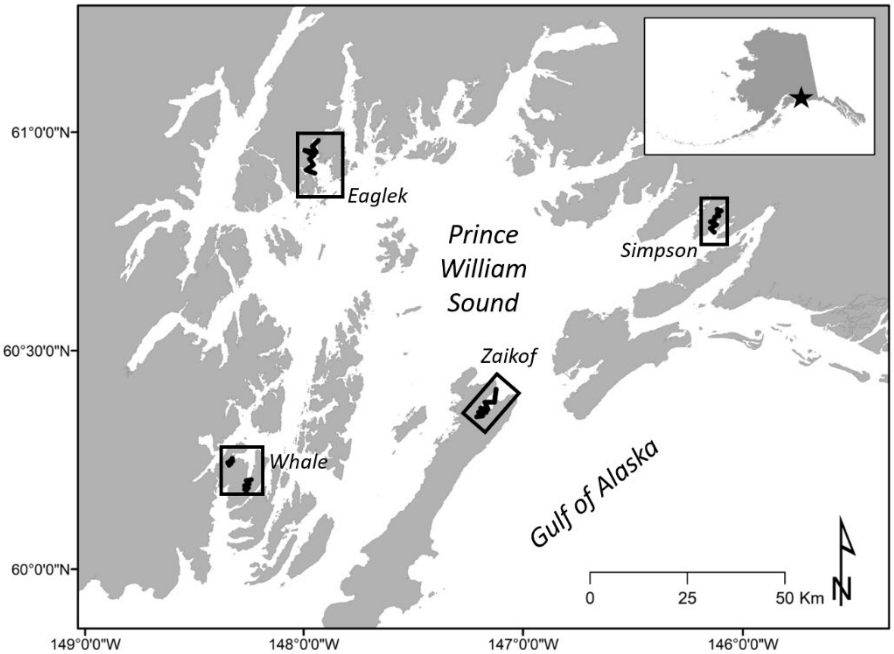

Figure 4. Location of fjords and bays surveyed for marine birds and fish schools in Prince William Sound, Alaska, November 2007 - March 2012. Zigzag transects within bays are indicated by black lines.

Data collection and preparation

Hydroacoustic surveys. Hydroacoustic surveys followed the methods outlined in Thorne (2010) and consisted of systematic zigzag transects in each bay during daylight hours of November and March. We used a 120 kHz split-beam hydroacoustic transducer (Biosonics DT-X system) mounted to a hydrodynamic fin towed alongside the survey vessel 1 m below the surface. The maximum depth of acoustic data collection was 120 m. The 17 m charter vessel travelled ~3.5-4 knots during surveys and generally stayed $\underset{\sim}{}$200 m from shore to avoid the shallow, rocky coastline.

Acoustic data were manually inspected and post-processed using Echoview 5.1 (Myriax Pty, Ltd., Tasmania, Australia) following the methods outlined in Rand (2018). We applied a minimum analysis threshold for integration of -60.00 dB to remove very small targets (<2 cm). The bottom signal and upper 5 m of data were excluded from analysis to remove unwanted acoustic backscatter (e.g., benthic habitat, noise near the transducer). We used the school detection module of Sonardata Echoview (Coetzee 2000) to identify discrete forage fish schools using the following minimum criteria: school length >2 m, school height >1 m, vertical linking distance <5 m, and horizontal linking distance <5 m. Linking distance refers to the maximum distance allowed between two school candidates being connected to form one school. In addition to identifying individual forage fish schools, we identified prey patches, or areas in which fish schools were spatially clumped. For this study, we defined prey patches as fish schools located within 30 m of one another.

Marine bird surveys. Marine bird surveys were performed concurrently with and on the same vessel as the hydroacoustic surveys and followed established United States Fish and Wildlife Service (USFWS) protocols (USFWS 2007). One observer using 10x binoculars recorded the number, species, and behavior of all marine birds occurring within a 300 m fixed-width strip (150 m both sides and ahead of boat) from a clear observation platform 2.5 m above the water line. Observations were recorded into a laptop computer integrated with a global positioning system (GPS) using the program dLOG (Ford 1999). Location data (latitude, longitude) were automatically recorded at 20 s intervals and for every entered observation. For each survey, we subset our marine bird data to only include piscivorous species observed on the water or actively foraging.

Statistical analyses

School analysis. To understand the factors influencing marine bird presence and abundance at individual fish schools, we first tallied the total number of birds within 150 m of each ensonified fish school and classified each school as “bird-associated” (one or more birds) or “bird-absent”. Because marine bird count data are often zero-inflated due to irregular distribution of individuals, we implemented two-step hurdle models for the analysis (Arab 2015). The first step used the binomial distribution to model the probability of observing zero birds at the school, while the second step used a truncated Poisson distribution to estimate the probability of the observation value (the number of birds observed) given a non-zero observation. To account for spatial autocorrelation of observations, we included spatially correlated error terms based on the Matérn covariance function in all models. For a more complete definition of the hurdle model framework and development see Arab (2015) and Stocking et al. (2018).

Explanatory variables included in the model set were selected based on previous research identifying spatial and temporal patterns of marine bird (Dawson et al. 2015, Stocking et al. 2018) and juvenile Pacific herring distributions (Lewandoski and Bishop 2018) in PWS during winter. We related marine bird presence and abundance at fish schools to 2 temporal, 4 habitat, and 5 school variables. Temporal terms included month (November, March) and winter (five winters, 2007/08 – 2011/12). Habitat covariates included bay (categorical: Eaglek, Simpson, Whale, Zaikof), bottom depth (m), distance to shore (m), and distance to eel grass (*Zostera marina*) habitat (m). We obtained bottom depth from the Alaska Ocean Observing System bathymetry grid modeled to a horizontal resolution of 500 m (Alaska Ocean Observing System 2010). Eel grass habitat data were obtained from the National Oceanic and Atmospheric Administration (NOAA) ShoreZone coastal inventory and mapping project (NOAA 2010). Distance to shore was calculated as the Euclidean distance to the nearest shoreline and was included in the models as a quadratic term.

We obtained fish school variables from the Echoview school detection model output and included in the model set terms for the minimum school depth (m), school height (m), and the nautical area scattering coefficient (NASC). NASC provides an index of fish biomass in the water column but does not account for differences in species composition or fish size. We also included prey patch length (m) and the number of schools within each prey patch as model terms.

We standardized all continuous variables to improve model convergence and performed thorough exploratory data analysis to identify correlations among predictor variables. Due to high collinearity, we did not include distance to shore and distance to eel grass within the same models. We assigned non-informative prior distributions to unknown parameters and fit models using R-INLA (Lindgren and Rue 2015). We used backward variable selection for model development, beginning with the full model and dropping non-significant terms until all remaining parameters were significant. The Deviance Information Criterion (DIC) and principle of parsimony were used to drive model selection and compare candidate models. We obtained posterior distributions for all variables included in the top model and examined statistical significance. Variables with 95% credible intervals that did not overlap zero were deemed significant, while estimates with distributions spanning zero were non-significant. Full model selection results are available online in Supplemental Table 1 (Appendix B).

Within bay analysis. To relate marine bird abundance to fish school characteristics and habitat variables within bays, we developed linear models using observed counts of marine birds as the response variable against 2 temporal, 2 habitat, and 4 fish school covariates. We aggregated marine bird observations into two foraging groups: diving birds (loon, cormorant, murre, and murrelet species) and gulls (all large and small gulls, and kittiwakes). We standardized bird counts by survey effort (birds/km surveyed) and developed separate model sets for each foraging group.

Temporal variables included in the models were month and winter. The habitat terms included were the total amount of eel grass habitat in the bay (linear m of shoreline) and the mean bottom depth of recorded fish school locations (m). Four fish school variables were included and standardized by km survey effort: mean minimum school depth (m), total number of fish schools, total number of prey patches, and fish biomass (NASC) in the bay summed over water depth bins to estimate the biomass available within the foraging ranges of the two marine bird foraging groups. For the gull model set we summed NASC over the first 10 m of recorded water depth (NASC10), and for the diving bird model set we summed NASC over the first 40 m (NASC40) and the first 60 m (NASC60).

We standardized all continuous explanatory variables and log-transformed response variables to meet assumptions of normality, which we verified using the Shapiro-Wilk normality test (Shapiro and Wilk 1965). We did not include the terms for number of prey patches and number of schools or the terms for NASC40 and NASC60 within the same models due to high collinearity. We used backward variable selection for model development, beginning with the full model and dropping non-significant terms until all remaining terms were significant. We used Akaike's Information Criterion (Akaike 1973) corrected for small sample sizes (AIC_C; Hurvich and Tsai 1989) to direct model selection. Parameter estimates with 95% confidence intervals that did not overlap zero were considered significant. Full model selection results are available online in Supplemental Tables 2 and 3 (Appendix B).

We performed all spatial data extraction, interpolation, and summarization using ArcMap 10.6 (ESRI 2018) and all statistical analyses using R version 3.5.3 (R Core Team 2019).

Results

We completed 10 synoptic hydroacoustic and marine bird surveys over five years (2007 – 2012) during early (November) and late (March) winter, covering ~561 km total within the four surveyed bays (Table 4).

Table 4. Length of total survey effort (km) for each survey and fjord/bay of Prince William Sound, Alaska, November 2007 – March 2012.

	2007-2008		**2008-2009**		**2009-2010**		**2010-2011**		**2011-2012**		**Total**
Fjord/Bay	**Nov**	**Mar**	**Nov**	**Mar**	**Nov**	**Mar**	**Nov**	**Mar**	**Nov**	**Mar**	
Eaglek	17.8	17.8	16.5	15.4	14.2	16.1	18.7	18.1	19.2	18.8	172.6
Simpson	11.6	11.4	11.2	10.6	11.7	12.1	11.9	11.0	11.5	12.1	115.1
Whale	10.1	9.0	9.9	8.0	10.6	10.5	11.1	10.7	10.7	6.8	97.4
Zaikof	17.0	17.9	17.3	16.4	18.6	18.3	21.5	19.0	16.9	12.8	175.7
Total	56.5	56.1	54.9	50.4	55.1	57.0	63.2	58.8	58.3	50.5	560.9

We detected 1,947 individual fish schools during surveys, of which 387 (20%) were associated with marine birds. More schools were detected during November (*n* = 1,430) compared to March (*n* = 517) (Table 5). The number of schools detected each winter was also variable (Fig. 5i), ranging from 228 (winters 2008/09 and 2011/12) up to 668 (winter of 2007/08). Overall, 1,390 of the 1,947 schools (71%) were part of a prey patch. The mean number of schools per patch was 9.0 (± 0.3 standard error (SE); range 1-59) and mean patch length was 200.4 m (± 5.0 SE; range 60.0-1027.4). On average, Simpson Bay had the highest density of schools (6.8 schools/km), followed by Whale (3.8 schools/km), Zaikof (2.8 schools/km), and Eaglek (1.7 schools/km). There was a strong seasonal influence on the number of schools recorded in bays, particularly in Simpson and Zaikof (Fig. 6).

Table 5. Mean and standard deviation (SD) values of habitat and fish school covariates for bird-absent and bird-associated fish schools by month, 2007 – 2012, Prince William Sound, AK. Variables marked with an asterisk (*) were significant in the binomial portion of the most supported hurdle model. NASC = nautical area scattering coefficient.

	Bird-absent fish schools		**Bird-associated fish schools**	
Variable	**November** ***n*** **=1180**	**March** ***n*** **= 380**	**November** ***n*** **= 250**	**March** ***n*** **= 137**
*Distance to land (m)	474.8 (288.4)	379.4 (221.9)	449.9 (254.5)	436.8 (225.5)
Distance to eel grass beds (m)	570.6 (418.7)	457.02 (303.80)	508.1 (314.6)	529.5 (288.5)
*Bottom depth (m)	53.3 (27.8)	57.1 (29.0)	42.1 (17.3)†	50.4 (26.1)
*Min. school depth (m)	50.5 (19.3)	50.5 (23.6)	44.5 (18.1)†	39.7 (23.0)
NASC	5,756.2 (75,939.3)	6,179.8 (43,298.1)	3,384.8 (14,476.4)	28,768.2 (303,563.6)
School height (m)	1.3 (1.5)	1.9 (2.0)	1.3 (1.3)	1.9 (2.1)
*Patch length (m)	243.6 (245.9)	120.0 (77.9)	185.4 (234.0)	78.3 (41.2)
No. schools/patch	11.4 (15.4)	4.8 (6.4)	7.7 (14.6)	2.0 (1.8)

†Discrepancy between bottom depth and minimum school depth due to the differences in the resolution of the data sources. Minimum school depth was measured in-situ by the echo-sounder. Bottom depth measurements were obtained from the Alaska Ocean Observing System bathymetry grid and were modeled to a horizontal resolution of 500 m.

We observed 3,156 birds over the five winters. Marine bird abundance varied by survey month (November *n* = 1,333, March *n* = 1,822) and winter (range = 282 - 937; Fig. 5ii). Overall, 44% of the birds observed (*n* = 1,382) were associated with at least one fish school. When birds were associated with a school, mean group size was 3.1 birds/school in November (range 1 – 42) and 4.5 birds/school (range 1 – 45) in March.

Altogether, common murres (*Uria aalge*) were the most abundant species group recorded during surveys (45% of observations), followed by marbled murrelets (*Brachyramphu*s *marmoratus*; 15%) and large gulls (*Larus* spp.; 11%) (Table 6). However, a strong seasonal signal was reflected in the marine bird observations. In November, murrelets were the most commonly recorded species (25% of observations), followed by large gulls (21%) and murres (12%). In March, murres were the overwhelmingly dominant species group, accounting for 68% of all observations. This same pattern held when examining just the birds associated with fish schools. In November, large gulls (26%), murrelets (21%), and murres (13%) represented the top three recorded species groups, whereas in March, murres again dominated observations (70%) (Fig. 7).

Table 6. Piscivorous marine bird species groups recorded during marine bird surveys of Prince William Sound, Alaska, November 2007 – March 2012. n = 3,156 total birds recorded, % = percent of n.

Species group	**Species included (common names)**	**%**
Cormorants	Pelagic, Double-crested	4.2
Grebes	Red-necked, Horned	4.7
Kittiwakes	Black-legged	5.2
Large Gulls	Glaucous-winged, Herring	10.6
Small Gulls	Mew, Bonaparte’s	3.9
Loons	Pacific, Common, Yellow-billed, Red-throated	5.8
Mergansers	Common, Red-breasted	6.0
Murres	Common	45.0
Murrelets	Marbled	14.6

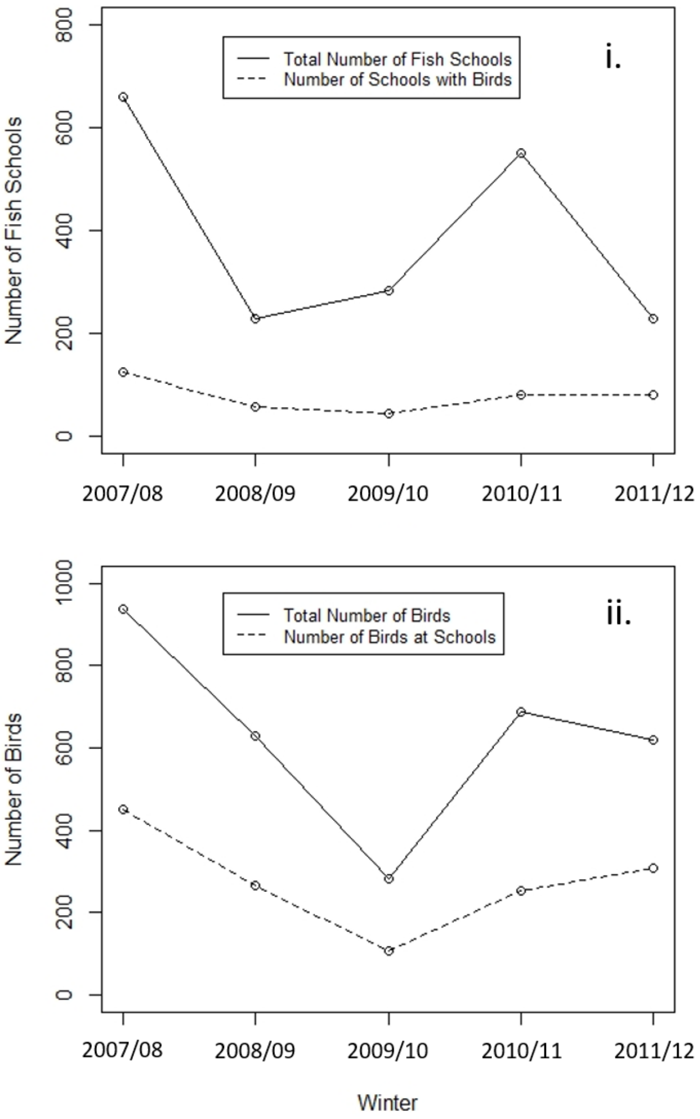

Figure 5. Total number of fish schools (i) and marine birds (ii) observed during November and March surveys in Prince William Sound, Alaska over 5 winters (2007/08 - 2011/12).

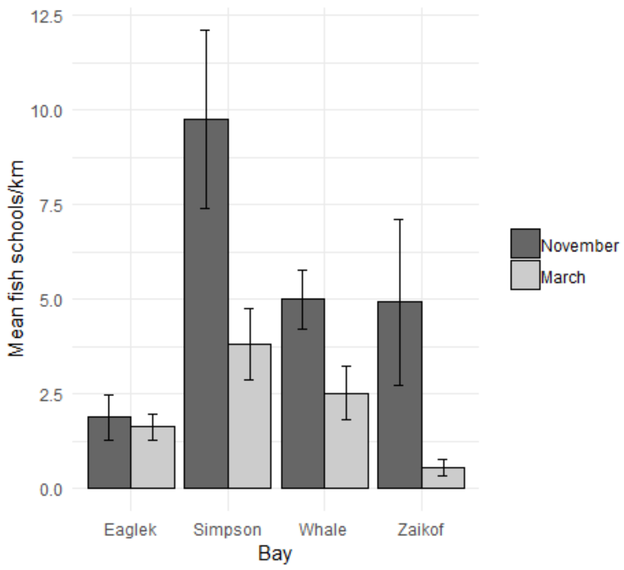

Figure 7. Mean number of fish schools/km ± SE of fish schools detected in each bay by month over five winter seasons, Prince William Sound, Alaska, November 2007 – March 2012.

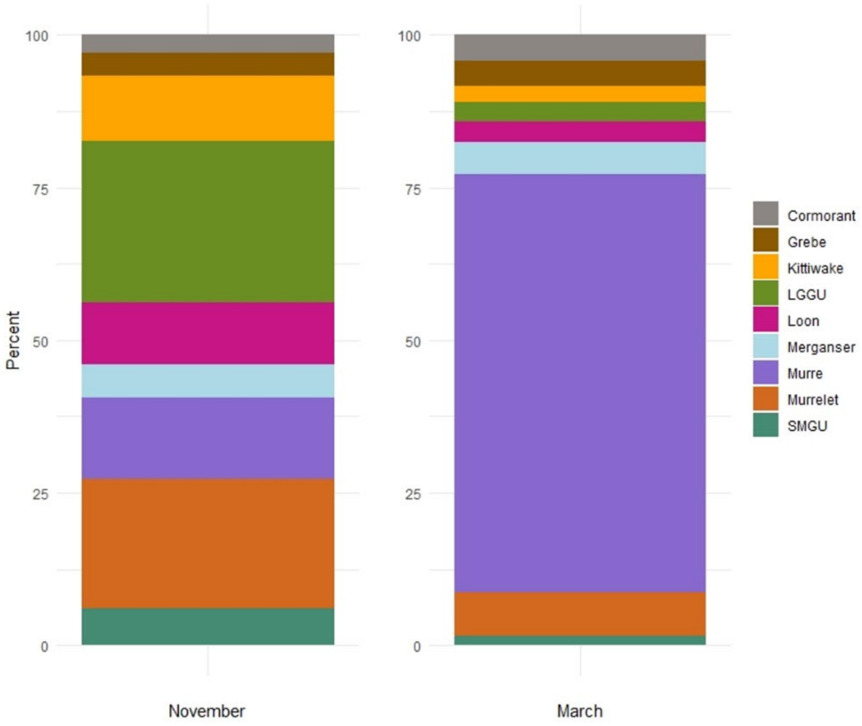

Figure 6. Species composition (%) of marine birds associated with fish schools in Prince William Sound bays and fjords during early (November) and late (March) winter, 2007 – 2012. LGGU = large gull; SMGU = small gull.

School analysis

The probability of bird presence at fish schools was associated with intermediate distances from shore, shallower bottom depths, shallower fish schools, and smaller prey patches. Birds were also more likely to be present at fish schools in March. Inclusion and significance of the winter term in the top model indicates unexplained interannual variation (Fig. 8i, Table 5).

For bird-associated fish schools, the model containing parameters for month, NASC, patch size, and number of schools in the prey patch best explained marine bird abundance at schools. The month term was the only significant parameter in the model, however, the credible intervals for NASC and patch size only slightly overlapped zero (Fig. 8ii). Marine birds were more abundant at fish schools in March, and potentially correlated with greater NASC and smaller prey patches.

Because temporal covariates are not physical measures and are likely correlated with some of the habitat and fish school variables, post-analyses we removed these factors (winter, month) from all models to better understand the mechanisms directly affecting bird presence and abundance at schools. Comparing the best fitting models when the temporal variables were either included or dropped, the same terms were found to have significant effects in the models explaining bird presence at schools (distance to land, bottom depth, minimum school depth, and prey patch size). In contrast, in the models explaining bird abundance at schools, the variables distance to land, minimum depth, NASC, and patch size were all significantly related in the absence of temporal covariates. The presence of these terms in the temporal-exclusion model explaining bird abundance indicates potential support for these variables, however, the model including the temporal variables had a much better fit than models excluding those terms (as measured by DIC; ΔDIC = 60.18).

Within bay analysis

Greater numbers of divers were associated with schools located in shallower bottom depths and higher in the water column and in bays with more eel grass habitat and fewer forage fish schools (Fig. 9). Winter was also included in the final model, suggesting unexplained annual variation. For gulls, model selection results indicated that gull abundance was positively and significantly related to the number of fish schools in the bay ($\beta = 0.33$, SE = 0.08).

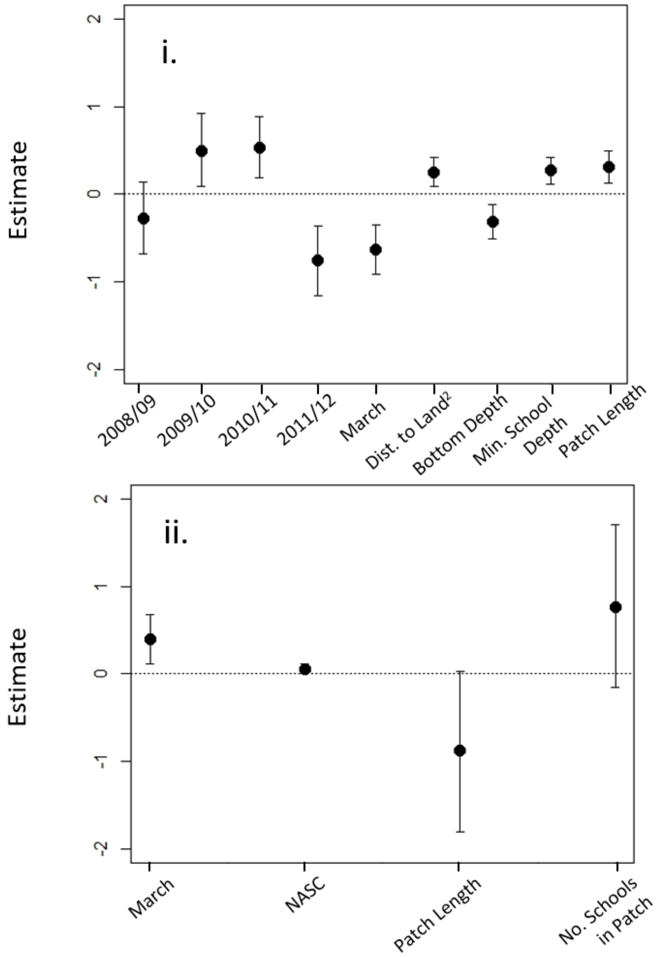

Figure 8. The effects of explanatory variables on presence (i.) and abundance (ii.) of piscivorous marine birds at fish schools in Prince William Sound, Alaska, November 2007- March 2012. In "i" the response variable estimates the probability of observing zero birds at the school, so a positive relationship indicates a decreased probability of bird presence. Error bars represent 95% credible intervals. NASC refers to the nautical area scattering coefficient and is an index of fish biomass in the water column.

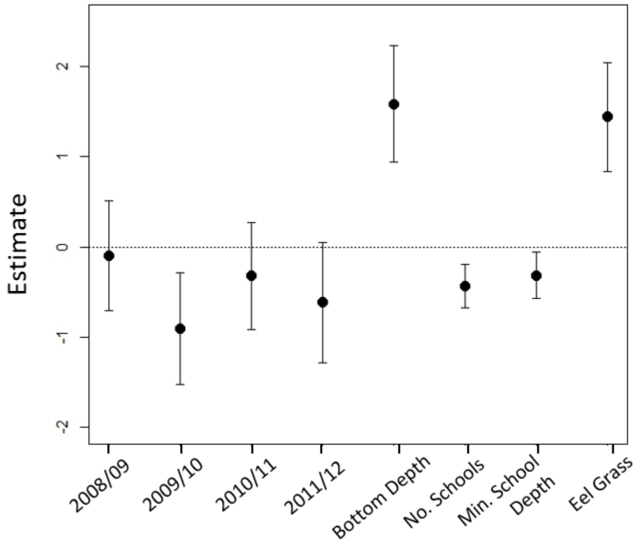

Figure 9. The effects of explanatory variables on abundance of diving marine birds in bays of Prince William Sound, Alaska, November 2007 – March 2012. Error bars represent 95% confidence intervals.

Discussion

Understanding predator-prey interactions is challenging, especially in the marine environment. Our results underscore this complexity, indicating support for seasonal, habitat, and fish school characteristics as drivers of marine bird presence and abundance at both the school-level and bay-level. Unlike most studies examining the relationship between marine bird predators and prey, our study occurred within juvenile herring and walleye pollock nursery bays, not open waters (e.g., Logerwell and Hargreaves 1996, Fauchald et al. 2000), thereby likely increasing our ability to identify relationships at a finer scale.

We documented strong seasonal variation in the marine bird community composition and the number of fish schools, but weaker relationships with direct prey measurements, such as NASC, school height, and number of schools per prey patch or bay. The lack of strong correlations with prey measurements could be due to imperfect sampling. While the echosounder detected schools directly under the research vessel, marine birds were recorded out to 150 m on either side. Despite being within 150 m of a recorded school, birds may have been targeting off-transect schools not captured by the hydroacoustics. Furthermore, although there was slight evidence for the effect of NASC on marine bird abundance (Fig. 8ii), the NASC term was highly variable across space and time (range = 19 – 3,555,245; Table 5, Fig. 10). The high variation in NASC combined with the reduced sample size of bird-associated schools in the Poisson portion of the model resulted in no clear signal.

Prior research in PWS supports the influence of seasonality on marine bird distribution and abundance during the nonbreeding season. Dawson et al. (2015) and Stocking et al. (2018) identified consistent, large-scale seasonal shifts in the marine bird community across all habitat types, including in bays, passages, and exposed open waters. Our results from PWS bays corroborate these previous studies: marbled murrelets and large gulls (primarily glaucous-winged gulls, *L. glaucescens*) were the most abundant species groups in our November surveys, while common murres overwhelmingly dominated the marine bird community in March (Fig. 7). The observed changes in community composition across seasons reflects the different feeding and migratory strategies of each species. For example, after breeding murrelets move offshore to molt, however ~25% remain in the protected waters of PWS through winter (Nelson 1997, McKnight et al. 2008). Murrelets begin returning to breeding areas in March, with arrivals peaking in April (Nelson 1997). Murres also move offshore after breeding to molt and overwinter, returning to nearshore areas in late winter, well before breeding (Ainley et al. 2002).

Marine birds were more strongly associated with fish schools during March, when birds were more likely to be present and in greater numbers at schools. When birds were present, there were on average 1.4 more birds/school in March compared to November. Birds may be more tied to prey resources during this period because they are still enduring harsh winter conditions while also preparing for the upcoming breeding season. We also may have observed this pattern of larger group sizes in March because there were considerably fewer fish schools, thereby concentrating birds at the available schools. A similar pattern has been documented previously in

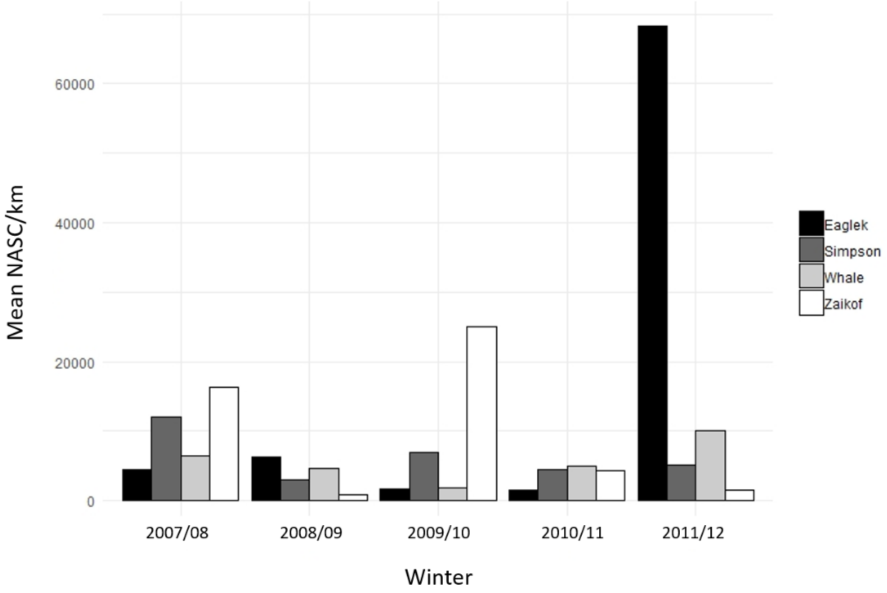

Figure 10. Mean nautical area scattering coefficient (NASC) per kilometer for surveyed bays across the five winter seasons of the study (November 2007 – March 2012). NASC is an index for fish biomass in the water column, Prince William Sound, Alaska.

this study area: murrelets in PWS during summer foraged in larger groups when prey was scarce, but as pairs or individuals when prey was more abundant (Kuletz 2005).

The reduction in fish school detections in March could be related to high overwinter mortality of juvenile fish. Juvenile herring fast during winter in response to low forage availability (Norcross et al. 2001). If individuals do not accumulate sufficient energy stores leading up to this period of fasting, their energy content declines to the point of starvation (Paul and Paul 1998). In fact, juvenile herring sampled over nine winters in PWS were near the minimum energy threshold capable of supporting life during late winter (Gorman et al. 2018). We recorded fewer schools during March in all bays except Eaglek, with Simpson and Zaikof bays demonstrating the greatest seasonal contrasts (Fig. 6). Similarly, Norcross et al. (2001) recorded high fish abundance and low overwinter survival in Simpson Bay. In that study fish sampled from Simpson Bay were smaller and had lower energy content than fish from other bays, indicating competition for food resources as the underlying driver of the observed high mortality. An energetics model developed to predict overwinter survival of age-0 herring also predicted the lowest survival rates for Zaikof and Simpson bays, compared to Whale and Eaglek (Patrick 2000).

Spatial and temporal variation of fish predators could also influence overwinter survival of juvenile herring. The primary piscine predators of herring in PWS are Pacific cod (*Gadus macrocephalus*), yellowfin sole (*Limanda aspera*), walleye pollock, great sculpin (*Myoxocephalus polyacanthocephalus*), and big skate (*Raja binoculata*) (Bishop and Powers 2013). In shallower areas, such as Simpson Bay, yellowfin sole target age-0 herring. In deeper regions, such as Whale Bay, cod, pollock, and skate forage on a wider size range of herring. Seasonal shifts in forage fish consumption by fish predators has also been documented, with herring comprising a larger portion of the cod diet in late compared to early winter (Bishop and Powers 2013).

Birds were more likely to be present and in greater numbers when fish schools were higher in the water column and bottom depths were shallower (Figs. 8i and 9). During November fish schools were mostly detected on or near the sea floor, while in March, schools were slightly off the bottom (Table 5). This is not surprising, given that our surveys occurred during daylight hours when diel-migrating forage fish reside deeper in the water column. Nevertheless, our results show that forage fish were selecting for shallow areas in bays despite the availability of deeper habitat (Fig. 11) and birds were then targeting schools occurring in these shallow areas. Foraging at schools in shallow water would limit the predator avoidance capabilities of fish, thereby increasing the accessibility of fish to marine birds.

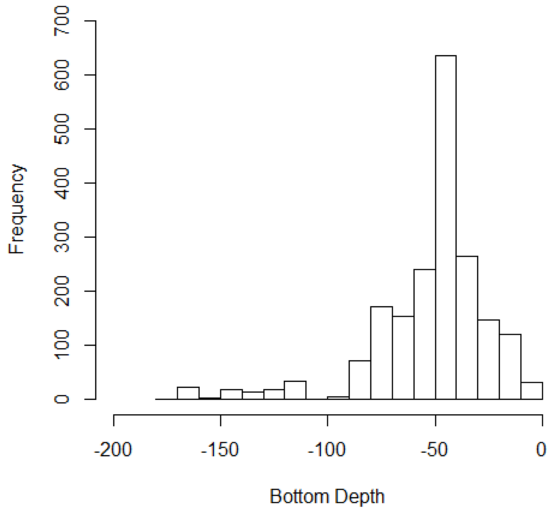

Figure 11. Frequency distribution of bottom depths at detected fish schools in Prince William Sound, Alaska, November and March 2007 – 2012 (n = 1947).

The minimum school depth represents the depth at which the fish school first becomes available to marine bird predators and has been an important factor explaining fish school selection by marine birds in previous studies (e.g., Hunt et al. 1999, Ostrand et al. 2004, Benoit-Bird et al. 2011). Targeting schools that are more easily accessible maximizes the potential energy return from the prey item by minimizing the energy expenditure by the predator. For example, during summer marbled murrelets in PWS selectively foraged at schools higher in the water column (Ostrand et al. 1998, 2004). Similarly, pollock in areas without foraging murres were 15 m deeper (but still within diving range) than pollock in areas with two or more diving murres (Benoit-Bird et al. 2011). In our study, marine birds were associated with schools that were 6 m (November) and 10.8 m (March) higher in the water column than schools without birds (Table 5). Zooplankton abundance reaches its nadir in January and February (Foy and Norcross 1999, McKinstry and Campbell 2018) when juvenile fish are in energetically poor condition due to prolonged winter fasting (Norcross et al. 2001, Gorman et al. 2018). Zooplankton abundance rises slightly in March (Foy and Norcross 1999, McKinstry and Campbell 2018) coincidental with increased feeding documented in an analysis of juvenile herring stomach contents (Norcross et al. 2000). Therefore, in late winter marine birds appear to take advantage of juvenile fish shifting their distribution in the water column in response to increased forage availability.

In March, marine birds foraged at schools that were farther offshore compared to schools without birds (Table 5). Throughout the winter, age-0 herring remain near the heads of bays, while age-1 herring move from inner to outer bay habitats (Lewandoski and Bishop 2018), likely to exploit a wider range of prey resources than is available in the inner bay (Norcross et al, 2001). During March, the marine bird community is dominated by common murre (70% of observations; Fig. 7) which tend to aggregate in the highest densities near historical spring spawning sites associated with adult herring overwintering habitat (Bishop, unpubl. data). Although marine bird diets are more varied in winter when prey is less plentiful (Ainley et al. 2002) murres tend to forage on herring 100 – 190 mm long when available (Ainley et al. 1996), corresponding to larger age-0 through age-4 herring (Lewandoski and Bishop 2018, Haught, Alaska Department of Fish and Game, unpubl. data). Therefore, we suggest murres were selectively targeting schools consisting of older, larger individuals located further from shore than younger herring schools.

We observed contrasting responses by divers and gulls to the number of fish schools in the bay, highlighting the differences in foraging strategies of the two groups. Diver abundance was negatively correlated with the number of schools in the bay (Fig. 9), while gulls demonstrated the opposite pattern. In fact, the number of schools in the bay was the only variable important in explaining gull abundance, indicating that limited survey coverage at the top of the water column may have affected our ability to fully evaluate the factors influencing gull abundance patterns. Nevertheless, diving birds may key into habitat cues consistently associated with prey instead of direct prey measures. For example, bottom depth and the amount of eel grass in the bay were both highly significant and positive in the most supported diver model (Fig. 9), which may have driven the associations of parameters with smaller effect sizes. Juvenile herring occur in higher densities in areas with eel grass habitat compared to kelp or rocky substrates (Johnson et al. 2010, Lewandoski and Bishop 2018). In addition to providing protection, eel grass beds are associated with areas of high productivity in PWS, thereby also providing increased forage resources for juvenile fish (Dean et al. 2000, Johnson et al. 2010).

Marine birds were more likely to be associated and more abundant at fish schools within smaller prey patches throughout the winter (Table 5, Fig. 8). Ostrand et al. (2004) reported similar results for marbled murrelets in PWS in summer. They concluded that murrelets were choosing less abundant but higher energy prey over more abundant but less energy dense prey regardless of other school characteristics, such as school size. This could explain the selection for smaller prey patches observed in our study. Although we do not have species-level data of the fish schools in this study, the results from other studies in this area suggest detected schools are likely either juvenile Pacific herring or walleye pollock (Stokesbury et al. 2000, Lewandoski and Bishop 2018, Rand 2018). The energetic content of juvenile herring is almost double that of juvenile walleye pollock (Foy and Norcross 1999, Van Pelt et al. 1997), therefore, birds could be preferentially targeting smaller patches of herring over larger patches of pollock.

Conclusions

In this study, we broadened our understanding of the spatial and temporal drivers of marine bird distribution in PWS during the nonbreeding season by using spatially explicit hurdle models including synoptic measures of prey. Marine birds foraged at shallower schools within smaller prey patches and in areas with shallower bottom depths and more eel grass habitat. We also observed seasonal patterns, with birds more likely to be found at schools and in greater numbers in March, an important period for both bird and forage fish survival. Further research efforts should explore overwinter survival of juvenile herring as climate conditions change and explore whether other forage fish species (such as pollock or capelin) can mediate variation in herring abundance for marine predators. Additional research should also incorporate community dynamics that have been found to influence predator-prey relationships in other systems, such as local enhancement and interactions with marine mammals (e.g., Anderwald et al. 2011, Fauchald 2009, Viet and Harrison 2017, Goyert et al. 2018). Further understanding of these relationships will facilitate the identification of critical areas and time periods for marine birds and their prey and may increase our insight of the status of the marine ecosystem.

Acknowledgements

We are grateful to Captain D. Janka and the crew of the *R/V Auklet*, to our observers K. Brenneman, N. Dawson, B. Hsu, R. Kaler, A. Lang, T. Morgan, and E. Owen, to P. Rand and A. Zenone for their assistance processing the hydroacoustic data, and J. Bernard and S. Williams for their input on data analyses. We also thank two anonymous reviewers for providing constructive comments that improved the manuscript. Funding for this research was provided by the *Exxon Valdez* Oil Spill Trustee Council, however the findings and conclusions of the authors are their own and do not necessarily reflect the views or position of the Trustee Council.

CHAPTER 3: DRIVERS OF MARINE BIRD DISTRIBUTION AND ABUNDANCE IN PELAGIC REGIONS OF PRINCE WILLIAM SOUND DURING THE POST-BREEDING PERIOD

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Introduction

Pacific herring (*Clupea pallasii*) has been identified as a resource injured by the 1989 *Exxon Valdez* oil spill in PWS. Concurrent with the decline in Pacific herring abundance, several marine birds wintering in PWS demonstrated a reduced capacity to recover post-oil spill, a phenomenon that may be related to decreased forage fish availability (Agler et al. 1999, Irons et al. 2000, Kuletz 2005). Further, the herring population in PWS has not recovered (*Exxon Valdez* Oil Spill Trustee Council 2014). In addition to disease and the lingering effects of oil contamination, the lack of herring recovery could also be due to predation pressure.

Despite the dynamic association between marine predators and forage fish, few studies have addressed these relationships outside of the breeding season (but see Fauchald et al. 2000, Suryan et al. 2006, Amélineau et al. 2018, Schaefer et al. 2020) and the potential for effects on population recovery. Therefore, the objectives of this study were to characterize the drivers of marine bird distribution in offshore humpback whale (*Megaptera novaeangliae*) foraging areas of PWS. Simultaneous surveys of predators and prey are important for understanding how predator communities respond to variation in prey availability and quality and to inform our understanding of top-down forcing on prey communities. We focused this study on the fall season (September) to provide a better understanding of predator-prey interactions at a crucial time when forage fish energy is maximized and while marine birds are provisioning for the upcoming winter.

Methods

Data collection

Marine bird surveys: We conducted marine bird surveys concurrent with hydroacoustic sampling (see below) annually during September 2017-2019, and 2021. Fixed transects were located in three pelagic sub-regions of PWS (Bainbridge Passage, Port Gravina, Montague Strait) that typically contain foraging aggregations of humpback whales and high densities of marine birds (Fig. 12) We also included data from a 2014 pilot study that was reduced in effort but overlapped spatially with the later surveys. Marine bird observations followed established USFWS protocols (USFWS 2007). One observer using 10x binoculars recorded the number, species, and behavior (flying, on water, foraging) of all marine birds occurring within a 300 m fixed-width strip (150 m both sides and ahead of vessel) into a laptop computer integrated with GPS using the programs Dlog (Ford 1999) and later SeaLog (ABR, Inc). These programs record location data at 15 s intervals as well as for every entered observation. Additionally, sea and weather conditions were tracked on site by the observer. For analysis, flying birds and non-marine birds were removed from the dataset.

Hydroacoustic surveys: We classified macrozooplankton and forage fish along diurnal acoustic transects following the methods outlined in Arimitsu et al. (2021). Briefly, acoustic surveys were conducted using Simrad EK60 (Kongsberg Maritime) echosounder with towed (2014, 2017-2018) or hull mounted (2019, 2021) split-beam transducers (38 and 120 kHz). The echosounder was calibrated each survey by suspending a 38.1 mm tungsten carbide sphere. Acoustic backscatter in the water column were classified in 10-m depth bins for depths between 4 m below the surface and 1 m above the bottom using frequency response methods for inshore waters (De Robertis and Ormseth 2018).

Fish were sampled opportunistically using midwater trawls and jigging to identify acoustic targets. Catches were sorted by species and age-group and measured (length, weight). We computed the acoustic macrozooplankton index as the nautical area scattering coefficient (NASC, m^2 nmi^{-2}) from the 120 kHz data for each 300 m interval of surveyed transect. Fish density per area (fish/m^2) was calculated from the 38 kHz for each 300 m interval and identified to the following species and age groups when possible: adult/juvenile Pacific herring, adult/juvenile walleye pollock (*Gadus chalcogrammus*), capelin (*Mallotus villosus*), or Pacific sand lance (*Ammodytes hexapterus*).

Analysis

We performed all spatial data extraction and interpolation using ArcMap 10.8.2 (ESRI 2021) and all statistical analyses using R version 4.2.2 (R Core Team 2022).

Fine-scale: To understand the fine-scale drivers of marine bird distribution and abundance we classified each 300 m interval of surveyed transect as either “bird-associated” (one or more birds) or “bird-absent” (no birds recorded within interval). Because these data were zero-inflated due to the irregular distribution of individuals, we used two-step hurdle models similar to the frameworks described in Chapter 1 and 2 of this report to model marine bird occupancy and abundance in relation to physical and prey (forage fish and euphausiids) characteristics. For a more thorough definition of the hurdle model framework and development, see Chapters 1 and 2 of this report, as well as Arab (2015) and Stocking et al. (2018). Briefly, in the first step of the model, the binomial distribution modeled the probability of observing zero birds within the interval, while the second step used the truncated Poisson distribution to estimate the intensity (the number of birds observed) within the interval given a non-zero observation.

We developed three model sets to describe marine bird distribution and abundance (Table 7). The first included physical habitat explanatory variables such as region (Bainbridge Passage, Port Gravina, Montague Strait), wave exposure (exposed, semi-exposed, semi-protected, protected), depth (m), distance to shore (m), and sea surface temperature (°C). The second model set included prey covariates, such as macrozooplankton biomass (m^2 nmi^{-2}) and mean fish density by species and by depth layers, and the minimum depth of prey availability (macrozooplankton or fish; m). This second set of models (n = 3) included one model for each depth layer. The third model set included macrozooplankton biomass (m^2 nmi^{-2}) and mean density of all fish (fish/m^2) by depth layers (0-60 m, 0-120 m, all depths) and the minimum depth of prey availability (macrozooplankton or fish; m). This model set also consisted of 3 models, including one model for each depth layer.

Table 7. Variables included in the fine-scale hurdle model analyses to explain variation in marine bird distribution and abundance in three pelagic regions of Prince William Sound.

Explanatory Variable	Model Set 1	Model Set 2	Model Set 3
Bathymetry	X		
Distance to land	X		
SST	X		
Exposure	X		
Region	X		
MZ[1] (60, 120, All)		X	X
Fish (60, 120, All)			X
AH[2] (60, 120, All)		X	
JH[3] (60, 120, All)		X	
AP[4] (60, 120, All)		X	
JP[5] (60, 120, All)		X	
CAP[6] (60, 120, All)		X	
SL[7] (60, 120, All)		X	
Min Prey depth		X	X

[1] Macrozooplankton
[2] Adult herring
[3] Juvenile herring
[4] Adult pollock
[5] Juvenile pollock
[6] Capelin
[7] Sand lance

We standardized all continuous variables to improve model convergence and conducted exploratory data analyses to identify correlations among explanatory variables. We assigned non-informative prior distributions to unknown parameters and fit models using R-INLA (Lindgren and Rue 2015). We ran full models for each model set (*n* = 7 models: habitat model set (1), prey model set (6) [by species at each depth layer (3), total prey by depth layer (3)]) as well as a null model. Model support was determined based on the Widely Applicable Information Criterion (WAIC) (Watanabe 2010). We obtained posterior distributions for the variables included in the most supported model of each model set and examined statistical significance. Variables with 95% credible intervals not overlapping zero were deemed significant.

Broad-scale: To relate marine bird abundance to habitat and prey characteristics at a larger scale, we developed three linear model sets using observed counts of marine birds as the response variable against two habitat and five prey variables (Table 8). We aggregated all marine bird observations for each region (Bainbridge Passage, Port Gravina, Montague Strait) and survey year (2014, 2017-2019, 2021) and standardized the counts by survey effort (birds/km).

Table 8. Variables included in the model sets to explain broad-scale variation in marine bird density in three regions of Prince William Sound. A third model set was developed based on the most supported parameters determined from the model sets below.

Explanatory Variable	Model Set 1	Model Set 2
Mean Bathymetry	X	
SST	X	
MZ[1] (60, 120)		X
AH[2] (60, 120)		X
JH[3] (60, 120)		X
AP[4] (60, 120)		X
JP[5] (60, 120)		X

[1] Macrozooplankton
[2] Adult herring
[3] Juvenile herring
[4] Adult pollock
[5] Juvenile pollock

The first model set consisted of habitat characteristics only and included variables for mean bottom depth and mean SST for each region. The second model set consisted of prey biomass indices by species in the upper 60 m and 120 m of the water column for each region. Variables included mean density of adult and juvenile herring (AH60, AH120, JH60, JH120), adult and juvenile pollock (AP60, AP120, JP60, JP120), as well as macrozooplankton biomass in each depth strata corrected for survey effort (Mz60, Mz120). Capelin and sand lance were excluded from this analysis due to low sample sizes. Separate models were developed for each depth strata due to collinearity. The third model set was developed based on the most supported models and parameters from the habitat and prey model sets.

We standardized all continuous explanatory variables and log-transformed response variables to meet assumption of normality, which we verified using the Shapiro-Wilk normality test (Shapiro and Wilk 1965). We constructed full models and used backward variable selection for model development. Akaike's Information Criterion (Akaike 1973) corrected for small sample sizes (AICc; Hurvich and Tsai 1989) was used to direct model selection. Parameter estimates with 95% confidence intervals that did not overlap zero were considered significant.

Results and Discussion

Between 2014 and 2021, we conducted five concurrent marine bird and hydroacoustic forage fish and macrozooplankton surveys in areas of high marine bird density and persistent whale feeding activity during September. A pilot survey was conducted in 2014 in two regions of PWS (Bainbridge Passage, Montague Strait), followed by the full survey in three regions of PWS (Bainbridge Passage, Montague Strait, Port Gravina) in 2017-2019, and 2021 (Fig. 12). We surveyed 605 km of transects, resulting in 2036 300-m sampling intervals.

Fish densities were identified on 65% of the sampled intervals (*n* = 1,333). Adult pollock were observed on the highest number of intervals (56%), followed by juvenile pollock (7%), juvenile herring (4%), adult herring (4%), capelin (2%), and sand lance (0.1%). Fish density was highly variable among years and regions (Fig. 13). The highest and lowest observed densities were observed in Bainbridge Passage (2017 and 2018, respectively). Community composition also varied by region and year (Fig. 14). In Bainbridge Passage, the fish community seemed to be dominated by one species each survey year. Juvenile herring were the dominant species in 2014, followed by juvenile pollock in 2017. By 2018, the Bainbridge Passage community transitioned to adult pollock (2018-2019) and then to adult herring (2021). The Port Gravina forage fish community was more mixed. Juvenile herring was present in all years and was the dominant species in all years except 2017, when adult herring had the highest densities. The fish community in Montague Strait was also mixed but transitioned from a community dominated by juvenile pollock in the early years of the survey to a community dominated by adult herring in the later years of the survey.

Macrozooplankton biomass was broadly distributed along transects and was observed on 95% of all sampled segments. Macrozooplankton biomass was highest in 2014, and generally declined each subsequent survey year (Fig. 13).

We recorded 838 birds of 24 species during the surveys (Table 9). Kittiwakes were the most abundant species group observed (30.0%), followed by murres (21.0%) and shearwaters (16.5%). Marine birds were present on 12.9% of intervals (n = 262) and when present, the mean group size was 3 (±1 standard error, SE = 0.35) birds. Encounter rates were typically much lower in Bainbridge Passage compared to Port Gravina and Montague Strait (Fig. 13). From 2014-2019, encounter rates generally increased during each subsequent survey. However, in 2021, encounter rates in Montague Strait and Port Gravina decreased.

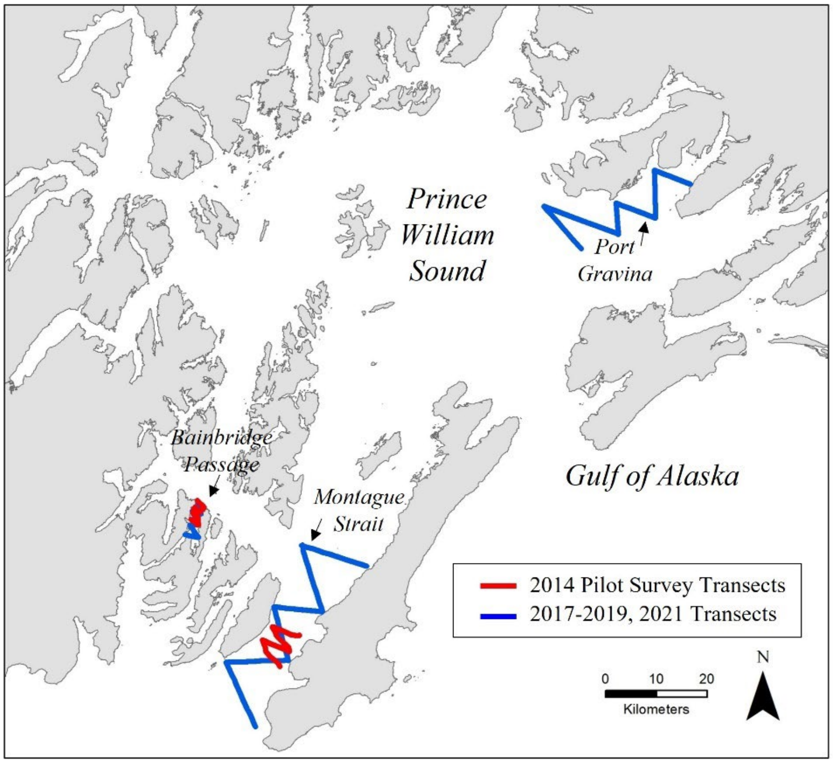
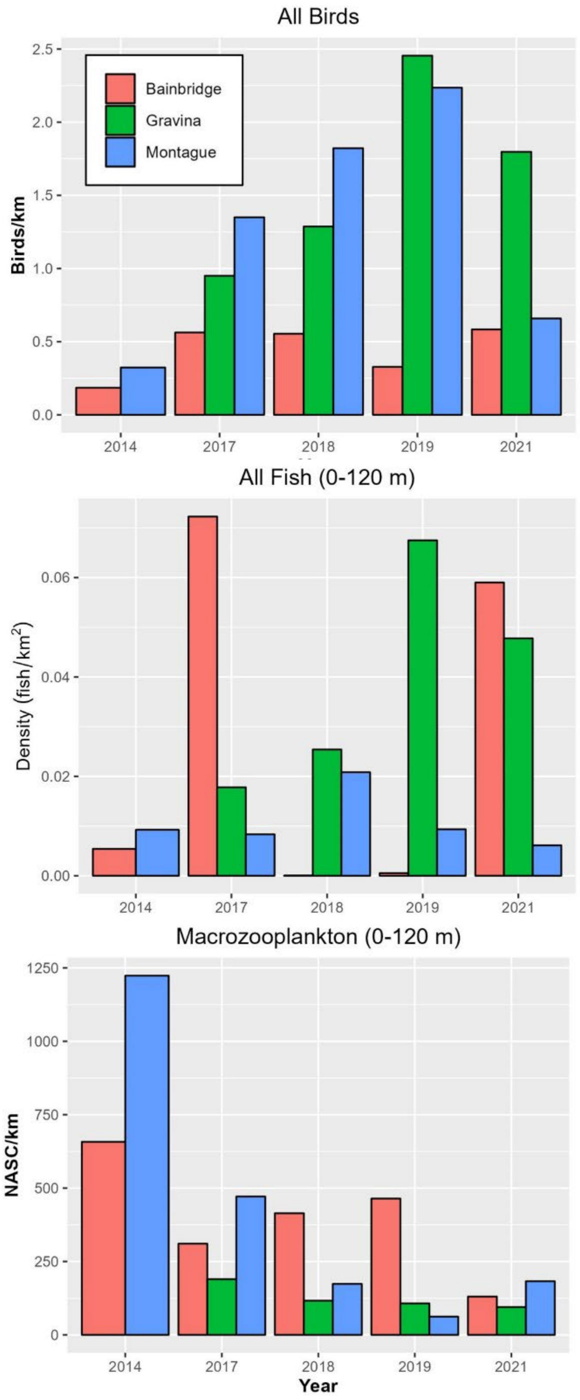


Figure 12. Concurrent marine bird and hydroacoustic surveys were conducted in September 2014 (red line), 2017-2019 and 2021 (blue line) in three regions of Prince William Sound, Alaska: Bainbridge Passage, Montague Strait, and Port Gravina.

Table 9. Species composition of the birds observed during at-sea surveys in Prince William Sound, Alaska, in September 2014, 2017-2019, and 2021.

Species Group	**Common Name**	**Scientific name**	**Percent of Species group**	**Percent of observed marine bird community**
Loons	Pacific loon	*Gavia pacifica*	3.0	3.9
	Unid. loon		97.0	
Grebes	Unidentified grebe	*Podiceps* spp.	100.0	0.1
Fulmars	Northern fulmar	*Fulmarus glacialis*	100.0	0.1
Shearwaters	Sooty shearwater	*Ardenna grisea*	45.7	16.5
	Short-tailed shearwater	*Puffinus tenuirostris*	0.7	

Species Group	**Common Name**	**Scientific name**	**Percent of Species group**	**Percent of observed marine bird community**
	Unid. shearwater		53.6	
Storm-petrels	Fork-tailed storm-petrel	*Oceanodromo furcata*	100.0	3.8
Cormorants	Pelagic cormorant	*Phalacrocorax pelagicus*	100.0	0.4
Scoters	Surf scoter	*Melanitta perspicillata*	33.3	0.7
	White-winged scoter	*Melanitta deglandi*	66.7	
Phalaropes	Red-necked phalarope	*Phalaropus lobatus*	11.8	6.1
	Unid. phalarope		88.2	
Larus gulls	Glaucous-winged gull	*Larus glaucescens*	2.3	5.1
	Herring gull	*Larus argentatus*	20.9	
	Short-billed gull	*Larus brachyrhynchus*	2.3	
	Unid. large gull		2.3	
	Unid. small gull		72.1	
Kittiwakes	Black-legged kittiwake	*Rissa tridactyla*	99.6	30.0
	Red-legged kittiwake	*Rissa brevirostris*	0.4	
Terns	Arctic tern	*Sterna paradisaea*	100.0	0.2
Jaegers	Parasitic jaeger	*Stercorarius parasiticus*	52.2	2.7
	Pomarine jaeger	*Stercorarius pomarinus*	39.1	
	Unidentified jaeger		8.7	
Murres	Common murre	*Uria aalge*	100.0	21.0
Murrelets	Marbled murrelet	*Brachyramphus marmoratus*	2.4	4.9
	Ancient murrelet	*Synthliboramphus antiquus*	4.9	
	Unidentified *Brachyramphus* murrelet		92.7	
Guillemots	Pigeon guillemot	*Cepphus columba*	100.0	1.6
Puffins	Horned puffin	*Fratercula corniculata*	91.7	2.9
	Tufted puffin	*Fratercula cirrhata*	8.3	



All Birds

All Fish (0-120 m)

Macrozooplankton (0-120 m)

Figure 13. Marine birds observed per kilometer, mean fish density in the upper 120 m of the water column, and macrozooplankton biomass (NASC) per kilometer in the upper 120 m of the water column during at-sea surveys in three regions of Prince William Sound, Alaska. September 2014, 2017-2019, and-2021.

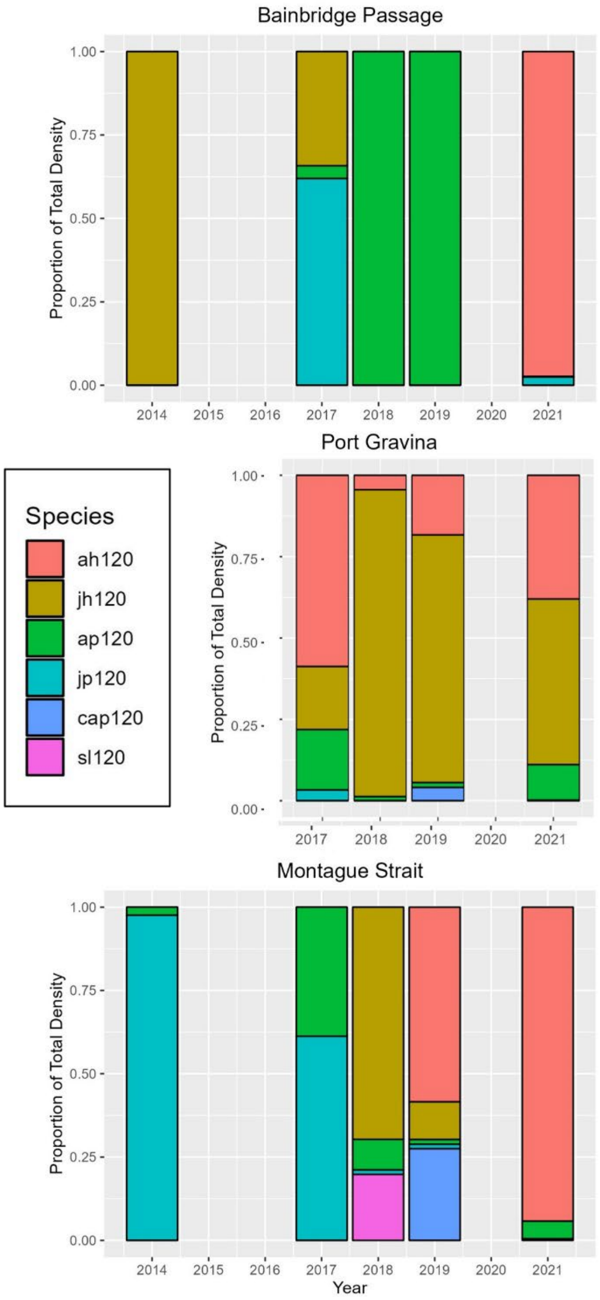


Figure 14. Summary of fish backscatter of each species classification in the upper 120 m of the water column by region and year for hydroacoustic surveys in Prince William Sound, Alaska, 2014-2021. Species were classified as: adult herring (ah), juvenile herring (jh), adult pollock (ap), juvenile pollock (jp), capelin (cap), and sand lance (sl).

Fine-scale analysis

The most supported model explaining fine-scale marine bird distribution and abundance was the habitat model (Table 10). Compared to the null model, the habitat model resulted in a 10.9-unit reduction in WAIC. Marine birds were more likely to be present in shallower water, closer to shore, and in semi-exposed, semi-protected, and protected habitats compared to exposed habitats (Fig. 15). Marine birds were more abundant with warmer sea surface temperatures (Fig. 15).

None of the prey models received more support than the null model (Table 10). The prey model with the lowest WAIC value was the model that included the variables for macrozooplankton at all depths, all fish across all depths, and minimum prey depth. This model resulted in a WAIC value 18.4 units higher than the null model and all covariates had credible intervals that overlapped zero.

Table 10. Model selection results for the hurdle model analysis to characterize marine bird presence and abundance in Prince William Sound, Alaska, September 2014-2021.

Model Terms	**ΔWAIC[1]**
Depth + Distance to land + SST[2] + Wave exposure + Region	0.00
(null)	10.92
Mz[3] (all depths) + All Fish (all depths) + Min. prey depth	29.30
Mz60 + All Fish 60+ Min. prey depth	40.63
Mz120 + All Fish 120 + Min. prey depth	55.46
Mz120 + AH[4]120 + JH[5]120 + AP[6]120 + JP[7]120 + CAP[8]120 + SL[9]120 + Min. prey depth	204.58
Mz (all depths) + AH (all depths) + JH (all depths) + AP (all depths) + JP (all depths) + CAP (all depths) + SL (all depths) + Min. prey depth	209.52
Mz60 + AH60 + JH60 + AP60 + JP60 + CAP60 + SL60 + Min. prey depth	290.63

[1] Widely Applicable Information Criterion
[2] Sea surface temperature
[3] Macrozoooplankton
[4] Adult herring
[5] Juvenile herring
[6] Adult pollock
[7] Juvenile pollock
[8] Capelin
[9] Sand lance

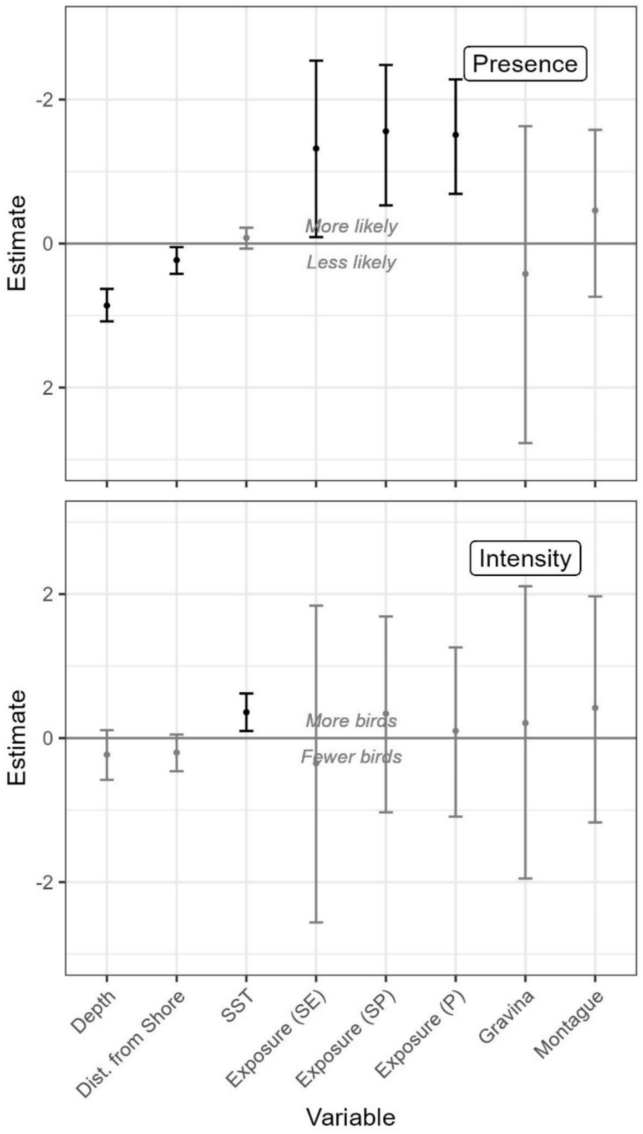


Figure 15. Estimates and 95% credible intervals for the coefficients of the variables for the binomial (Presence) and Poisson (Intensity) portions of the most supported model describing marine bird distributions in Prince William Sound, Alaska, during September 2014, 2017-2019, and 2021. Because the binomial portion of the model estimated the probability of absence rather than presence, we flipped the y-axis to aid interpretation of the estimates. Negative estimates, which correspond to an increased probability of presence, are on top. Gray variables are those whose credible intervals overlap with zero. Estimates are on the log odds and log scale for the binomial and Poisson portions of the model, respectively.

Broad-scale analysis

The most supported model explaining broad-scale marine bird abundance included the term for mean bottom depth (bathymetry; Table 11). Marine birds were more abundant in areas with shallower bottom depths on average (β=0.23, SE=0.08, *p*=0.01).

Table 11. Model selection results for the region level analysis to characterize marine bird abundance in pelagic areas of Prince William Sound, Alaska, September 2014-2021.

Model Terms	ΔAICc[1]
Bathymetry	0.00
Bathymetry + Mz[2]120	1.40
Bathymetry + Mz120 + AP[3]60	5.19
Bathymetry + Mz120 + AP60 + JH[4]120	11.22

[1] Akaike's Information Criterion corrected for small sample sizes
[2] Macrozooplankton
[3] Adult pollock
[4] Juvenile herring

Conclusions

In this study, physical variables rather than prey variables, better explained marine bird distribution and abundance in pelagic regions of PWS during September post-breeding season surveys. At the fine-scale, marine birds were more likely to be present in areas that were shallower, closer to shore, and more protected from wave action and were more abundant in warmer waters. Similarly, at the broader spatial scale, marine birds were more abundant in areas with shallower mean bottom depths. Previous studies in PWS have also found that habitat variables related to protection from winter storms better explained marine bird distribution than variables used as proxies for foraging (Dawson et al. 2015, Chapter 1 of this report). Taken together, these studies emphasize the importance of PWS as a refuge from the harsher conditions in the Gulf of Alaska during the nonbreeding season.

However, the lack of correlation with prey variables may indicate a mismatch in scales. While strong associations between marine birds have been documented at large spatial scales (tens of kilometers; Fauchald 2009, Fauchald et al. 2000), these relationships can break down at smaller scales. In this study, we examined marine bird and forage fish distributions concurrent in space and time at two spatial scales. Disruptions in the relationship between predators and prey could be caused by an incomplete knowledge of prey density and distribution by the predator or antipredator behaviors by the prey species (Logerwell and Hargreaves 1996, Hunt et al. 1999, Fauchald et al. 2000, Fauchald 2009, Hentati-Sundberg et al. 2018).

Interestingly, this study occurred at the onset (2014) and then immediately following (2017 onward) a Pacific marine heatwave event (Di Lorenzo and Mantua 2016). This marine heatwave was notable in both spatial extent and temporal persistence and led to disruptions at all levels of the PWS marine ecosystem. The forage fish community in PWS, which is typically buffered from environmental variability through variation in the life history strategies of each species, collapsed, resulting in reduced prey quality and quantity for predators (Arimitsu et al. 2021). The increasing marine bird encounter rates from 2017-2019 in these areas of PWS that are important humpback whale feeding locations may signal the beginning of ecosystem recovery following the heatwave. Further quantitative measures of predator density and distribution relative to prey availability during the fall season will inform our understanding of how predator communities respond to variation in prey quantity and quality and our understanding of top-down forcing on prey communities as the marine habitat continues to change and experience perturbations.

Acknowledgements

We are very grateful to our vessel captains D. Beam (*M/V Montague*), A. Schroeder and T. Jones (*R/V Island C*), and P. Tate (*R/V Alaskan Gyre*) and crews for their assistance with this work. Funding for this research was provided by the *Exxon Valdez* Oil Spill Trustee Council, however the findings and conclusions of the authors are their own and do not necessarily reflect the views or position of the Trustee Council.

CHAPTER 4: MULTI-SPECIES FORAGING DYNAMICS IN PRINCE WILLIAM SOUND DURING FALL AND WINTER

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Introduction

Multi-species feeding aggregations have been documented broadly across taxa and habitats and serve several functions, such as increased predator avoidance and increased foraging efficiency (Diamond 1981, Goodale et al. 2020). As upper trophic-level predators in the marine environment where foraging resources are ephemeral and patchily distributed, the foraging efficiency benefit is important to marine birds (Hoffman et al. 1981). Seabirds commonly gather into mixed-species forage flocks to feed on prey concentrations. The benefits of flock feeding include reduction in individual time spent searching for prey via local enhancement (Hoffman et al. 1981, Grünbaum and Veit 2003) and increased foraging efficiency through complementary interactions with other flock participants (Goodale et al. 2020). According to the *feeding efficiency theory*, complementary roles are those in which individuals take on qualitatively distinct functions due to different feeding strategies, thereby reducing interspecific competition and increasing access to the prey resource (Diamond 1981, Camphuysen and Webb 1999, Gosticha et al. 2021). For example, “catalyst” species (Hoffman et al. 1981) such as gulls and kittiwakes are highly visible and signal the presence of food resources to others by circling above and performing shallow surface dives onto prey. Diving seabirds, or “producers” (Hoffman et al. 1981) such as alcids and loons, access prey by pursuit diving underwater and driving prey upwards toward the surface. Working together, the contrasting capture techniques of catalysts and divers prolong contact with the prey, benefitting flock participants as long as capture rates remain high. Potential drawbacks of flock feeding are interference competition by “suppressors (e.g., large gulls and shearwaters) that behaviorally hinder the feeding of other flock members, and kleptoparasitism wherein “kleptoparasites” (e.g., jaegers, gulls) steal food from other members of the flock (Hoffman et al. 1981, Bayer 1983, Maniscalco et al. 2001).

Seabirds also form feeding aggregations with other taxa, including predatory fish such as tuna (e.g., Ashmole and Ashmole 1967, Hebshi et al. 2008), dolphins (e.g., Pitman and Ballance 1992, Camphuysen and Webb 1999, Clua and Grosvalet 2001), and whales (e.g., Obst and Hunt 1990, Anderwald et al. 2011, Gostischa et al. 2021). These inter-taxa associations are primarily commensal or mutual, with seabirds exploiting a temporary food source resulting from the subsurface predators also acting as “facilitators” by aggregating and trapping prey near the ocean surface (e.g., Obst and Hunt 1990, Pitman and Balance 1992, Degrati et al. 2014). Conversely, whales and other subsurface predators can take advantage of seabird feeding activity by using the visual and auditory cues associated with forage flocks to locate prey concentrations (e.g., Anderwald et al. 2011, Haynes et al. 2011). When prey resources are scarce or limited, this type of interaction can be disruptive to the flock or end the feeding event altogether (Haynes et al. 2011), resulting in interspecific competition and increased foraging costs for the avian participants.

Most studies documenting mixed-species and mixed-taxa feeding aggregations have occurred during the summer season, when resources are relatively abundant. During this period, breeding seabirds are central place foragers, constrained in their foraging habitat by the need to return to their nest or colony. In contrast, less research on the dynamics of feeding aggregation has been conducted during winter when marine birds are not tied to a specific location (but see Baltz and Morejohn 1977, Guillemette et al. 1993, Anguita and Simeone 2015). The nonbreeding season (September – April) represents the majority of the annual cycle and is the period in which marine birds face the greatest environmental and physiological pressures. Marine birds overwintering at higher latitudes experience colder temperatures, shorter days, and more extreme climate (Daunt et al. 2006) reducing opportunities for foraging at time when metabolic energy demands are increased (Fort et al. 2009).

In Prince William Sound (PWS), Alaska, a sub-arctic embayment on the Gulf of Alaska, forage flock dynamics have been characterized during the summer season and have focused exclusively on seabirds. Marbled murrelets (*Brachyramphus marmoratus*), the dominant summer species, were the main producers ("initiators") with larid species joining once murrelets began feeding (Ostrand 1999). However, seabird forage flock dynamics have not been examined in PWS during the nonbreeding season nor have flock interactions with other taxa, such as humpback whales (*Megaptera novaengliae*) been evaluated. PWS is a winter refugia for seabirds, providing protection from the harsher conditions of the Gulf of Alaska (Stocking et al. 2018) for ~40 species of marine birds (McKnight et al. 2008, Schaefer and Bishop 2016). Humpback whales also inhabit PWS during the fall and winter to feed on lipid-rich forage fish prior to migrating to their Hawaiian calving grounds (Rice et al. 2011, Moran et al. 2018, Straley et al. 2018). In addition to euphausiids, the main prey species in PWS for marine birds and humpback whales include Pacific herring (*Clupea pallasii*), Pacific sand lance (*Ammodytes personatus*), juvenile walleye pollock (*Gadus chalcogrammus*), and capelin *(Mallotus villosus*) (Rand 2018), though Pacific herring is the dominant prey species during winter (Stokesbury et al. 2000, Lewandoski and Bishop 2018, Rand 2018).

Understanding the functional relationships between marine birds and mammals during winter is important in light of limited direct knowledge of prey resources and changing marine ecosystem conditions. For this study, we sought to examine foraging dynamics of mixed-species feeding aggregations during the nonbreeding season in PWS. Our goals were to understand if humpback whales use marine bird foraging flocks as signals of available prey and vice versa, and to identify flock characteristics associated with whale presence at a flock.

Methods

Observations of marine birds and marine mammals were collected in PWS during the nonbreeding season (September – March) in conjunction with multiple projects, including the Alaska Department of Fish and Game spot shrimp survey (October), NOAA pollock surveys (December and March), Ocean Tracking Network maintenance cruises (February), Gulf Watch Alaska (GWA) monitoring ocean conditions in PWS project (November and March; principal investigator Campbell), and PWS Regional Citizens' Advisory Council tanker lane surveys (March). Additionally, we conducted an annual Integrated Predator Prey survey in September with the GWA forage fish project (PIs Arimitsu and Piatt) and humpback whale project (PIs Straley and Moran) with the specific goal of recording marine predators (marine birds and humpback whales) in the same space and time as their prey (forage fish and euphausiids).

Strip-transect surveys were conducted following established USFWS protocols (USFWS 2007). One observer recorded the number of birds or mammals occurring within a strip transect width of 300 m (150 m both sides and ahead of boat) into a laptop computer integrated with a GPS using the program dLOG (R.G. Ford Consulting) or SeaLog (ABR, Inc). All birds within the strip were counted continuously and their behavior recorded (on water, flying, foraging). Additionally, observers recorded any observations of note beyond the survey strip out to 1000 m, particularly those of marine mammals and forage flocks. Whales and forage flocks observed beyond the strip width were included in data summaries and analyses described below (see Statistical Analysis section). A forage flock was defined as an aggregation of >10 individuals of one or more species actively foraging or flying but showing a clear interest in the water surface by either circling or hovering (Anderwald et al. 2011). When a forage flock was encountered, the observer noted if there were any associated marine mammals. A marine mammal was considered associated with a seabird aggregation if it surfaced ≤150 m from the group. Following the methods outlined in Anderwald et al. (2011), the observer recorded the time and position of the encounter, species composition, and number of individuals in the feeding aggregation. When time and observation conditions allowed, the number of individuals of each species was counted. If there was insufficient time to approach the birds close enough for a direct count, only the presence of each species was recorded.

Focal follows of individual humpback whales were conducted opportunistically and primarily (although not exclusively) during Integrated Predator Prey surveys during September. During focal follows, the observer went off formal strip transect survey effort but recorded every encounter between focal humpback whales and feeding seabird aggregations using the methods described above. Surfacing behavior (e.g., traveling, loafing) and feeding events (e.g., surface lunging, diving) by whales associated with a forage flock were also recorded. However, only the subset of foraging events visible from the surface were detectable. While, each seabird group was counted only once, a single whale could be associated with more than one group of birds, although not simultaneously. Focal follow whales and flocks observed during focal follows were included in data summaries and analyses described below (see Statistical Analysis section).

Whale and forage flock observations were also collected opportunistically during research cruises when neither strip transect surveys or focal follows were occurring. These data have been incorporated into the data summaries and analyses described below (see Statistical Analysis section).

Covariate data

We evaluated the relative contribution of physical parameters and variables describing the composition of the forage flock on the variation of humpback whale presence or absence at the aggregation. Physical covariates included habitat type (bay, mouth of bay or passage, passage, open water), wave exposure of the nearest shoreline (exposed [E], semi-exposed [SE], semi-protected [SP], protected [P], very protected [VP]), depth (m), and distance from shore (m). Wave exposure values were obtained from the NOAA ShoreZone coastal inventory and mapping project (NOAA 2010). Bathymetry data were obtained from the Alaska Regional Digital Elevation Model v.2.0 (Danielson et al. 2015) bathymetry grid, modeled to a horizontal resolution of 1 km and distance to shore was calculated as the Euclidean distance to the nearest shoreline.

Based on their feeding strategies, marine birds observed in foraging groups were divided into six guilds following de Graaf et al. (1985) and Camphuysen and Webb (1999): pursuit divers, shallow plungers, surface seizers, aerial pursuers, benthic gleaners, and hawkers. The dominant guild was determined for each group and was defined as the foraging guild comprising >50% of the total number of individuals in the group. For each marine bird aggregation, we calculated the group size of each of the three main guilds (pursuit divers, shallow plungers, surface seizers).

Each flock was categorized following the classification system of Hoffman et al. (1981). Type I flocks are relatively small (often <50 individuals, up to 500 individuals), transient aggregations that form over fish schools or other clumped prey resources within 5 km of shore. Type II flocks are much larger (5,000-50,000 individuals) and longer lasting and form over less cohesive and less reactive concentrations of prey. Type III flocks form along current rips where zooplankton and small fish are concentrated by downwelling.

We originally intended to evaluate if there were certain whale characteristics, such as the number of humpback whales present and whale behavior (e.g., feeding, surface active, transiting), correlated with presence at a mixed-species aggregation. However, in all instances in which humpback whales were associated with a marine bird aggregation, there was always a single whale present, and the behavior category was always “feeding”.

Statistical Analysis

We fit generalized linear models with a Poisson error structure to test the relationship between the number of forage flock-whale interactions observed each survey (response variable) and the total number of humpback whales observed during each survey corrected for survey effort (km), the total number of forage flocks observed each survey corrected for survey effort (km), season, and fall/winter-year (e.g., 2017/18, 2018/19). Seasons were defined as fall (September, October), early winter (November, December), and late winter (February, March).

Following methods outlined in Anderwald et al. (2011), we developed three logistic regression model sets to assess the contribution of quantitative factors (including group sizes of each guild), qualitative factors (including presence/absence of each guild), and overall composition of the forage flock (total number of individuals, number of guilds, dominant guild) on variation in whale presence at the aggregation (Table 12). Forage flocks where species or foraging guilds could not be recorded due to large observation distances were excluded from the regression analyses.

We also built a fourth model set of to evaluate the importance of physical habitat variables on humpback whale presence or absence at a flock (Table 12). We developed a final model set based on the most supported terms from the preceding modeling exercises. In all models, the presence or absence of a humpback whale at the aggregation was the response variable. We square-root transformed the group-sizes of each guild to meet assumptions of Poisson-distributed residuals and standardized continuous variables (e.g., distance to land, depth) to z-scores. We used backward variable selection for model development, beginning with the full model of each model set and dropping non-significant terms until all remaining parameters were significant. Variables with 95% confidence intervals that did not overlap zero were considered significant. Akaike's Information Criterion (Akaike 1973) corrected for small sample sizes (AICc; Hurvich and Tsai 1989) was used to drive model selection and compare candidate models. The MuMIn package in R (Barton 2020) was used to conduct full model averaging and estimate weighted parameter estimates and likelihoods. Finally, we used Spearman's rank correlation to describe the relationships between the foraging guilds within the aggregations.

Table 12. Variables included in logistic regressions to explain variation in humpback whale presence at forage flocks.

Explanatory Variable	Model Set 1	Model Set 2	Model Set 3	Model Set 4
Group size of:				
Total flock			X	
Pursuit divers	X			
Shallow plungers	X			
Surface seizers	X			
Number of guilds	X	X	X	
Dominant guild	X		X	
Presence/absence of:				
Pursuit divers		X		

Explanatory Variable	**Model Set 1**	**Model Set 2**	**Model Set 3**	**Model Set 4**
Shallow plungers		X		
Surface seizers		X		
Habitat type				X
Wave exposure				X
Depth				X
Distance to shore				X

Results

We conducted 15 cruises over 5,221 km of survey effort from September 2017 – November 2021 (Table 13). During these surveys we observed 73 forage flocks, 12 of which were associated with humpback whales (16%; Fig. 17). Flocks and whales were distributed throughout the survey area, however, interactions between flocks and whales were primarily observed at the entrance of Port Gravina and in Montague Strait (Fig. 17).

Based on the classification system of Hoffman et al. (1981), all feeding groups observed during the study were Type I, meaning they were small, ephemeral flocks occurring over relatively dense aggregations of prey. The overwhelming majority of feeding aggregations were observed in September (n = 49, 67%), followed by November (n = 10, 14%) and March (n = 6, 8%) (Fig. 18).

Overall, flocks were dominated numerically by species representing the shallow-plunging (e.g., black-legged kittiwakes, *Rissa tridactyla*) guild, followed by the surface seizing (e.g., glaucous-winged gulls, *Larus glaucescens*), and pursuit diving (e.g., common murre, *Uria aalge*) guilds (Table 14). Although glaucous-winged gulls were more frequent flock participants, common murre were more abundant when present. We found no correlation between the numbers of pursuit divers with shallow plungers or surface seizers. However, there was a significant negative correlation between the number of shallow plungers and surface seizers (rho = -0.39, p = 0.001).

Twenty-three (31.5%) of the 73 observed aggregations consisted of a single species, usually black-legged kittiwake (n = 19). The other monospecific flocks were comprised of short-billed gull (*L. brachyrhynchus*, n = 3) and glaucous-winged gull (n = 1). The average group size was 48.8 individuals (range 10 – 265), and the mean number of avian species per aggregation was 2.4 (range 1 – 5).

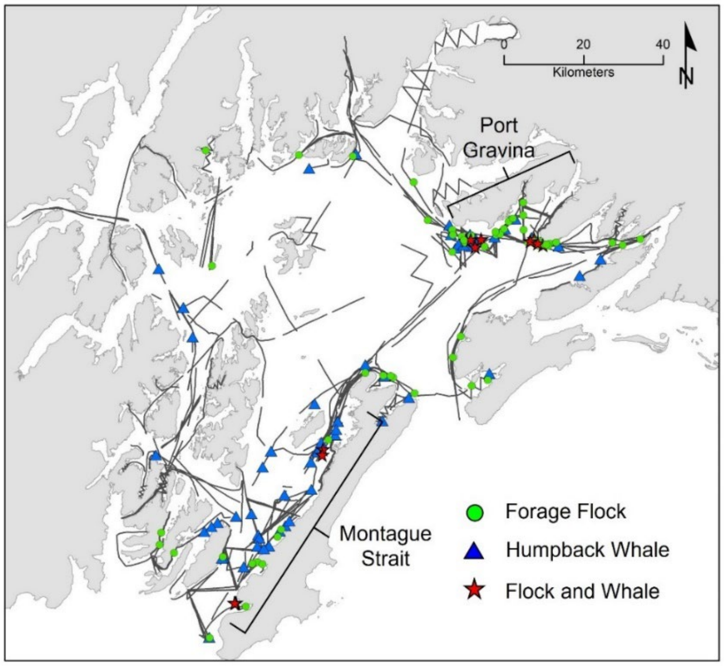

Figure 16. Location of forage flocks with whales (red stars), without whales (green circle), and humpback whales without forage flocks (blue triangles) observed on surveys in Prince William Sound, Alaska, September 2017 – March 2021. Transects surveyed are shown as black lines.

Table 13. Temporal allocation of marine bird and marine mammal survey effort in Prince William Sound, Alaska during the nonbreeding season, 2017-2021. Each survey is indicated with the number of kilometers of formal survey effort conducted, and months are grouped by fall/winter (e.g., 2017/2018: September 2017 – March 2018).

	2017/2018	**2018/2019**	**2019/2020**	**2020/2021**	**2021/2022**	**Total**
September	347	550	551		397	1845
October	334	277				611
November			328	323	308	959
December	81					81
January						0
February	301					301
March	320	306	305	493		1424

Table 14. Avian species recorded in forage flocks during surveys in Prince William Sound, Alaska, September 2017 – November 2021 in order of frequency of occurrence in flocks without whales. The number of aggregations in which species were observed is reported separately for flocks with (n = 61) and without (n = 12) whale interactions, as well as the mean group size (and ±1 standard deviation (SD)) when present.

Species	**Guild classification**	**Role(s) in mixed species group**	**Freq. of presence in flocks without whales (%)**	**Birds/flock (mean ± SD)**	**Freq. of presence in flocks with whales (%)**	**Birds/flock (mean ± SD)**
Black-legged kittiwake	Shallow plunging	Catalyst, Kleptoparasite	78.7	38.0 ± 42.3	75.0	54.4 ± 62.8
Glaucous-winged gull	Surface seizing	Catalyst, Suppressor, Kleptoparasite	39.3	8.5 ± 7.8	16.7	9.0 ± 9.9
Common murre	Pursuit diving	Producer	24.6	16.0 ± 21.3	25.0	12.3 ± 6.7
Pelagic cormorant	Pursuit diving	Producer, Suppressor	14.8	2.9 ± 2.9	16.7	3.0 ± 0
Pacific loon	Pursuit diving	Producer	11.5	6.0 ± 7.3	16.7	5.0 ± 1.4
Short-billed gull	Surface seizing	Catalyst	9.8	11.7 ± 8.4		
Marbled murrelet	Pursuit diving	Producer	8.2	2.8 ± 1.3	8.3	4.0 ± 0
Horned puffin	Pursuit diving	Producer	6.6	3.3 ± 1.5	16.7	8.0 ± 2.8
Unid. loon	Pursuit diving	Producer	4.9	5.0 ± 4.6		
Brachyramphus murrelet	Pursuit diving	Producer	4.9	4.3 ± 1.5		
Unid. Gull			3.3	40.0 ± 0	25.0	54.4 ± 62.8
Double-crested cormorant	Pursuit diving	Producer, Suppressor	3.3	1.5 ± 0.7	8.3	1.0 ± 0
Pigeon guillemot	Pursuit diving	Producer	3.28	1.5 ± 0.7		
Unid. large gull	Surface seizing	Catalyst, Suppressor, Kleptoparasite	1.6	30.0 ± 0		
Unid. cormorant	Pursuit diving	Producer, Suppressor	1.6	2.0 ± 0		
Herring gull	Surface seizing	Catalyst	1.6	1.0 ± 0		
Red-breasted merganser	Pursuit diving	Producer	1.6	2.0 ± 0		
Unid. grebe	Pursuit diving	Producer	1.6	4.0 ± 0		
Bald eagle	Hawker		1.6	2.0 ± 0	8.3	2.0 ± 0
Parasitic jaeger	Aerial pursuit	Kleptoparasite	1.6	2.0 ± 0		

Species	Guild classification	Role(s) in mixed species group	Freq. of presence in flocks without whales (%)	Birds/flock (mean ± SD)	Freq. of presence in flocks with whales (%)	Birds/flock (mean ± SD)
Unid. jaeger	Aerial pursuit	Kleptoparasite	1.6	3.0 ± 0		
Unid. shearwater	Shallow plunging	Catalyst, Suppressor	1.6	4.0 ± 0		
Surf Scoter	Benthic gleaning				8.3	3.0 ± 0
Unid. Bird			1.6	250.0 ± 0		

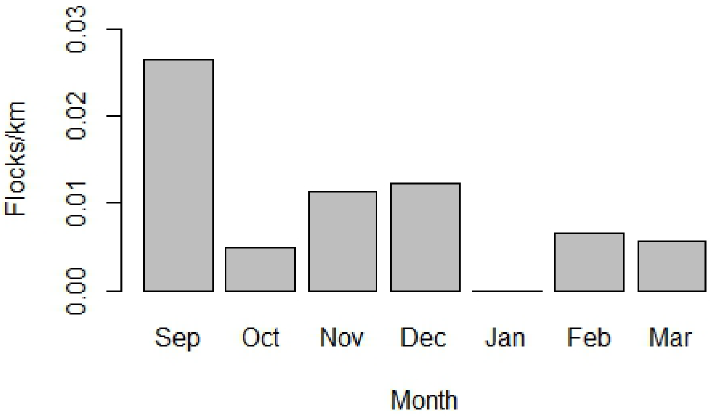

Figure 17. Temporal distribution of forage flocks (corrected for monthly effort) observed during September – March surveys in Prince William Sound, 2017 – 2021.

Comparison: characteristics of flocks without and with humpback whale interactions

Most forage flocks recorded during surveys (84%) were not associated with a humpback whale. Approximately 62% of these "non-whale flocks" were observed within the survey strip, while 38% were observed beyond the survey strip (Table 15). The mean group size was 46.3 birds (SD: 51.6, range: 10 - 225) representing on average 2.3 species (SD: 1.3, range: 1 – 5; Table 15). We recorded 16 species total as non-whale flock participants (Table 15). Black-legged kittiwakes were the dominant flock participants, followed by glaucous-winged gull, common murre, pelagic cormorant, and Pacific loon (Table 14).

Humpback whales were associated with 12 of the 73 observed flocks (16.4%). In all cases, a single whale was observed surface lunging through an already established flock, after which the flock dispersed. Of the 12 recorded flock interactions, 11 occurred in September during the Integrated Predator Prey Surveys. Two interactions were recorded during strip-transect surveys, three during focal follow whale surveys, and six interactions were observed opportunistically during surveys (neither during strip transect surveys or during focal follows). The only non-September interaction observed was recorded in December 2017 during a focal follow.

Forage flocks occurring with humpback whales averaged 61.8 birds (SD: 66.1, range: 25 – 265) and on average, consisted of 2.3 species (SD: 1.4, range: 1 – 5) (Table 15). In all, 10 species were recorded in flocks associated with humpback whales (Table 15). Similar to non-associated flocks, black-legged kittiwakes were the overwhelmingly dominant species recorded at forage flocks with whale interactions, followed by unidentified gulls and common murre (Table 14). Glaucous-winged gulls were more common when whales were not present (Table 14). Kittiwakes were observed at 75% of whale-associated flocks with an average of 54 birds (SD: 62.8) per flock. Unidentified gulls and common murres were recorded at 25% of flocks and when present, there were on average 51.7 (SD: 22.6) and 12.3 individuals (SD: 6.7), respectively. I

Humpback whale-forage flock dynamics

The number of forage flocks observed during each survey corrected for effort was the most important factor influencing the number of whale-flock interactions observed (Table 16). The probability of observing a whale-flock interaction increased with the number of forage flocks observed during a survey ($\beta = 80.12$, SE = 18.40, $p = <0.001$) (Fig. 19).

Six feeding aggregations were not included in the regression analyses to evaluate the influence of flock and habitat characteristics on whale presence because we were unable to record the species or number of participants in the flock due to distance. Of those, three included humpback whale-flock interactions. Thus, the final sample size for regression analyses was 67 forage flocks, including nine flocks associated with a humpback whale. Based on the 67 forage flocks, our final model set included covariates for the number of shallow plungers in the flock, the presence of surface seizers, depth, and distance to land.

All models (n = 3) were within 2 AIC units and received more support than the null model (Table 17), so we conducted full model averaging to estimate the weighted parameter estimates and likelihoods. Distance to land was the only term explaining whale presence at a flock with confidence intervals that did not overlap zero (Table 18). Humpback whales were more likely to be associated with forage flocks that were farther from shore. The mean distance from shore for foraging flocks with an associated whale was 2.72 (SD: 0.56) km, compared to 1.51 (SD: 0.16) km for flocks where no whales were present.

Table 15. Comparison of forage flocks with and without humpback whale associations in Prince William Sound, Alaska, 2017-2021.

	With Whales	**Without Whales**
Number of Flocks	12	61
Percent of Flocks within 300m Survey Strip	41.7%	62.3%
Mean (±1SD) Number of Birds/Flock	61.8 (66.1)	46.3 (51.6)
Mean (±1SD) Number of Species/Flock	2.3 (1.4)	2.3 (1.3)
Total Number of Species Observed	10	16

Table 16. Model selection results for the Poisson regression evaluating the factors influencing the number of whale-forage flock interactions observed during surveys in Prince William Sound, Alaska, 2017 – 2021.

Explanatory variable(s)	**Number of parameters**	**ΔAICc**	***w***
Number of flocks/km	2	0.00	0.74
Number of flocks/km + Number of whales/km	3	2.15	0.25
Season	3	8.34	0.01
(null)	1	15.26	0.00
Number of whales/km	2	15.55	0.00
Winter	5	26.65	0.00

AICc: Akaike's Information Criterion corrected for small sample sizes

w: Akaike weight

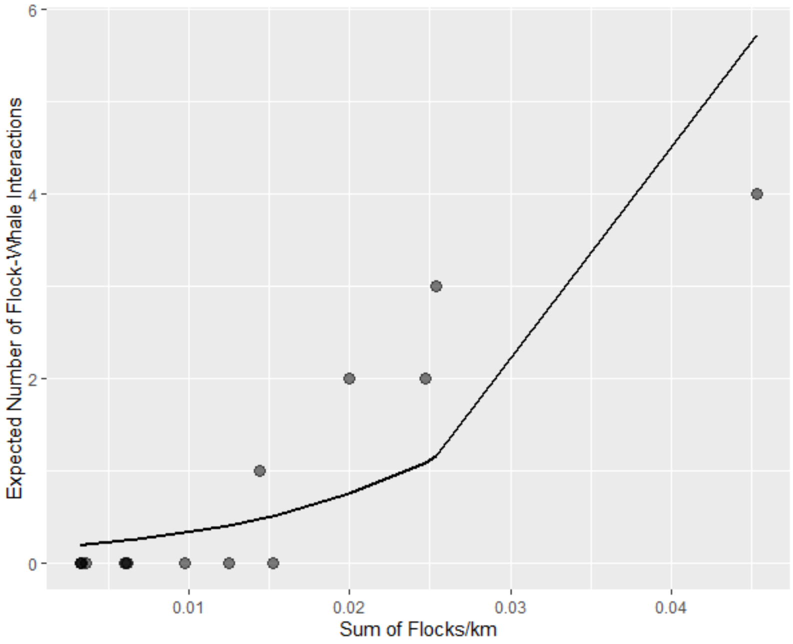

Figure 18. Based on regression results, the number of whale-forage flock interactions observed is expected to be higher when more forage flocks are observed during a survey. The graph displays the expected values (line) and the actual observed values (points).

Table 17. Model selection results for the final logistic regression model set testing the effects of forage flock and habitat characteristics on whale presence at a flock during surveys in Prince William Sound, Alaska, 2017 – 2021.

Explanatory variable(s)	**Number of parameters**	**ΔAICc**	***w***
Number of Species + Depth + DistLand	4	0.00	0.44
Depth + DistLand	3	0.63	0.32
Presence SS + Number of Species + Depth + DistLand	5	1.18	0.24
(null)	1	12.20	0.00

AICc: Akaike's Information Criterion corrected for small sample sizes
w: Akaike weight
SP: Shallow Plunger
DistLand: Distance to land
SS: Surface Seizer

Table 18. Parameter estimates, 95% confidence intervals (CI), and Parameter Likelihoods for candidate models explaining humpback whale presence or absence at a forage flock during surveys in Prince William Sound, Alaska, 2017 – 2021. Bolded values indicate coefficient estimates with confidence intervals that do not overlap zero.

Explanatory Variable	Estimate (CI)	Parameter Likelihood
Sum SP	0.18 (-0.04 – 0.58)	0.68
Presence SS	-0.26 (-3.21 – 1.04)	0.24
Depth	5.01 (-0.20 – 10.21)	1.00
DistLand	**1.22 (0.22 – 2.22)**	1.00

SP: Shallow Plunger

SS: Surface Seizer

DistLand: Distance to land

Discussion

Fall and winter flocks in Prince William Sound

All mixed-species feeding aggregations recorded during this study were relatively small aggregations that formed over a clumped and temporary food source, such as a school of fish. As has been documented previously in PWS during summer (Ostrand and Maniscalco 1997, Ostrand 1999), Type I forage flocks during fall and winter in PWS were smaller on average than those encountered in more oceanic areas (Hoffman et al. 1981).

During summer, when marbled murrelets are the most numerous species in PWS (McKnight et al. 2006), Ostrand (1999) found that marbled murrelets and black-legged kittiwakes were the most abundant flock participants. Marbled murrelets acted as the primary flock initiators by diving on sub-surface prey, concentrating it, and forcing it towards the surface within range of surface plunging kittiwakes. In our study in the fall and winter, the species composition of observed feeding aggregations was dominated by black-legged kittiwake and in contrast to summer, marbled murrelets were less common. Over two-thirds of all feeding aggregations recorded during this study were observed in September, which is when kittiwakes are the most abundant species encountered during at-sea surveys and murrelets are less plentiful (M. A. Bishop and A. Schaefer, unpublished data).

In contrast to Ostrand (1999), we found no evidence supporting a complementary association between pursuit divers and surface feeders (shallow plungers and surface seizers). Instead, our results revealed a negative relationship between shallow plungers (kittiwakes) and surface seizers (*Larus* spp.), suggesting the presence of passive interference competition. Unlike active interference competition (e.g., aggression, kleptoparasitism), passive interference competition occurs when one species obstructs the availability of a resource to another species using nonaggressive behavior (Charnov et al. 1976, Maurer 1984). Shallow plungers, such as glaucous-winged gulls, have been identified as flock suppressors (Camphuysen and Webb 1999) because they often sit on the water in the center of the flock and directly over the fish school. This behavior blocks access to the school for smaller gulls and kittiwakes or forces other flock participants to adjust their foraging behavior in response (Maniscalco and Ostrand 1997, Maniscalco et al. 2001, Haynes et al. 2011).

Associations of forage flocks with humpback whales

The number of interactions between humpback whales and forage flocks observed was positively associated with the total number of flocks observed during the survey. Humpback whales were also associated with feeding aggregations that were larger than aggregations without whales. Anderwald et al. (2011) recorded a similar positive relationship between probability of whale presence and flock size. A greater number of feeding birds may indicate the presence of a larger fish school or may create a larger auditory or visual signal into which the whales can cue. Although more flocks were present when whales were associated, there were fewer marine bird species present, likely because whale associations occurred farther from shore. Nearshore species, such as mergansers and grebes, were never observed foraging in aggregations associated with a humpback whale (Table 14).

Humpback whales acted as flock disrupters (Hoffman et al. 1981, Haynes et al. 2011, Goodale et al. 2020), rather than facilitators (Obst and Hunt 1990, Pitman and Balance 1992, Degrati et al. 2014) during fall and winter in PWS. In all cases of recorded observations, a whale surface lunged through an already established feeding aggregation, after which the aggregation would disperse. This behavior was also documented in southeast Alaska, with whales targeting prey that had been located and concentrated at the surface by birds (Haynes et al 2011). A single feeding event by a whale at a forage flock can reduce or completely eliminate prey availability to foraging birds. Additionally, the mouth-open surface lunge of a whale through the flock can disrupt flock configurations, and in some instances result in accidental ingestion of seabirds by whales (Haynes et al. 2011, J. Straley unpublished data, A. L. Schaefer, unpublished data). In our study, flocks typically did not re-form after a whale feeding event. However, in the single instance in which we did observe flock reformation, the whale also returned and consumed the prey.

The seasonal use of PWS by humpback whales is primarily driven by movement patterns of lipid-rich Pacific herring. Whale numbers are low in PWS during mid- and late-winter when most whales migrate to breeding grounds in Hawaii, increase in PWS in spring during herring spawn, decline during the summer as herring disperse out to the Gulf of Alaska, and peak in the fall and early winter as herring move back into PWS to overwinter (Moran and Straley 2018, Moran et al. 2018, Straley et al. 2018, Bishop and Bernard 2021). This peak in whale abundance in PWS corresponds to the time in which forage fish energy content is maximized, as both adult and juvenile herring accumulate energy stores throughout the summer and fall in preparation for over-winter fasting (Norcross et al. 2001). Almost all (11 of 12) observed whale-flock interactions occurred during this fall timeframe, when whales and marine birds are provisioning for the upcoming winter. While most humpback whales do undertake seasonal migrations, some proportion of the population remains in PWS throughout the winter (Straley et al. 2018). Currently whales do not appear to impact flocks during winter (only one interaction observed outside of September), however changes in the rate of winter residency of humpback whales in PWS could have implications for foraging dynamics of marine birds.

Interestingly, this study occurred immediately following the dissipation the Pacific Marine Heatwave of 2014-2015 (Di Lorenzo and Mantua 2016), which caused disruptions at all levels of the PWS marine ecosystem. The forage fish community, usually buffered from environmental variability by differences in life history strategies, collapsed, with fewer prey that were smaller and lower quality (Arimitsu et al. 2021). Small, scattered, fast-moving schools replaced the large overwintering shoals of herring on which humpback whales typically feed (Moran and Straley 2018). Coinciding with the disruption to the prey base, a key pursuit-diving marine bird predator in PWS, the common murre, experienced widespread mass mortalities, breeding colony failures, and distribution shifts (Piatt et al. 2020), and murre densities in PWS during fall and winter remain below the long-term average (Bishop 2021). Prior to the heatwave, humpback whale populations in the North Pacific and in PWS, specifically, had recovered to pre-whaling levels (Calambokidis et al. 2008, Teerlink et al. 2015). A study conducted in the mid-2000s estimated that ~64-134 humpback whales were present in PWS during fall and early winter, with <10 whales remaining from January through March (Rice 2011). During the heatwave event, whale numbers in PWS began to decline (Moran and Straley 2018) and have not recovered (Suryan et al. 2021, Moran and Straley 2021). Only seven individuals were counted during the recent September 2020 survey (Moran and Straley 2021). Continued exploration of multi-species feeding associations as the ecosystem recovers may provide insight into how upper trophic level species and their prey recover from the impacts of the heatwave and how upper trophic level foraging dynamics may alter as the marine climate continues to shift and heatwaves increase in frequency and intensity.

Limitations

The 73 recorded feeding aggregations included those observed beyond the 300 m survey strip and observations recorded while off survey strip-transect survey effort (e.g., during focal follows or opportunistic observations). Because these observations include distant feeding groups, there was likely bias towards high visibility species such as gulls, and against less visible species such as alcids. Therefore, in the current study we may have underestimated the role of pursuit divers, as has been documented elsewhere (e.g., Ostrand 1999, Anderwald et al. 2011, Haynes et al. 2011).

Almost all (11 of 12) whale-flock interactions were observed during September. However, the lack of observations during the rest of the winter may not reflect an absence of whale-flock interactions but instead reveal limitations in the sampling design. The surveys conducted in September were a collaboration between the forage fish (PIs Arimitsu and Piatt, project

21120114-C), humpback whale (PIs Moran and Straley, project 21120114-O), and fall and winter seabird (PI Bishop, this project) projects. These surveys were designed to sample in historical whale hotspots and included dedicated time to conduct focal follows of individual whales and other opportunistic surveying (neither strip transect surveys or focal follows). Consequently, 9 of the 11 interactions observed during the September surveys were either during focal follows (n = 3) or opportunistic off-effort observations (n = 6). Moreover, the only interaction observed outside of September occurred during a focal follow conducted during the December 2017 survey. These results emphasize the importance of dedicated surveys focused on forage flock and humpback whale interactions.

Conclusions

Continued research is necessary to understand the role of multi-species feeding aggregations and the functional relationships within those aggregations in PWS during the nonbreeding season, particularly in light of changing ocean conditions. In the current study, when whale, seabird, and forage fish abundances were suppressed following a heatwave event, we observed humpback whales using forage flocks of seabirds as cues to locate scattered prey resources. As the ecosystem recovers and predator and prey populations begin to rebound, questions remain as to the level of plasticity of the functional roles documented in this study. If functional roles shift in response to changes in the prey base, upper trophic-level foraging dynamics could be used as in indicator of the productivity of the marine ecosystem.

Acknowledgments

We are thankful to our survey collaborators M. Arimitsu and J. Piatt (U. S. Geological Survey), J. Moran (National Oceanic and Atmospheric Administration), and J. Straley (University of Alaska Sitka). We are also grateful to our vessel captains R. Campbell (*R/V New Wave*), P. Tate (*R/V Alaskan Gyre*), A. Schroeder and T. Jones (*R/V Island C*), D. Anderson (*R/V Solstice*), and D. Beam (*M/V Montague*) and crews for their assistance. Funding for this research was provided by the *Exxon Valdez* Oil Spill Trustee Council, however the findings and conclusions of the authors are their own and do not necessarily reflect the views or position of the Trustee Council.

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APPENDIX A: MARINE BIRD RESPONSE TO FORAGE FISH DURING WINTER IN SUBARCTIC BAYS

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Received: 27 November 2019 | Revised: 6 March 2020 | Accepted: 9 March 2020
DOI: 10.1111/fog.12472

ORIGINAL ARTICLE

Marine bird response to forage fish during winter in subarctic bays

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Funding information
Exxon Valdez Oil Spill Trustee Council

Abstract

Despite the importance of understanding marine bird response to prey fish, few studies have examined this relationship during winter. Over a 5-year period, we conducted synoptic marine bird and hydroacoustic forage fish surveys during early (November) and late (March) winter to characterize the factors influencing marine bird and forage fish dynamics at two spatial scales (fish school and bay) within subarctic bays of coastal Alaska, USA. Over 40% of observed marine birds were associated with a fish school (within 150 m of a fish school), although only 20% of fish schools were associated with birds. Seasonally, we recorded significantly more schools during early winter. The marine bird community also shifted from being comprised primarily of marbled murrelets (*Brachyramphus marmoratus*) and large gulls (*Larus* spp.) in early winter to common murres (*Uria aalge*) in late winter. At the school level, marine birds were more likely to be associated with shallow fish schools within 500 m of shore and in smaller prey patches. At the bay level, gull abundance was positively associated with the total number of fish schools recorded, while diving birds were more abundant when fish schools were higher in the water column, in shallower bottom depths, and in areas with more eel grass habitat. Our results indicate the importance of temporal, habitat, and fish school variables as drivers of marine bird presence and abundance, underscoring the complexity of predator–prey dynamics in the marine environment during winter.

KEYWORDS
Alaska, bays, forage fish, hydroacoustics, marine birds, piscivorous, predator–prey dynamics, Prince William Sound

1 | INTRODUCTION

Most free-living animals inhabit environments with patchily distributed resources (Johnson, Wiens, Milne, & Crist, 1992; Wiens, 1976). This is especially true for birds foraging in the marine environment, where prey is highly mobile, elusive, and dispersed. At-sea distribution of marine birds is driven by the distribution and availability of prey (Becker & Beissinger, 2003; Birkhead & Furness, 1985; Hunt et al., 1999), which is contingent on a range of factors, such as light and nutrient availability, sea and surface air temperature, sea level pressure, surface winds, water depth, and upwelling strength (Behrenfeld et al., 2006; Brown, Dijken, & Arrigo, 2011). Strong associations between forage fish and marine birds have been documented at broad spatial scales (10s of km; Fauchald, 2009; Fauchald, Erikstad, & Skarsfjord, 2000). However, at finer spatial scales (10s of m), these relationships tend to break down, possibly due to incomplete information on prey densities by the

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[†] Recently deceased.

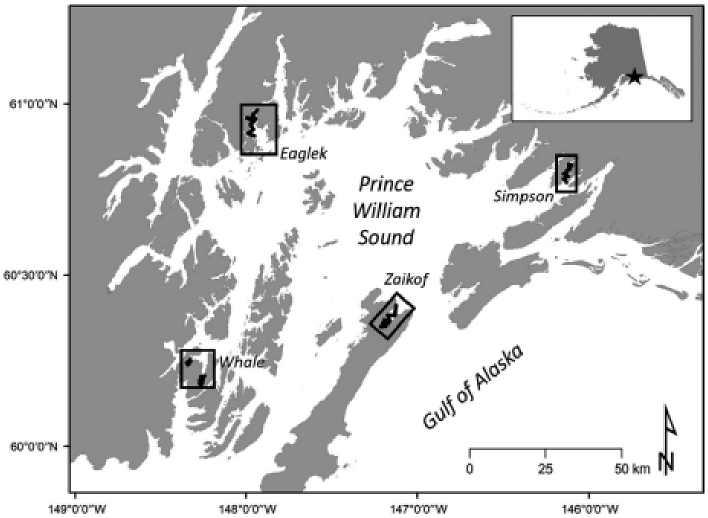


FIGURE 1 Location of fjords and bays surveyed for marine birds and fish schools in Prince William Sound, Alaska, November 2007–March 2012. Zigzag transects within bays are indicated by black lines

predator or antipredator behavior of prey (Fauchald, 2009; Fauchald et al., 2000; Hentati-Sundberg et al., 2018; Hunt et al., 1999; Logerwell & Hargreaves, 1996).

Most research on marine bird and fish dynamics has focused on the effect of prey availability and quality on the productivity or foraging behavior of birds during the breeding season (e.g., Hentati-Sundberg et al., 2018; Kuletz, 2005; Ostrand, Coyle, Drew, Maniscalco, & Irons, 1998; Piatt, 2002; Suryan et al., 2002) when birds must rely on prey resources and foraging locations within commuting distance of their nest. When prey is scarce or highly variable, the restricted foraging range of nesting birds can have cascading effects that impact foraging behavior, reproductive success, and abundance (Suryan et al., 2002).

Less emphasis has been placed on marine bird and forage fish dynamics during winter (although see Amélineau et al., 2018; Fauchald et al., 2000; Suryan et al., 2006) especially including measures of prey (Hunt et al., 1999). Understanding this relationship during winter is important because this is the time period during which marine birds face the greatest environmental and physiological pressures. Marine birds overwintering at higher latitudes experience colder temperatures, shorter days, and more extreme climate (Daunt, Afanasyev, Silk, & Wanless, 2006), limiting foraging activities at a time when metabolic energy demands are higher (Fort, Porter, & Grémillet, 2009). Additionally, for many animals, the non-breeding season is a time when breeding-capable individuals accumulate energy stores in preparation for future reproductive events (Sorensen, Hipfner, Kyser, & Norris, 2009). Poor conditions encountered during the winter may carry over into other parts of the year (Barbraud & Weimerskirch, 2003; Daunt et al., 2006; Sorensen et al., 2009); therefore, the association between marine birds and prey during winter may have important implications for subsequent survival and reproductive decisions.

In this study, we collected marine bird observations synoptic with hydroacoustic forage fish surveys to characterize the distribution and abundance of birds in relation to forage fish abundance and habitat characteristics in bays of Prince William Sound (PWS), Alaska, during early and late winter. Prior research identified spatial and temporal patterns of marine birds in PWS throughout the non-breeding season (Dawson, Bishop, Kuletz, & Zuur, 2015; Stocking, Bishop, & Arab, 2018), but recognized the lack of direct prey information as a gap. To address this, we first used a two-step approach to understand how fish school and habitat characteristics influence bird presence and abundance at individual fish schools. We then took a larger-scale approach and evaluated predator–prey relationships at the bay level.

2 | METHODS

2.1 | Study area

Prince William Sound is a subarctic sound located along the south central coast of Alaska (primarily between 60° and 61°N) comprised of more than 70 bays and fjords. PWS is separated from the Gulf of Alaska by large, mountainous barrier islands and provides access to extensive and protected ice-free habitat for wintering populations of at least 18 species of piscivorous marine birds (Bishop, Watson, Kuletz, & Morgan, 2015; McKnight, Sullivan, Irons, Stephensen, & Howlin, 2008). During winter, marine birds occur primarily in semi-protected and protected nearshore habitats, preferring shallower, warmer waters (Stocking et al., 2018). Our surveys occurred in two fjords (hereafter referred to bays: Eaglek and Whale Bays) and two bays (Simpson and Zaikof Bays) (Gay & Vaughan, 2001; Figure 1). The study bays vary in depth from 90 m (Simpson Bay) to 300 m (Whale

Bay) and basin area from 25.7 km^2 (Whale Bay) to 50.0 km^2 (Eaglek Bay).

The primary forage fish species in PWS include Pacific herring (*Clupea pallasii*), walleye pollock (*Gadus chalcogrammus*), and capelin (*Mallotus villosus*) (Rand, 2018), with Pacific herring the dominant species during winter (Lewandoski & Bishop, 2018; Rand, 2018; Stokesbury, Kirsch, Brown, Thomas, & Norcross, 2000). Adult herring overwinter in deep protected waters near their spring spawning grounds (Rand & Thorne, 2018; Thomas & Thorne, 2003; Thorne, 2010) and near entrances to the Gulf of Alaska (Bishop, PWS Science Center, unpubl. data), while juvenile herring prefer eelgrass beds and the shallow waters of fjords and bays (Lewandoski & Bishop, 2018; Norcross et al., 2001; Thorne, 2010).

2.2 | Data collection and preparation

2.2.1 | Hydroacoustic surveys

Hydroacoustic surveys followed the methods outlined in Thorne (2010) and consisted of systematic zigzag transects in each bay during daylight hours of November and March. We used a 120 kHz split-beam hydroacoustic transducer (Biosonics DT-X system) mounted to a hydrodynamic fin towed alongside the survey vessel 1 m below the surface. The maximum depth of acoustic data collection was 120 m. The 17 m charter vessel travelled ~3.5–4 knots during surveys and generally stayed ≃200 m from shore to avoid the shallow, rocky coastline.

Acoustic data were manually inspected and post-processed using ECHOVIEW 5.1 (Myriax Pty, Ltd.) following the methods outlined in Rand (2018). We applied a minimum analysis threshold for integration of −60.00 dB to remove very small targets (<2 cm). The bottom signal and upper 5 m of data were excluded from analysis to remove unwanted acoustic backscatter (e.g., benthic habitat, noise near the transducer). We used the school detection module of Sonardata Echoview (Coetzee, 2000) to identify discrete forage fish schools using the following minimum criteria: school length >2 m, school height >1 m, vertical linking distance <5 m, and horizontal linking distance <5 m. Linking distance refers to the maximum distance allowed between two school candidates being connected to form one school. In addition to identifying individual forage fish schools, we identified prey patches, or areas in which fish schools were spatially clumped. For this study, we defined prey patches as fish schools located within 30 m of one another.

2.2.2 | Marine bird surveys

Marine bird surveys were performed concurrently with and on the same vessel as the hydroacoustic surveys and followed established United States Fish and Wildlife Service (USFWS) protocols (USFWS, 2007). One observer using 10× binoculars recorded the number, species, and behavior of all marine birds occurring within a 300 m fixed-width strip (150 m both sides and ahead of boat) from a clear observation platform 2.5 m above the water line. Observations were recorded into a laptop computer integrated with a global positioning system (GPS) using the program dLOG (Ford, 1999). Location data (latitude, longitude) were automatically recorded at 20-s intervals and for every entered observation. For each survey, we subset our marine bird data to only include piscivorous species observed on the water or actively foraging.

2.3 | Statistical analyses

2.3.1 | School analysis

To understand the factors influencing marine bird presence and abundance at individual fish schools, we first tallied the total number of birds within 150 m of each ensonified fish school and classified each school as "bird-associated" (one or more birds) or "bird-absent." Because marine bird count data are often zero-inflated due to irregular distribution of individuals, we implemented two-step hurdle models for the analysis (Arab, 2015). The first step used the binomial distribution to model the probability of observing zero birds at the school, while the second step used a truncated Poisson distribution to estimate the probability of the observation value (the number of birds observed) given a non-zero observation. To account for spatial autocorrelation of observations, we included spatially correlated error terms based on the Matérn covariance function in all models. For a more complete definition of the hurdle model framework and development, see Arab (2015) and Stocking et al. (2018).

Explanatory variables included in the model set were selected based on previous research identifying spatial and temporal patterns of marine bird (Dawson et al., 2015; Stocking et al., 2018) and juvenile Pacific herring distributions (Lewandoski & Bishop, 2018) in PWS during winter. We related marine bird presence and abundance at fish schools to 2 temporal, 4 habitat, and 5 school variables. Temporal terms included month (November, March) and winter (five winters, 2007/08–2011/12). Habitat covariates included bay (categorical: Eaglek, Simpson, Whale, Zaikof), bottom depth (m), distance to shore (m), and distance to eel grass (*Zostera marina*) habitat (m). We obtained bottom depth from the Alaska Ocean Observing System (AOOS) bathymetry grid modeled to a horizontal resolution of 500 m (AOOS, 2010). Eel grass habitat data were obtained from the National Oceanic and Atmospheric Administration (NOAA) ShoreZone coastal inventory and mapping project (NOAA, 2010). Distance to shore was calculated as the Euclidean distance to the nearest shoreline and was included in the models as a quadratic term.

We obtained fish school variables from the Echoview school detection model output and included in the model set terms for the minimum school depth (m), school height (m), and the nautical area scattering coefficient (NASC). NASC provides an index of fish biomass in the water column but does not account for differences in species composition or fish size. We also included prey patch length

TABLE 1 Length of total survey effort (km) for each survey and fjord/bay of Prince William Sound, Alaska, November 2007–March 2012

	2007–2008		2008–2009		2009–2010		2010–2011		2011–2012		
Fjord/Bay	Nov	Mar	Nov	Mar	Nov	Mar	Nov	Mar	Nov	Mar	Total
Eaglek	17.8	17.8	16.5	15.4	14.2	16.1	18.7	18.1	19.2	18.8	172.6
Simpson	11.6	11.4	11.2	10.6	11.7	12.1	11.9	11.0	11.5	12.1	115.1
Whale	10.1	9.0	9.9	8.0	10.6	10.5	11.1	10.7	10.7	6.8	97.4
Zaikof	17.0	17.9	17.3	16.4	18.6	18.3	21.5	19.0	16.9	12.8	175.7
Total	56.5	56.1	54.9	50.4	55.1	57.0	63.2	58.8	58.3	50.5	560.9

(m) and the number of schools within each prey patch as model terms.

We standardized all continuous variables to improve model convergence and performed thorough exploratory data analysis to identify correlations among predictor variables. Due to high collinearity, we did not include distance to shore and distance to eel grass within the same models. We assigned non-informative prior distributions to unknown parameters and fit models using R-INLA (Lindgren & Rue, 2015). We used backward variable selection for model development, beginning with the full model and dropping non-significant terms until all remaining parameters were significant. The deviance information criterion (DIC) and principle of parsimony were used to drive model selection and compare candidate models. We obtained posterior distributions for all variables included in the top model and examined statistical significance. Variables with 95% credible intervals that did not overlap zero were deemed significant, while estimates with distributions spanning zero were non-significant. Full model selection results are available online in Table S1.

2.3.2 | Within bay analysis

To relate marine bird abundance to fish school characteristics and habitat variables within bays, we developed linear models using observed counts of marine birds as the response variable against 2 temporal, 2 habitat, and 4 fish school covariates. We aggregated marine bird observations into two foraging groups: diving birds (loon, cormorant, murre, and murrelet species) and gulls (all large and small gulls, and kittiwakes). We standardized bird counts by survey effort (birds/km surveyed) and developed separate model sets for each foraging group.

Temporal variables included in the models were month and winter. The habitat terms included were the total amount of eel grass habitat in the bay (linear m of shoreline) and the mean bottom depth of recorded fish school locations (m). Four fish school variables were included and standardized by km survey effort: mean minimum school depth (m), total number of fish schools, total number of prey patches, and fish biomass (NASC) in the bay summed over water depth bins to estimate the biomass available within the foraging ranges of the two marine bird foraging groups. For the gull model set, we summed NASC over the first 10 m of recorded water depth (NASC10), and for the diving bird model set, we summed NASC over the first 40 m (NASC40) and the first 60 m (NASC60).

We standardized all continuous explanatory variables and log-transformed response variables to meet assumptions of normality, which we verified using the Shapiro–Wilk normality test (Shapiro & Wilk, 1965). We did not include the terms for number of prey patches and number of schools or the terms for NASC40 and NASC60 within the same models due to high collinearity. We used backward variable selection for model development, beginning with the full model and dropping non-significant terms until all remaining terms were significant. We used Akaike's information criterion (Akaike, 1973) corrected for small sample sizes (AIC_C; Hurvich & Tsai, 1989) to direct model selection. Parameter estimates with 95% confidence intervals that did not overlap zero were considered significant. Full model selection results are available online in Tables S2 and S3.

We performed all spatial data extraction, interpolation, and summarization using ArcMap 10.6 (ESRI, 2018) and all statistical analyses using R version 3.5.3 (R Core Team, 2019).

3 | RESULTS

We completed 10 synoptic hydroacoustic and marine bird surveys over 5 years (2007–2012) during early (November) and late (March) winter, covering ~561 km total within the four surveyed bays (Table 1).

We detected 1,947 individual fish schools during surveys, of which 387 (20%) were associated with marine birds. More schools were detected during November (*n* = 1,430) compared with March (*n* = 517) (Table 2). The number of schools detected each winter was also variable (Figure 2a), ranging from 228 (winters 2008/09 and 2011/12) up to 668 (winter of 2007/08). Overall, 1,390 of the 1,947 schools (71%) were part of a prey patch. The mean number of schools per patch was 9.0 (±0.3 standard error [*SE*]; range 1–59), and mean patch length was 200.4 m (±5.0 *SE*; range 60.0–1,027.4). On average, Simpson Bay had the highest density of schools (6.8 schools/km), followed by Whale (3.8 schools/km), Zaikof (2.8 schools/km), and Eaglek (1.7 schools/km). There was a strong seasonal influence on the number of schools recorded in bays, particularly in Simpson and Zaikof (Figure 3).

TABLE 2 Mean and standard deviation (*SD*) values of habitat and fish school covariates for bird-absent and bird-associated fish schools by month, 2007–2012, Prince William Sound, AK

	Bird-absent fish schools		Bird-associated fish schools	
Variable	November *n* = 1,180	March *n* = 380	November *n* = 250	March *n* = 137
*Distance to land (m)	474.8 (288.4)	379.4 (221.9)	449.9 (254.5)	436.8 (225.5)
Distance to eel grass beds (m)	570.6 (418.7)	457.02 (303.80)	508.1 (314.6)	529.5 (288.5)
*Bottom depth (m)	53.3 (27.8)	57.1 (29.0)	42.1 (17.3)†	50.4 (26.1)
*Min. school depth (m)	50.5 (19.3)	50.5 (23.6)	44.5 (18.1)†	39.7 (23.0)
NASC	5,756.2 (75,939.3)	6,179.8 (43,298.1)	3,384.8 (14,476.4)	28,768.2 (303,563.6)
School height (m)	1.3 (1.5)	1.9 (2.0)	1.3 (1.3)	1.9 (2.1)
*Patch length (m)	243.6 (245.9)	120.0 (77.9)	185.4 (234.0)	78.3 (41.2)
No. schools/patch	11.4 (15.4)	4.8 (6.4)	7.7 (14.6)	2.0 (1.8)

Note: Variables marked with an asterisk (*) were significant in the binomial portion of the most supported hurdle model.

†Discrepancy between bottom depth and minimum school depth due to the differences in the resolution of the data sources. Minimum school depth was measured in situ by the echosounder. Bottom depth measurements were obtained from the Alaska Ocean Observing System bathymetry grid and were modeled to a horizontal resolution of 500 m.

We observed 3,156 birds over the five winters. Marine bird abundance varied by survey month (November *n* = 1,333, March *n* = 1,822) and winter (range = 282–937; Figure 2b). Overall, 44% of the birds observed (*n* = 1,382) were associated with at least one fish school. When birds were associated with a school, mean group size was 3.1 birds/school in November (range 1–42) and 4.5 birds/school (range 1–45) in March.

Altogether, common murres (*Uria aalge*) were the most abundant species group recorded during surveys (45% of observations), followed by marbled murrelets (*Brachyramphus marmoratus*; 15%) and large gulls (*Larus* spp.; 11%) (Table 3). However, a strong seasonal signal was reflected in the marine bird observations. In November, murrelets were the most commonly recorded species (25% of observations), followed by large gulls (21%) and murres (12%). In March, murres were the overwhelmingly dominant species group, accounting for 68% of all observations. This same pattern held when examining just the birds associated with fish schools. In November, large gulls (26%), murrelets (21%), and murres (13%) represented the top three recorded species groups, whereas in March, murres again dominated observations (70%) (Figure 4).

3.1 | School analysis

The probability of bird presence at fish schools was associated with intermediate distances from shore, shallower bottom depths, shallower fish schools, and smaller prey patches. Birds were also more likely to be present at fish schools in March. Inclusion and significance of the winter term in the top model indicates unexplained interannual variation (Figure 5a; Table 2).

For bird-associated fish schools, the model containing parameters for month, NASC, patch size, and number of schools in the prey patch best explained marine bird abundance at schools. The month term was the only significant parameter in the model; however, the credible intervals for NASC and patch size only slightly overlapped zero (Figure 5b). Marine birds were more abundant at fish schools in March and potentially correlated with greater NASC and smaller prey patches.

Because temporal covariates are not physical measures and are likely correlated with some of the habitat and fish school variables, post-analyses we removed these factors (winter, month) from all models to better understand the mechanisms directly affecting bird presence and abundance at schools. Comparing the best fitting models when the temporal variables were either included or dropped, the same terms were found to have significant effects in the models explaining bird presence at schools (distance to land, bottom depth, minimum school depth, and prey patch size). In contrast, in the models explaining bird abundance at schools, the variables distance to land, minimum depth, NASC, and patch size were all significantly related in the absence of temporal covariates. The presence of these terms in the temporal-exclusion model explaining bird abundance indicates potential support for these variables; however, the model including the temporal variables had a much better fit than models excluding those terms (as measured by DIC; ΔDIC = 60.18).

3.2 | Within bay analysis

Greater numbers of divers were associated with schools located in shallower bottom depths and higher in the water column and in bays with more eel grass habitat and fewer forage fish schools (Figure 6). Winter was also included in the final model, suggesting unexplained annual variation. For gulls, model selection results indicated that gull abundance was positively and significantly related to the number of fish schools in the bay ($\beta = 0.33$, $SE = 0.08$).

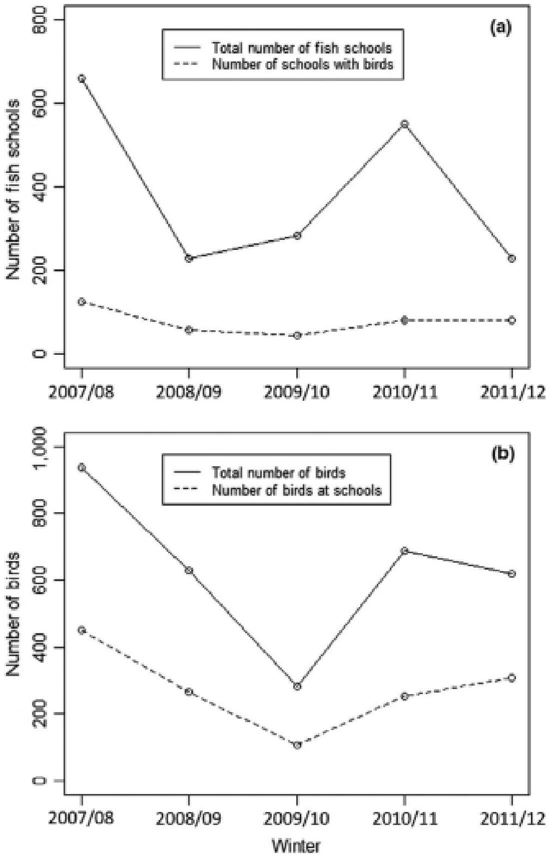


FIGURE 2 Total number of fish schools (a) and marine birds (b) observed during November and March surveys in Prince William Sound, Alaska, over five winters (2007/08–2011/12)

4 | DISCUSSION

Understanding predator–prey interactions is challenging, especially in the marine environment. Our results underscore this complexity, indicating support for seasonal, habitat, and fish school characteristics as drivers of marine bird presence and abundance at both the school level and bay level. Unlike most studies examining the relationship between marine bird predators and prey, our study occurred within juvenile herring and walleye pollock nursery bays, not open waters (e.g., Fauchald et al., 2000; Logerwell & Hargreaves, 1996), thereby likely increasing our ability to identify relationships at a finer scale.

W documented strong seasonal variation in the marine bird community composition and the number of fish schools, but weaker relationships with direct prey measurements, such as NASC, school height, and number of schools per prey patch or bay. The lack of strong correlations with prey measurements could be due to imperfect sampling. While the echosounder detected schools directly under the research vessel, marine birds were recorded out to 150 m on either side. Despite being within 150 m of a recorded school, birds may have been targeting off-transect schools not captured by the hydroacoustics. Furthermore, although there was slight evidence for the effect of NASC on marine bird abundance (Figure 5b), the NASC term was highly variable across space and time (range = 19–3,555,245; Table 2; Figure 7). The high variation in NASC combined with the reduced sample size of bird-associated schools in the Poisson portion of the model resulted in no clear signal.

Prior research in PWS supports the influence of seasonality on marine bird distribution and abundance during the non-breeding season. Dawson et al. (2015) and Stocking et al. (2018) identified consistent, large-scale seasonal shifts in the marine bird community across all habitat types, including in bays, passages, and exposed open waters. Our results from PWS bays corroborate these previous

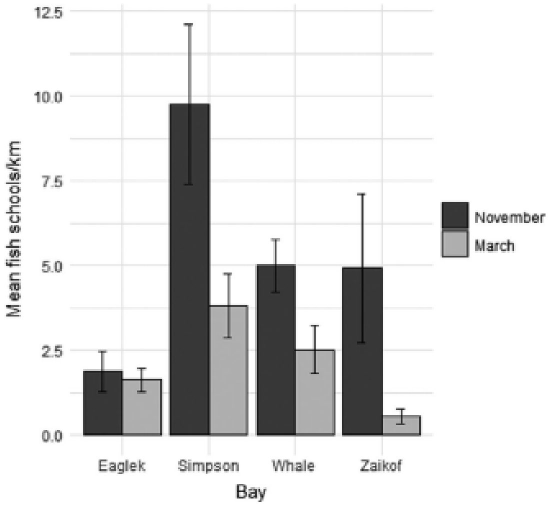
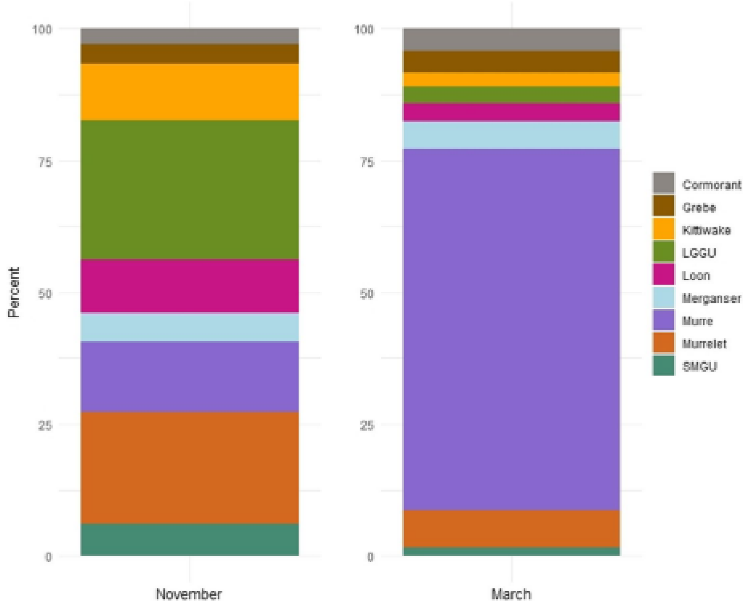


FIGURE 3 Mean number of fish schools/km ± *SE* of fish schools detected in each bay by month over five winter seasons, Prince William Sound, Alaska, November 2007–March 2012

TABLE 3 Piscivorous marine bird species groups recorded during marine bird surveys of Prince William Sound, Alaska, November 2007–March 2012. *n* = 3,156 total birds recorded; % = percent of *n*

Species group	Species included (common names)	%
Cormorants	Pelagic, Double-crested	4.2
Grebes	Red-necked, Horned	4.7
Kittiwakes	Black-legged	5.2
Large Gulls	Glaucous-winged, Herring	10.6
Small Gulls	Mew, Bonaparte's	3.9
Loons	Pacific, Common, Yellow-billed, Red-throated	5.8
Mergansers	Common, Red-breasted	6.0
Murres	Common	45.0
Murrelets	Marbled	14.6

FIGURE 4 Species composition (%) of marine birds associated with fish schools in Prince William Sound bays and fjords during early (November) and late (March) winter, 2007–2012. LGGU, large gull; SMGU, small gull



studies: marbled murrelets and large gulls (primarily glaucous-winged gulls, *Larus glaucescens*) were the most abundant species groups in our November surveys, while common murres overwhelmingly dominated the marine bird community in March (Figure 4). The observed changes in community composition across seasons reflect the different feeding and migratory strategies of each species. For example, after breeding murrelets move offshore to molt, however, ~25% remain in the protected waters of PWS through winter (McKnight et al., 2008; Nelson, 1997). Murrelets begin returning to breeding areas in March, with arrivals peaking in April (Nelson, 1997). Murres also move offshore after breeding to molt and overwinter, returning to nearshore areas in late winter, well before breeding (Ainley, Nettleship, Carter, & Storey, 2002).

Marine birds were more strongly associated with fish schools during March, when birds were more likely to be present and in greater numbers at schools. When birds were present, there were on average 1.4 more birds/school in March compared with November. Birds may be more tied to prey resources during this period because they are still enduring harsh winter conditions while also preparing for the upcoming breeding season. We also may have observed this pattern of larger group sizes in March because there were considerably fewer fish schools, thereby concentrating birds at the available schools. A similar pattern has been documented previously in this study area: Murrelets in PWS during summer foraged in larger groups when prey was scarce, but as pairs or individuals, when prey was more abundant (Kuletz, 2005).

The reduction in fish school detections in March could be related to high overwinter mortality of juvenile fish. Juvenile herring fast during winter in response to low forage availability (Norcross et al., 2001). If individuals do not accumulate sufficient energy stores leading up to this period of fasting, their energy content declines to the point of starvation (Paul & Paul, 1998). In fact, juvenile herring sampled over nine winters in PWS were near the minimum energy threshold capable of supporting life during late winter (Gorman et al., 2018). We recorded fewer schools during March in all bays except Eaglek, with Simpson and Zaikof bays demonstrating the greatest seasonal contrasts (Figure 3). Similarly, Norcross et al. (2001) recorded high fish abundance and low overwinter survival in Simpson Bay. In that study, fish sampled from Simpson Bay were smaller and had lower energy content than fish from other bays, indicating competition for food resources as the underlying driver of the observed high mortality. An energetics model developed to predict overwinter survival of age-0 herring also predicted the lowest survival rates for Zaikof and Simpson bays, compared with Whale and Eaglek (Patrick, 2000).

Spatial and temporal variation in fish predators could also influence overwinter survival of juvenile herring. The primary piscine predators of herring in PWS are Pacific cod (*Gadus macrocephalus*), yellowfin sole (*Limanda aspera*), walleye pollock, great sculpin (*Myoxocephalus polyacanthocephalus*), and big skate (*Raja binoculata*) (Bishop & Powers, 2013). In shallower areas, such as Simpson Bay, yellowfin sole target age-0 herring. In deeper regions, such as Whale Bay, cod, pollock, and skate forage on a wider size range of herring. Seasonal shifts in forage fish consumption by fish predators have also been documented, with herring comprising a larger portion of the cod diet in late compared with early winter (Bishop & Powers, 2013).

Birds were more likely to be present and in greater numbers when fish schools were higher in the water column and bottom depths were shallower (Figures 5a and 6). During November, fish schools were mostly detected on or near the sea floor, while in March, schools were slightly off the bottom (Table 2). This is not

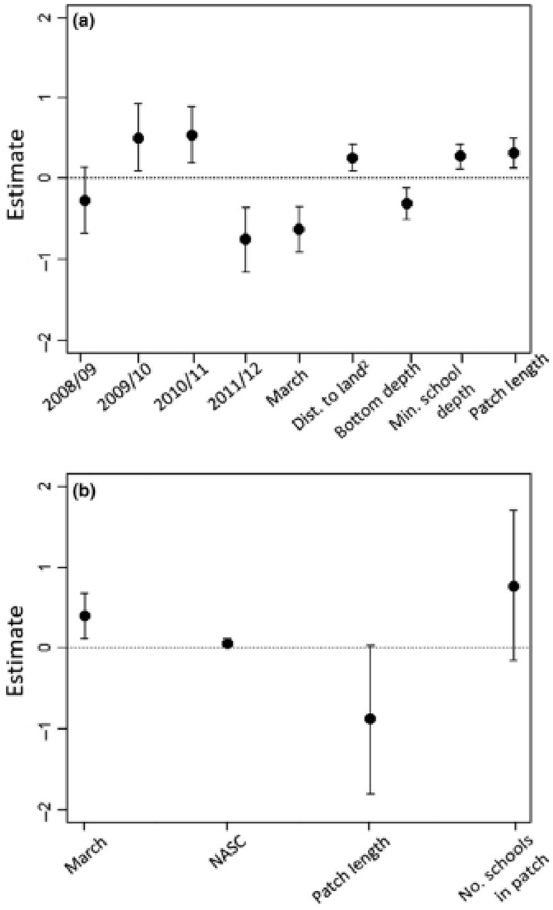


FIGURE 5 The effects of explanatory variables on presence (a) and abundance (b) of piscivorous marine birds at fish schools in Prince William Sound, Alaska, November 2007–March 2012. For Figure (a), the response variable estimates the probability of observing zero birds at the school, so a positive relationship indicates a decreased probability of bird presence. Error bars represent 95% credible intervals. NASC refers to the nautical area scattering coefficient and is an index of fish biomass in the water column

surprising, given that our surveys occurred during daylight hours when diel-migrating forage fish reside deeper in the water column. Nevertheless, our results show that forage fish were selecting for shallow areas in bays despite the availability of deeper habitat (Figure 8) and birds were then targeting schools occurring in these shallow areas. Foraging at schools in shallow water would limit the predator avoidance capabilities of fish, thereby increasing the accessibility of fish to marine birds.

The minimum school depth represents the depth at which the fish school first becomes available to marine bird predators and has been an important factor explaining fish school selection by marine birds in previous studies (e.g., Benoit-Bird, Kuletz, Heppell, Jones, & Hoover, 2011; Hunt et al., 1999; Ostrand, Howlin, & Gotthardt, 2004). Targeting schools that are more easily accessible maximizes the potential energy return from the prey item by minimizing the energy expenditure by the predator. For example, during summer, marbled murrelets in PWS selectively foraged at schools higher in the water column (Ostrand et al., 1998, 2004). Similarly, pollock in areas without foraging murres were 15 m deeper (but still within diving range) than pollock in areas with two or more diving murres (Benoit-Bird et al., 2011). In our study, marine birds were associated with schools that were 6 m (November) and 10.8 m (March) higher in the water column than schools without birds (Table 2). Zooplankton abundance reaches its nadir in January and February (Foy & Norcross, 1999; McKinstry & Campbell, 2018) when juvenile fish are in energetically poor condition due to prolonged winter fasting (Gorman et al., 2018; Norcross et al., 2001). Zooplankton abundance rises slightly in March (Foy & Norcross, 1999; McKinstry & Campbell, 2018) coincidental with increased feeding documented in an analysis of juvenile herring stomach contents (Norcross et al., 2001). Therefore, in late winter, marine birds appear to take advantage of juvenile fish shifting their distribution in the water column in response to increased forage availability.

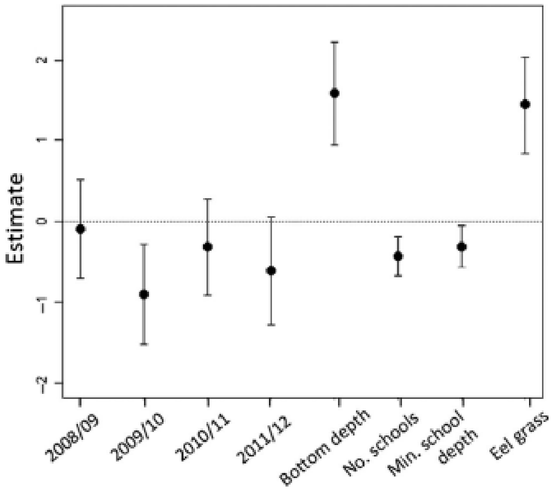
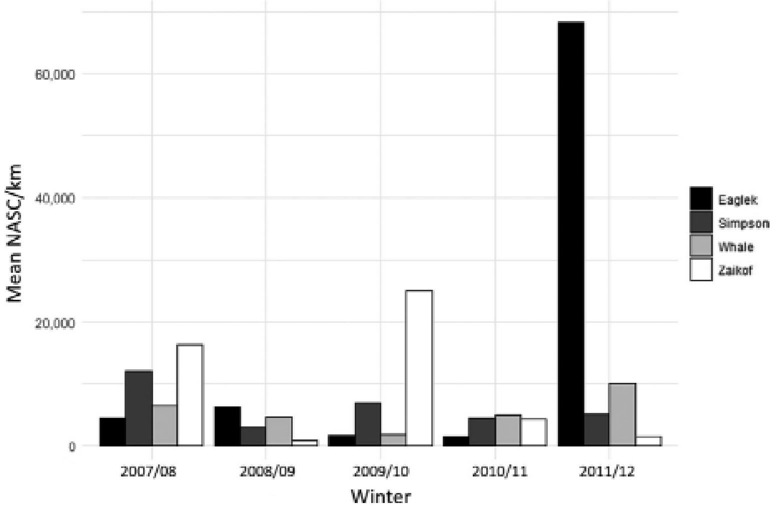


FIGURE 6 The effects of explanatory variables on abundance of diving marine birds in bays of Prince William Sound, Alaska, November 2007–March 2012. Error bars represent 95% confidence intervals

In March, marine birds foraged at schools that were farther offshore compared with schools without birds (Table 2). Throughout the winter, age-0 herring remain near the heads of bays, while age-1 herring move from inner to outer bay habitats (Lewandoski & Bishop, 2018), likely to exploit a wider range of prey resources than is available in the inner bay (Norcross et al., 2001). During March, the marine bird community is dominated by common murre (70% of observations; Figure 4) which tend to aggregate in the highest densities near historical spring spawning sites associated with adult herring overwintering habitat (Bishop, unpubl. data). Although marine bird diets are more varied in winter when prey is less plentiful

FIGURE 7 Mean nautical area scattering coefficient (NASC) per kilometer for surveyed bays across the five winter seasons of the study (November 2007–March 2012). NASC is an index for fish biomass in the water column. Prince William Sound, Alaska



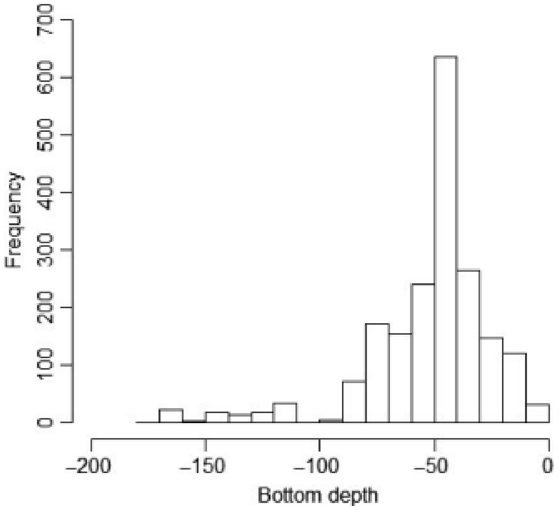


FIGURE 8 Frequency distribution of bottom depths at detected fish schools in Prince William Sound, Alaska, November and March 2007–2012 (*n* = 1,947)

(Ainley et al., 2002), murres tend to forage on herring 100–190 mm long when available (Ainley, Spear, Allen, & Ribic, 1996), corresponding to larger age-0 through age-4 herring (Lewandoski & Bishop, 2018; Haught, Alaska Department of Fish and Game, unpubl. data). Therefore, we suggest murres were selectively targeting schools consisting of older, larger individuals located further from shore than younger herring schools.

We observed contrasting responses by divers and gulls to the number of fish schools in the bay, highlighting the differences in foraging strategies of the two groups. Diver abundance was negatively correlated with the number of schools in the bay (Figure 6), while gulls demonstrated the opposite pattern. In fact, the number of schools in the bay was the only variable important in explaining gull abundance, indicating that limited survey coverage at the top of the water column may have affected our ability to fully evaluate the factors influencing gull abundance patterns. Nevertheless, diving birds may key into habitat cues consistently associated with prey instead of direct prey measures. For example, bottom depth and the amount of eel grass in the bay were both highly significant and positive in the most supported diver model (Figure 6), which may have driven the associations of parameters with smaller effect sizes. Juvenile herring occur in higher densities in areas with eel grass habitat compared with kelp or rocky substrates (Johnson et al., 2010; Lewandoski & Bishop, 2018). In addition to providing protection, eel grass beds are associated with areas of high productivity in PWS, thereby also providing increased forage resources for juvenile fish (Dean, Haldorson, Laur, Jewett, & Blanchard, 2000; Johnson et al., 2010).

Marine birds were more likely to be associated and more abundant at fish schools within smaller prey patches throughout the winter (Table 2, Figure 5). Ostrand et al. (2004) reported similar results for marbled murrelets in PWS in summer. They concluded that murrelets were choosing less abundant but higher energy prey over more abundant but less energy dense prey regardless of other school characteristics, such as school size. This could explain the selection for smaller prey patches observed in our study. Although we do not have species-level data of the fish schools in this study, the results from other studies in this area suggest detected schools are likely either juvenile Pacific herring or walleye pollock (Lewandoski & Bishop, 2018; Rand, 2018; Stokesbury et al., 2000). The energetic content of juvenile herring is almost double that of juvenile walleye pollock (Foy & Norcross, 1999; Van Pelt, Piatt, Lance, & Roby, 1997); therefore, birds could be preferentially targeting smaller patches of herring over larger patches of pollock.

5 | CONCLUSIONS

In this study, we broadened our understanding of the spatial and temporal drivers of marine bird distribution in PWS during the non-breeding season by using spatially explicit hurdle models including synoptic measures of prey. Marine birds foraged at shallower schools within smaller prey patches and in areas with shallower bottom depths and more eel grass habitat. We also observed seasonal patterns, with birds more likely to be found at schools and in greater numbers in March, an important period for both bird and forage fish survival. Further research efforts should explore overwinter survival of juvenile herring as climate conditions change and explore whether other forage fish species (such as pollock or capelin) can mediate variation in herring abundance for marine predators. Additional research should also incorporate community dynamics that have been found to influence predator–prey relationships in other systems, such as local enhancement and interactions with marine mammals (e.g., Anderwald, Evans, Gygax, & Hoelzel, 2011; Fauchald, 2009; Goyert et al., 2018; Viet & Harrison, 2017). Further understanding of these relationships will facilitate the identification of critical areas and time periods for marine birds and their prey and may increase our insight of the status of the marine ecosystem.

ACKNOWLEDGEMENTS

We are grateful to Captain D. Janka and the crew of the R/V Auklet, to our observers K. Brenneman, N. Dawson, B. Hsu, R. Kaler, A. Lang, T. Morgan, and E. Owen to P. Rand and A. Zenone for their assistance processing the hydroacoustic data, and J. Bernard and S. Williams for their input on data analyses. We also thank two anonymous reviewers for providing constructive comments that improved the manuscript. Funding for this research was provided by the Exxon Valdez Oil Spill Trustee Council; however, the findings and conclusions of the authors are their own and do not necessarily reflect the views or position of the Trustee Council.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare. This manuscript is the result of original research and has not been previously published by any other journal.

AUTHOR CONTRIBUTIONS

Anne Schaefer is the corresponding author and was responsible for data management and processing, statistical analysis, interpretation of data, and manuscript preparation. Mary Anne Bishop made substantial contributions to project development, design, and interpretation of data. She has also been involved in manuscript preparation and revision. Richard Thorne was integral to research design and development and data acquisition. Unfortunately, Richard passed away in an accident in October 2019 so he was unable to review a final draft of the manuscript. All authors (with the exception of Richard Thorne) approved the manuscript version to be published and have agreed to be accountable for all aspects of the work.

DATA AVAILABILITY STATEMENT

The data that support the findings from this study are available on request from the corresponding author.

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SUPPORTING INFORMATION

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

How to cite this article: Schaefer AL, Bishop MA, Thorne R. Marine bird response to forage fish during winter in subarctic bays. *Fish Oceanogr*. 2020;00:1–12. https://doi.org/10.1111/fog.12472

APPENDIX B: MARINE BIRD RESPONSE TO FORAGE FISH DURING WINTER IN SUBARCTIC BAYS SUPPLEMENTARY TABLES

Supplemental Table 1. Model selection results for the school-level hurdle models. DistLand: distance to land (m); MinDepth: minimum school depth (m); PatchSize: prey patch length (m); NumSchools: number of schools within prey patch; NASC: nautical area scattering coefficient; DistEelGrass: distance to eel grass (m).

Binomial Covariates	**Truncated Poisson Covariates**	**DIC**
Winter, Month, DistLand^2, Bathymetry, MinDepth, PatchSize	Month, NASC, PatchSize, NumSchools	3118.69
Winter, Month, DistLand^2, Bathymetry, MinDepth, PatchSize	Month, NASC, PatchSize,	3120.45
Winter, Month, Bay, DistLand^2, Bathymetry, MinDepth, NASC, PatchSize	Winter, Month, DistLand^2, Bathymetry, MinDepth, NASC, Height, PatchSize, NumSchools	3120.5
Winter, Month, DistLand^2, Bathymetry, MinDepth, PatchSize	Month, DistLand^2, MinDepth, NASC, PatchSize,	3121.55
Winter, Month, DistLand^2, Bathymetry, MinDepth, PatchSize	Month, DistLand^2, MinDepth, NASC, PatchSize, NumSchools	3121.6
Winter, Month, DistLand^2, Bathymetry, MinDepth, PatchSize	Month, DistLand^2, MinDepth, NASC	3121.95
Winter, Month, DistLand^2, Bathymetry, MinDepth, PatchSize	Month, MinDepth, NASC	3122.06
Winter, Month, Bay, DistLand^2, Bathymetry, MinDepth, PatchSize	Winter, Month, DistLand^2, MinDepth, NASC, PatchSize, NumSchools	3123.06
Winter, Month, Bay, DistLand^2, Bathymetry, MinDepth, NASC, Height, PatchSize	Winter, Month, DistLand^2, Bathymetry, MinDepth, NASC, Height, PatchSize, NumSchools	3123.67
Winter, Month, Bay, DistLand^2, Bathymetry, MinDepth, NASC, Height, PatchSize, NumSchools	Winter, Month, Bay, DistLand^2, Bathymetry, MinDepth, NASC, Height, PatchSize, NumSchools	3123.67

Binomial Covariates	**Truncated Poisson Covariates**	**DIC**
Winter, Month, DistLand^2, Bathymetry, MinDepth, PatchSize	DistLand^2, MinDepth, NASC, PatchSize	3123.69
Winter, Month, Bay, Bathymetry, MinDepth, NASC, PatchSize	Month, DistEelGrass, Bathymetry, MinDepth, NASC, PatchSize, NumSchools	3123.71
Winter, Month, DistLand^2, Bathymetry, MinDepth, PatchSize	Month, NASC	3127.11
Winter, Month, Bay, Bathymetry, MinDepth, PatchSize	Month, DistEelGrass, Bathymetry, NASC, PatchSize, NumSchools	3127.22
Winter, Month, Bay, Bathymetry, MinDepth, NASC, Height, PatchSize	Month, DistEelGrass, Bathymetry, MinDepth, NASC, Height, PatchSize, NumSchools	3129.85
Winter, Month, Bay, DistEelGrass, Bathymetry, MinDepth, NASC, Height, PatchSize	Winter, Month, DistEelGrass, Bathymetry, MinDepth, NASC, Height, PatchSize, NumSchools	3130.33
Winter, Month, Bay, DistEelGrass, Bathymetry, MinDepth, NASC, Height, PatchSize, NumSchools	Winter, Month, Bay, DistEelGrass, Bathymetry, MinDepth, NASC, Height, PatchSize, NumSchools	3134.99

Supplemental Table 2. Model Selection results for the influence of temporal, habitat, and fish school covariates at the bay-level on gull abundance (large and small gulls, kittiwakes). NumSchools = number of fish schools in bay; NumPatches: number of prey patches in bay; MinDepth: mean minimum fish school depth (m); EelGrass = amount of eel grass in bay (m); NASC10: nautical area scattering coefficient summed over the first 10 meters of recorded water column.

Explanatory Variables	**AIC$_C$**
NumSchools	59.61
Winter, Month, NumSchools	59.70
Winter, NumSchools	61.20
Winter, Month, NumSchools, MinDepth	61.27
Winter, Month, Bathymetry, NumSchools, MinDepth	64.73
Winter, Month, Bathymetry, NumSchools, MinDepth, EelGrass	68.22
Winter, Month, Bathymetry, NumPatches, MinDepth, EelGrass	72.02
Winter, Month, Bathymetry, NASC10, NumSchools, MinDepth, EelGrass	72.34
Winter, Month, Bathymetry, NASC10, NumPatches, MinDepth, EelGrass	75.98

Supplemental Table 3: Model selection results for the influence of temporal, habitat, and fish school variables at the bay-level on diving bird abundance (loons, cormorants, murres, murrelets). NumSchools = number of fish schools in bay; NumPatches: number of prey patches in bay; MinDepth: mean minimum fish school depth (m); EelGrass = amount of eel grass in bay (m); NASC40 & NASC60: nautical area scattering coefficient summed over the first 40 and 60 meters of recorded water column.

Explanatory Variables	**AIC$_C$**
Winter, Bathymetry, NumSchools, MinDepth, EelGrass	83.54
Bathymetry, NumSchools, MinDepth, EelGrass	84.31
Bathymetry, NumPatches, EelGrass	86.95
Winter, Month, Bathymetry, NumSchools, MinDepth, EelGrass	86.96
Winter, Bathymetry, NumPatches, EelGrass	87.74
Bathymetry, NumSchools, EelGrass	87.95
Winter, Bathymetry, NumPatches, MinDepth, EelGrass	88.69
Winter, Bathymetry, NASC40, NumPatches, MinDepth, EelGrass	90.29
Winter, Month, Bathymetry, NASC40, NumSchools, MinDepth, EelGrass	90.36
Winter, Month, Bathymetry, NASC60, NumSchools, MinDepth, EelGrass	90.64
Winter, Bathymetry, NASC60, NumPatches, MinDepth, EelGrass	90.83
Winter, Month, Bathymetry, NASC40, NumPatches, MinDepth, EelGrass	93.79
Winter, Bathymetry, NASC60, NumPatches, MinDepth, EelGrass	94.24