Exxon Valdez Oil Spill
Restoration Project Final Report

Seabird Predation on Juvenile Herring in Prince William Sound

Restoration Project 090814
Final Report

Mary Anne Bishop*
Prince William Sound Science Center
P.O. Box 705
Cordova, AK 99574

Kathy J. Kuletz
U.S. Fish and Wildlife Service, Migratory Bird Management
1011 East Tudor Road
Anchorage, Alaska 99503

June 2011

*With contributions by: Neil Dawson[1], Tawna Morgan[1], Jordan Watson[1], Richard Thorne[1], Jordan Watson[1], and Alain Zuur[2,3]
[1]Prince William Sound Science Center, P.O. Box 705, Cordova, AK 99574
[2]Highland Statistics, 6 Laverock Road, Newburgh, Aberdeenshire, AB41 6FN, Scotland;
[3]Oceanlab, University of Aberdeen, Newburgh, UK

Exxon Valdez Oil Spill
Restoration Project Final Report

Seabird Predation on Juvenile Herring in Prince William Sound

Restoration Project 090814
Final Report

Mary Anne Bishop*
Prince William Sound Science Center
P.O. Box 705
Cordova, AK 99574

Kathy J. Kuletz
U.S. Fish and Wildlife Service, Migratory Bird Management
1011 East Tudor Road
Anchorage, Alaska 99503

June 2011

*With contributions by: Neil Dawson[1], Tawna Morgan[1], Jordan Watson[1], Richard Thorne[1], and Alain Zuur[2,3]
[1]Prince William Sound Science Center, P.O. Box 705, Cordova, AK 99574
[2]Highland Statistics, 6 Laverock Road, Newburgh, Aberdeenshire, AB41 6FN, Scotland;
[3]Oceanlab, University of Aberdeen, Newburgh, UK

Seabird Predation on Juvenile Herring in Prince William Sound

Restoration Project 090814
Final Report

Study History: A detailed project description for this project was approved for funding by the Trustee Council on 14 November 2006. Funding began in March 2007. Fieldwork for the project began in March 2007 and continued through March 2009. This is the final report on activities conducted by this project. Results of this project were used for developing a subsequent project being led by Drs. Bishop and Kuletz within the scope of the Prince William Sound Herring Monitoring program, which began in 2010.

Abstract: The collapse of the Prince William Sound (PWS) herring fishery has impacted not only the economy and well-being of PWS communities, but also several species of seabirds that depend on herring. We investigated seabird abundance and distribution during winter months (November through March) in PWS from March 2007 to March 2009. Seabird observations took place across nine cruises, with the primary purpose of cruises being either hydroacoustic surveys for herring (five cruises) or humpback whale surveys (four cruises). Using data from the nine cruises, we examined abiotic and biotic variables to identify habitat associations of the most common species, Common Murre, Glaucous-winged Gull, and Marbled Murrelet. We found that Murre and Murrelet numbers increased from November to January, while by March, Murre numbers peaked while Murrelet numbers declined. Gull abundance was not consistent, although both in March 2008 and 2009, numbers were low. Habitat association modelling revealed that winter climate conditions may influence distributional patterns more than variables providing proxies for foraging opportunities, such as substrate and benthic habitat type. We estimated the biomass of juvenile and adult herring consumed by marine birds in PWS during 10 winters between 1989 and 2007. As a group marine birds consumed an average of 2.8 – 10.2% of the total adult herring biomass (up to 5,013 t) in a given winter, indicating that avian consumption may represent a substantial and highly variable source of adult herring mortality. Total juvenile herring biomass is unknown, however, on average the avian consumption of juvenile herring was estimated at 1,572 $\pm$ 569 t. Common Murre (*Uria aalge*) consumed the greatest quantity of herring in all years (max = 4,055 t $\pm$) and like most other species investigated, they depredated a greater portion of juvenile herring than adult herring. Finally, we used seabird survey data conducted in conjunction with the hydroacoustic herring surveys to compare Pacific herring abundance spatially and temporally relative to the distribution and abundance of piscivorous birds. Analysis of presence/ absence of the most prevalent seabirds in PWS in winter revealed that at a 1 km^2 scale in the bays that we surveyed, fish predictability and bathymetric features were important to foraging seabirds. We found that the presence of Common Murre, Glaucous-winged Gull, Pelagic Cormorant and grebes were positively associated with the predictability of fish at depths >23m while Marbled Murrelet and mergansers were negatively associated with water depth . The association between presence of seabirds and predictable fish aggregations at the scale of 1 km^2 suggests a searching ability of seabirds to locate seasonally predictable resources among the bays of PWS.

Key Words: Marine birds, bioenergetics, fish consumption, predation, Pacific herring, nursery bays, Prince William Sound.

Project Data:

Description of data – Data on the at-sea distribution and abundance of seabirds and marine mammals were collected in Prince William Sound, Alaska. Bird and marine mammal data were collected during juvenile herring hydroacoustic surveys and humpback whale surveys. Juvenile herring data were collected during hydroacoustic surveys by R. Thorne at the Prince William Sound Science Center as part of Restoration Project 070830. March bird population data for all of Prince William Sound were collected by US Fish and Wildlife Survey as part of Restoration Project 080751.
Format –All at-sea bird and marine mammal survey data are available as Microsoft Access files.
Custodians – Mary Anne Bishop, Ph.D. Prince William Sound Science Center, P.O. Box 705, Cordova, AK 99574 or Kathy J. Kuletz, Migratory Bird Management, U.S. Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, Alaska 99503.

Citation:

Bishop, M.A. and K.J. Kuletz. 2011. Seabird Predation on Juvenile Herring in Prince William Sound. *Exxon Valdez* Oil Spill Restoration Project Final Report (Project 09081), Prince William Sound Science Center, Cordova, Alaska.

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1. HABITAT ASSOCIATIONS OF SEABIRDS DURING WINTER IN PRINCE WILLIAM SOUND, ALASKA

Neil Dawson[1], Mary Anne Bishop[1], Kathy Kuletz[2] And Alain Zuur[3,4]

[1] Prince William Sound Science Centre, Cordova, Alaska USA 99574, [2]U. S. Fish and Wildlife Service, Migratory Bird Management, 1011 East Tudor Road, Anchorage, Alaska USA 99503, [3]Highland Statistics, 6 Laverock Road, Newburgh, Aberdeenshire, AB41 6FN, Scotland, [4]Oceanlab, University of Aberdeen, Newburgh, UK

ABSTRACT

Winter may be the period during which seabirds face the greatest environmental and physiological pressures, yet little is known about seabird distribution at this time and what is known is often taken from snapshots at the beginning or end of the season. Using at-sea surveys on 'ships of opportunity' conducted in Prince William Sound, Alaska from November 2007 to March 2009, we investigated how habitat associations vary within and between winters for some common seabird species with extensive ranges: Common Murre *(Uria aalge)*, Black-legged Kittiwake (*Rissa tridactyla)*, Marbled Murrelet (*Brachyramphus marmoratus)* and Glaucous-winged (*Larus glaucescens)* and Herring Gulls (*Larus argentatus)*. Due to a large proportion of zeros in the survey data, hurdle models were performed using generalized additive mixed models. Densities varied greatly for all species across the period, suggesting that multiple surveys are required to estimate wintering populations and assess habitat associations. However, consistent trends were observed between the two winters for each species, revealing that there are species-distinct temporal patterns in distribution. Habitat association modelling revealed that winter climate conditions may influence these distributional patterns more than variables providing proxies for foraging opportunities, such as substrate and benthic habitat type. Common Murre and Marbled Murrelet both increased in number in midwinter, with Marbled Murrelet favoring bays and passages and Common Murres other semi-protected waters. The probability of encountering Marbled Murrelet was also positively linked to sea surface temperature in Prince William Sound. Our results suggest that if distributional data are to be effectively utilised to effect conservation of seabird populations, both fine-scale and species-specific temporal patterns must be considered.

INTRODUCTION

Seabird populations can be impacted by pollution events (Peterson *et al*. 2003), direct and indirect interactions with fisheries (Tasker *et al*. 2000, Okes *et al*. 2009) and increasingly through marine environmental change (Pichegru *et al*. 2010). Many species of seabird are currently under pressure from some and in many cases all of these threats. Improving our understanding of marine habitat requirements for seabirds can help predict the impacts from these events and assist in the selection of appropriate marine protected areas (Hooker and Gerber 2004, Amorim *et al*. 2009). Because most seabird studies occur during the summer breeding season, little is known about winter habitat requirements. Here we describe winter marine habitat use and variation through the winter period for seabirds in Prince William Sound, a large fjord-type estuary in southcentral Alaska.

Most seabirds time their breeding to coincide with favorable feeding conditions in the spring and summer, when prey may be concentrated near the surface. Because breeding seabirds are central-place foragers, distance to the colony restricts the habitat choices and

foraging distribution of seabirds during summer (Ashmole 1963, Garthe *et al*. 1997), but this is also a time when food is generally at its most plentiful. Winter may be the period during which seabirds face the greatest pressures and competition for food can be high (Lack 1968, Hunt et al. 2005). For those species at higher latitudes not migrating large distances, food tends to be relatively scarce or inaccessible, the climate more extreme, light levels reduced, day length shorter and water temperatures colder. Consequently daily energy requirements increase (Fort *et al*. 2009) and birds have to forage for a large proportion of daylight hours (Daunt *et al*. 2006). Wind and sea state are known to affect surface-feeding seabirds in particular (Dunn 1973, Taylor 1983) but diving birds can also be impacted and the effects of these conditions on survival have been observed in Common Murre and European Shag (Harris and Wanless 1996, Piatt and Van Pelt 1997, Frederiksen *et al*. 2008).

In response to these environmental challenges, seabirds may perform large-scale movements during winter and may aggregate in areas where high bird densities can be sustained for a limited period (Vaitkus 2001). Winter aggregations may also be a means to maintain warmth or keep ice from closing on marine birds, such as the aggregation of spectacled eiders (*Somateria fischeri*) in the north Bering Sea (Petersen *et al*. 1999). Rather than dispersing during this part of the year, spatial patterns can actually display a high degree of patchiness (Skov *et al*. 2000, Garthe *et al*. 2009) and discrete aggregations can occur at which large proportions of a geographic population may be found (Skov *et al*. 1995, Petersen *et al.* 1999).

While we may expect highly mobile seabirds to show a strong aggregative response towards concentrations of prey, attempts to explain the distribution of a variety of seabird species have shown that different factors are important at different spatial scales. Seabirds have been shown to be possible tools for predicting stocks of certain fisheries (Cairns 1992, Roth *et al*. 2007) and associations with concentrations of prey have been confirmed at large scales of tens to hundreds of square kilometres (Logerwell & Hargreaves 1996, Fauchald *et al*. 2000, Skov *et al*. 2000). At finer scales, however, seabirds may show no relationship (Vlietstra 2005, Fauchald 2009) or even negative relationships with prey availability (Suryan *et al*. 2002, Ainley *et al*. 2003).

During the nonbreeding season a number of seabird species feed upon a wider variety of prey than they do during summer (Shealer 2002). Sanger *et al*. (1987) found that Common Murre (*Uria aalge)* and Marbled Murrelet (*Brachyramphus marmoratus)* in southcentral Alaska fed on a variety of prey items in winter, and Ouwehand *et al*. (2004) recorded a varied winter diet in Murre in the North Sea. Black-legged Kittiwake (*Rissa tridactyla)* (hereafter 'Kittiwake') exploit a wider range of food sources in winter than they do in summer, including increased amounts of discards and offal (Camphuysen *et al*. 1995). Therefore, studying single predator-prey associations during the nonbreeding season may not yield strong results, because seabirds may congregate in areas with predictable concentrations of a variety of prey items based on benthic habitat, bathymetry or exposure to the elements (Hunt *et al*. 1999, Weimerskirch 2007, Garthe *et al*. 2009). Seabirds have been shown to associate with physical and biological ocean processes (Weichler *et al*. 2004, Ainley *et al*. 2005, Hyrenbach *et al*. 2006, Yen *et al*. 2006, Garthe *et al*. 2009) as well as with specific bathymetric features (Yen *et al*. 2004, Amorim *et al*. 2009). Such environmental factors may be better predictors of seabird distribution than prey abundance (Ainley *et al*. 2004).

In this study we define fine scale habitat associations (1 km^2) of the more abundant seabird species overwintering in Prince William Sound, Alaska. We investigate how habitat associations change through the winter for each species and discuss the possible causes of temporal variation. Finally, we examine the implications of our findings for incorporation of

biodiversity data into marine spatial planning and establishment of protected areas at sea. We relied on ships of opportunity to conduct surveys, thus our methods for analysing this type of data could be applied to studies with similar platforms of opportunity.

STUDY AREA AND METHODS

Study Area

Prince William Sound (PWS) lies on the coast of south-central Alaska, primarily between 60^{o} and 61^{o} N, and is separated from the adjacent Gulf of Alaska (GOA) by large, mountainous islands (Figure 1). The coastline is rugged and extensive and includes many islands, deep fjords and shallow bays. There are several large icefields with > 20 tidewater glaciers (Molnia 2001). Abundant rain, snow and glacial melt result in a strong cyclonic circulation that generally travels east to west (Neibauer *et al*. 1994). During summer the waters of PWS are highly stratified, but during winter months they are more mixed, with Gulf of Alaska surface waters pulsing into PWS via the Alaska Coastal Current (Niebauer *et al*. 1994). The northern half of PWS is strongly influenced by fjord waters and tends to be colder and fresher relative to the Alaska Coastal Current-influenced waters that are warmer and more saline (Wang *et al*. 2001).

Much of PWS is protected from the wave action that hits the exposed Alaskan coast, but winter can bring large storm systems. Annual precipitation can be as high as 5.4 m and sea surface temperatures in the fjords can be as low as 1^{o} C in late winter, with some inner bays and fjords choked with ice (Gay and Vaughan 2001). Fjords and bays are very diverse, with average depths ranging from <50 m to >400 m. Outside the bays are many basins and passages of varying depths up to 700m.

The fish assemblage of PWS is diverse, but is dominated in biomass by Pacific Herring (*Clupea pallasii)*, Pacific Cod (*Gadus macrocephalus)*, Walleye Pollock (*Theragra chalcogramma)* and various salmonids (*Oncorhynchus* spp.; Willette *et al*. 1997). Additionally, there are numerous other fish species important to seabirds, including Pacific Sandlance (*Ammodytes hexapterus)* and Capelin (*Mallotis villosus)* (Kuletz et al. 1996, Anthony et al. 2000). One major ecological event which provides concentrations of food for various seabirds in the nonbreeding season include herring spawning from late March through early May (Bishop and Green 2001; Norcross *et al*. 2001).

For this study w selected four common species or species groups with varying body size and feeding strategies: Common Murre, a deep-diving alcid, Black-legged Kittiwake, a medium-sized surface feeder, Marbled Murrelet, a globally endangered, small, diving alcid (IUCN 2010), and large gulls, predominantly Glaucous-winged (*Larus glaucescens)* along with small numbers of Herring Gull (*Larus argentatus)*, both of which are opportunistic surface-feeders. These species or species groups are the most abundant seabirds in PWS during winter. Surveys conducted in March 2005 estimated populations of these species of seabirds to be 90,902 Common Murre, 35,364 Glaucous-winged Gull, 15,903 Black-legged Kittiwake and 9432 Marbled Murrelet (McKnight *et al*. 2006).

Survey Methods

We conducted eight surveys of seabirds in PWS in November, January and March over two winters, 2007/08 and 2008/09. Surveys undertaken were: November 5 – 12, 2007 (292 km surveyed), November 24 – 29, 2007 (137 km), January 23 – 28, 2008 (246 km), March 12 – 19, 2008 (419 km), November 6 – 13, 2008 (200 km) January 23 – 28, 2009 (250

km), March 4 – 9, 2009 (221 km) and March 18 – 25, 2009 (518 km), totalling 2283 km. Seabird observations were conducted using established U.S. Fish and Wildlife Service protocols (USFWS 2007). One observer using 10x binoculars recorded number of birds occurring within a strip transect width of 300 m (150 m both sides and ahead of the boat, in 3 distance bins of 50m). Observers used rangefinders to check distances and were trained to estimate distances of birds from the center line at 50 m increments. All birds within the strip were counted continuously. Flying birds were included if deemed to be foraging rather than directly transiting. No birds of any species were deemed to have been attracted to or followed the survey vessel during surveys. All surveys were carried out using the same 17 m charter vessel with a clear observation platform 2.5 m above sea level. Surveys were only conducted while travelling on a direct course at a constant speed of ≤ 12 knots and only in calm sea conditions, (typically Beaufort Scale of 1 or 2, and not more than BS 4). The waters of PWS are relatively well protected with little swell and generally calm conditions, which provided good survey conditions. We assumed that all birds within the transect width were counted. This assumption was supported by our preliminary analysis of survey data for each species, which revealed no patterns in detectability across three 50 m survey bands (0-50 m, 51-100 m, 101-150 m). Therefore we assumed no bias in detection of birds across the 300 m transect width. The observer recorded observations into a laptop computer integrated with a global positioning system (GPS) using the program Dlog (Ford Consulting, Inc., Portland OR). The GPS-integrated program provided location data at 20-sec intervals and for every entered observation. We calculated density (birds • km^{-2}) of each seabird species for each km of survey trackline.

A-Priori Designation of Explanatory Variables

Data were obtained for a number of environmental variables, based on biological rationales supporting their ability to explain seabird distribution outside the breeding season. Using geographic information system (GIS) software (ArcMap 9.2), we spatially matched explanatory variables to survey data, thus building a detailed profile of each km of survey trackline. For continuous variables we also calculated the range, mean, and standard deviation (Table 1).

Marine habitat was included as a variable to capture use of different areas for foraging, such as bays where herring spawn in late winter or which may provide relative shelter during winter months (Thorne 2010), and mouths of bays and passages where tidal fronts regularly occur (Decker and Hunt 1996). Selected marine habitat categories were: within bay (685 of 2283 km), mouth of bay or passage (254 km), within passage (297 km) and open water (1047 km). Within bay reflects areas inside the mouth of an enclosed bay. The mouth of bays and passages refers to the area between two headlands and approximately 1 km in either direction. Passage refers only to narrower passes measured as < 3 km wide in GIS. Passages > 3 km wide are categorized as open water. Open water refers to all other areas. Winter weather events have the potential to influence seabird distribution (Vaitkus 2001). As a proxy we used wave exposure of the nearest point of land taken from ShoreZone coastal inventory and mapping project (NOAA Fisheries 2009). Categories included exposed/semi-exposed (570 out of 2283 km), semi-protected (1444 km) and protected (269 km). Points >3 km from shore were classified as semi-exposed.

Distance to shore was included as a variable because many juvenile fish are found in greater concentrations in nearshore environments (Beck *et al*. 2003) and fresh water runoff may also create fronts (Gay and Vaughn 2001). Depth was included because of its effect on fish assemblages (Johnson *et al*. 2008) and additionally because different seabird species are

restricted by their diving capabilities. Depth (in meters) was obtained from the Alaska Ocean Observing System (2010) grid of bathymetry for PWS that is modelled to a resolution of 500 m. Slope was included because bathymetric features can influence upwelling and can provide feeding opportunities for marine predators like seabirds (Yen *et al*. 2004). Slope is the angle of seabed in degrees, determined from GIS calculations based on the Alaska Ocean Observing System bathymetry grid.

Fish assemblages may differ strongly with substrate (Hamilton & Konar 2007) and details of substrate type were obtained from the ShoreZone coastal inventory and mapping project (NOAA Fisheries 2009) and included three categories: rock (455 out of 2283 km), rock and sediment (849 km) or sediment (979 km; including gravel, sand and mud). Kelp beds (*Nereocystis* spp., *Macrocystis* spp.) and eelgrass (*Zostera* spp.) are abundant in different areas of PWS, and are associated with high productivity as well as providing protection and food for a variety of juvenile fish (Dean *et al*. 2000, Johnson *et al*. 2010). Locations of coastal kelp and eelgrass beds were also obtained from the ShoreZone project (NOAA Fisheries 2009) and distance to them in meters calculated using GIS.

Sea surface temperature (SST), which may influence both prey availability and energetic requirements, was obtained from the NASA Giovanni website (GES DISC 2009), which provides monthly SST averages obtained from satellites for points in a 10 km grid. The resulting grid provided 233 points with SST measurements in PWS at each time point. Latitude and longitude were included as explanatory variables to determine if there was a geographical gradient to bird distribution. Temporal variables included month (November, January or March), year (whether winter 2007/08 or 2008/09) and month/year (combination of month and winter), which were included to account for possible changes in density seasonally and between winters.

Data Exploration

Following the protocol outlined in Zuur *et al*. (2010), we carried out data exploration to look for outliers, zero inflation (when there are too many zero observations), collinearity, and to investigate the type of relationships between birds and covariates. We plotted the spatial position of the sampling sites to visualise the consistency of sampling sites over time. To assess the presence of potential outliers, we used Cleveland dotplots, but we did not find extreme outliers. However, dotplots showed that values for the variable depth were not sampled along an equal-spaced gradient and therefore depth was converted into a categorical variable: 0 – 50 m (612 out of 2283 km), 50 – 100 m (665 out of 2283 km), 100 – 150 m (320 out of 2283 km), > 150 m (686 out of 2283 km).

Frequency plots were used to assess the proportion of zeros in the data and for each species the number of non-zero observations per km was calculated. The species with the most non-zero observations out of 2283 total km surveyed was Common Murre (n = 751). For other species the numbers of non-zero observations were: large gulls 521, Marbled Murrelet 343 and Kittiwake 198. Kittiwakes had so few positive observations that the data were not suitable for modelling habitat association. The Normal, Poisson and negative binomial distributions assume a considerably lower proportion of zeros in the response variable than occur in zero-inflated data. Applying generalised linear models (GLM) or generalised additive models (GAM) using one of these distributions on zero inflated data can produce biased parameters and cause overdispersion (Zuur *et al*. 2009).

Collinearity between covariates was investigated using pairplots (multi-panel scatterplots) and variance inflation factors (VIF). Pairplots only capture two-way relationships whereas VIF detect high-dimensional collinearity (Zuur *et al.* 2010). Based on

the pairplots, we determined the following pairs of variables to be collinear: distance to kelps and latitude (Pearson correlation; $r = 0.5$), distance to shore and distance to eelgrass ($r = 0.5$) and depth and slope ($r = -0.4$). Exploring VIFs showed the combinations time and SST, ocean habitat category and distance to eelgrass, SST and year to be collinear and therefore none of these combinations of covariates were used in the same model. Scatterplots for the presence-absence of each species and the presence-only data for each species showed that weak patterns can be expected for presence-absence data, and very weak patterns for the presence-only data. This provides an extra reason to deal with even the smallest amount of collinearity as it reduces the significance of the parameters.

Statistical exploration revealed a clear transect effect, and also a cruise effect, with observations made on the same transect and cruise being more closely related than otherwise. In addition, the locations of the sampled transects were not identical over time, although similar areas were visited (Figure 1). The interpretation of the temporal trends is therefore confounded with minor changes in spatial position of the sampling sites. For this reason latitude and longitude were included as explanatory variables to reveal any strong spatial bias in seabird density, occurrence, or geographical pattern to bird distribution. The large range in distances covered during each survey (minimum 137 km, total 2,283 km) provided a broad range of data across each variable (see explanatory variables section), which serves to limit the influence of spatial bias on statistical results for habitat association.

Statistical Analyses

The seabird distribution data were zero inflated for every species, thus regression techniques like generalised linear models (GLM) and generalised additive models (GAM) would likely produce biased estimated parameters. Because we assumed that zero observations were true zeros, hurdle models can be applied whereby data are analysed initially as presence-absence, followed by a separate analysis of presence-only data (Boucher and Guillén, 2009, Zuur *et al*. 2009). Hence, the first analysis attempted to determine which covariates were driving the presence and absence of birds, while the second analyses focused on the question of which covariates were driving the abundance of birds when they were present. All models were run using R software.

For the presence-absence data a binomial generalised additive mixed model (GAMM) was used with transect as a random intercept. That ensured that a correlation structure was imposed on the observations from the same 1 km transect. Observations from different transects were assumed to be independent as they were temporally and spatially distinct.

For the presence-only data we used a GAMM with a gamma distribution suitable for density data, and transect and cruise were used as random intercepts. The use of the random intercepts ensured that observations from the same multiple km transect were allowed to be correlated. For a detailed description of the statistical methods see Zuur *et al*. (in press). We used an Information Theoretic approach (Burnham and Anderson 2002), defining 15 or 16 models *a priori* separately for each species, which we then compared using Akaike (AIC) weights. Models selected for each species are detailed in Table 2 and hypotheses are listed in Appendix 1. There is some evidence to suggest that weakly significant variables ($p > 0.01$) should not be considered when using GAMMs (Wood 2006) and therefore only highly significant relationships ($p < 0.01$) were investigated further. Post-hoc testing was performed with Bonferroni corrections to investigate in more detail the nature of the relationships contained in the models. Values reported in the *Results* section represent means ± standard error.

RESULTS

Seabird Densities

Kittiwakes were scarce throughout the nonbreeding season and were almost nonexistent in January during both winters surveyed (Table 3). Kittiwake density was > 1 bird/km^{-2} in only two of the six time periods, March and November 2008. In contrast, Marbled Murrelet increased in abundance from early to mid winter, peaked in January in both years, but then decreased in late winter (Table 3). Common Murre increased between November and January of each year, and increased through March in 2008. Winter populations of Glaucous-winged Gull and Herring Gull were inconsistent, showing an extreme increase in January 2008, when abundance was more than four times greater than the next highest density in November 2008. In both winters, large gull density dropped in March (Table 3).

Modelling Seabird Distribution In Relation To Environmental Variables

Common Murre. For Common Murre presence-absence data the models M2 (SST), M12 (SST and year), M1 (month/year) and M11 (SST and exposure) are the preferred models (Table 4). For models 2, 11 and 12 none of the variables had *P*-values less than 0.05. The only model with a significant estimated parameter is model 1 (month/year), for which month/year is highly significant ($P < 0.001$), showing that density is higher for all other time periods than the November 2007 baseline. There were some patterns in the residuals for this model when plotted against depth or distance to kelps and this shows that the variable month/year also contains a spatial component because survey sites were not always consistent each period.

For presence-only data, model 5B (month/year and exposure), had the lowest AIC (Table 4), with a significant interaction ($P < 0.01$). Post-hoc testing with Bonferroni corrections found that within this interaction there were significant differences between January 2009 and January 2008 as well as January 2009 and March 2008, with the greater densities occurring in protected and semi-protected waters in each case.

Large Gulls. For large gulls, presence-absence data the models M6 (distance to shore and month/year) and M1 (month/year) were the optimal models (Table 5). However, the smoother for distance to shore in M6 has only a *P*-value of 0.06 (and one degree of freedom). For M1 the term month/year is highly significant ($P < 0.001$) in predicting gull presence. Post-hoc testing with Bonferroni corrections showed that there was significantly less likelihood of encountering large gulls during March during of both winters, compared to November 2008 and January 2009.

For presence-only data there are three competing models: M11B (exposure, distance to shore and year), M15B (distance to kelp, depth and month/year), and M16B (marine habitat and depth; Table 5). For M11B the interaction term between exposure and year was significant ($P = 0.01$) and post-hoc testing indicated that the major element of this relationship was higher gull densities in both semi-protected and protected areas during the first winter, compared to the second. Density of large gulls was on average much higher in the first (2007/08) year, though in both years density remained low in exposed waters. For model M15B (distance to kelp, depth and month/year) the term month/year is highly significant ($P < 0.01$), reflecting the higher density in January 2008 and lower densities in March of both years (Table 2). The smoother for distance to kelps is highly significant for January 2008 ($P < 0.001$), showing a preference for birds to be > 2 km from kelp. The

function of this relationship between birds and kelp has little biological grounding and reflects higher density of gulls in northern PWS in January 2008 rather than the south, where the vast majority of kelp beds were located. At other times there was no effect of distance to kelp beds (Figure 2). For model M16B (marine habitat and depth) marine habitat was significant ($P < 0.01$), reflecting a much higher density of birds in bays and passages during the nonbreeding season relative to open water or in the mouths of bays and passages.

Marbled Murrelet. For Marbled Murrelet presence-absence data, model M11 (latitude longitude, marine habitat and SST) was the best model with lowest AIC. In this model marine habitat was significant ($P < 0.005$) as was the smoother for SST ($P < 0.01$), whereas smoothers for latitude and longitude were not ($P > 0.9$). The SST effect is linear and positive (Figure 3). Post-hoc testing with Bonferroni corrections revealed that Marbled Murrelets were significantly more likely to be encountered in either bays or passages than in open water. In addition, the probability of encountering birds within bays was significantly greater at the 5% level than at the mouths of bays and passages. Density was higher in these habitats, particularly in January of both years.

For Marbled Murrelet presence-only data, the model M15B (marine habitat, depth, distance to shore, substrate and month/year) was the best fit, with lowest AIC (Table 6). The interaction between substrate and month/year was highly significant ($P < 0.001$). The post-hoc tests revealed that the main elements driving this relationship were the high densities of Marbled Murrelets encountered in January 2009 in several different areas with substrates consisting of sediment (gravel, sand, mud), whereas in January 2008 densities were higher in areas of mixed rock and sediment.

DISCUSSION

During winter, logistical limitations and the more varied diets of seabirds make it difficult and costly to study the association between seabirds and their prey. Furthermore at fine spatial scales, seabirds may show no relationship (Vlietstra 2005, Fauchald 2009) or even negative relationships with prey availability (Suryan *et al*. 2002, Ainley *et al*. 2003). Our results, from opportunistic surveys, suggest that environmental variables can provide useful indicators of potential overwintering habitat for seabirds and reveal drivers of habitat selection at both seasonal and annual temporal periods.

Proxies for prey availability included benthic habitat variables such as substrate composition (Hamilton & Konar 2007) and presence of eelgrass and kelp beds, which can provide information about likely prey assemblage and represent foraging opportunities for seabirds (Johnson *et al*. 2010), slope because bathymetric features can influence upwelling and can provide feeding opportunities for marine predators (Yen *et al*. 2004), distance to shore because many juvenile fish are found in greater concentrations in nearshore environments (Beck *et al*. 2003) and depth, which has an effect on fish assemblage (Johnson *et al*. 2008). For other variables, such as sea surface temperature or distance to shore, underlying causes may be difficult to disentangle.

Assuming our habitat features were useful proxies of prey abundance, we found little evidence to suggest that winter Common Murre distribution is related to prey. Common Murre are capable of taking large fish relative to murrelets and kittiwakes and they have been shown in late winter to associate with adult herring in PWS (Bishop *et al*. in prep.). Herring can be highly aggregated during late March and April, with up to 90% of the spawning population found within an area of < 10 km^2 (Thorne and Thomas 2008). Day (2006) studied abundance and distribution of seabirds in the northern GOA near PWS during winter and

noted high numbers of Common Murre flying inshore in late winter. However, our results show that variables which may have acted as proxies for prey availability in March did not feature in selected models. Furthermore, concentrations of murres did not occur in any particular habitat, distance to shore, or geographical location during our March cruises, whereas they did in midwinter. However, herring spawning occurred late both years of our study (Thorne 2010) and the impact of herring presence on the distribution of murre may have therefore been stronger in April 2008 and 2009, when larger aggregations of adult herring were recorded in PWS (Thorne 2010).

Marbled Murrelet distribution was related to a variety of factors, including those we considered proxies for prey availability. Marbled Murrelet use waters outside of PWS in early winter (Day 2006, NPPSD). As with the Common Murre, however, we found higher murrelet densities within PWS during midwinter. The probability of encountering Marbled Murrelets was greater within bays and passages, areas typically more sheltered from storms. The greater probability of finding Marbled Murrelets in bays and passages may also be related to prey availability. In particular, high densities of juvenile Pacific herring overwinter in the relatively warm, shallow waters of PWS bays (Stokesbury *et al*. 2000, Thorne 2010), where they would be accessible to Murrelets. In January, Murrelets were typically located in highest densities in areas with non-rocky substrates. Such areas are good habitat for a variety of juvenile and forage fish (Hamilton & Konar 2007, Thorne 2010) and may also contain a number of marine invertebrates.

Marbled Murrelets can dive and acquire food at up to 50 m depth, although most of their foraging occurs in the upper 25 m of the water column (Burger 1991, Jodice and Collopy 1999). Diving can be metabolically expensive in colder sea temperatures due to increased heat loss (Kooyman *et al*. 1976, Gremillet *et al*. 1998). We found that the probability of encountering Marbled Murrelets during the nonbreeding season was positively related to SST. In March, surface waters in PWS are coldest (average 2.88^{o} C in 2008 and 2.54^{o} C in 2009; Vaughan *et al*. 2001) while in the GOA, average March surface temperatures are comparatively warm, at 5.5^{o} C. This marked difference in sea surface temperatures could explain the late-winter decline in Marbled Murrelet numbers in PWS and the relatively high densities (for pelagic waters) of murrelets recorded in the GOA by Day (2006) during March.

Large gulls are opportunistic, generalist feeders and they exhibited large shifts in density in PWS, both within and between winters. During the 2007/08 winter, density of gulls increased by more than nine times between November and January, whereas the following winter their density decreased during that same time period. The disappearance of large gulls in late winter is likely due not just to the onset of breeding behaviour but also to the potential abundance of food outside PWS such as on the Copper River Delta. During February and March, Eulachon (*Thaleichthys pacificus)* begin to enter the freshwater habitats of the Copper River Delta (Moffitt et al. 2002), and during March 2008, Dawson observed up to 100,000 large gulls feeding there on large numbers of eulachon. However, although the large gulls showed high inter-annual variance, even they had lower densities in waters with greater exposure to wave action, particularly in January. As with the two alcid species, Day (2006) found an opposite trend during surveys of the northern GOA, with sightings of Glaucous-winged Gull lowest between October and April compared to summer months. The opposing trends in seasonal seabird abundance in PWS and the GOA support the finding that seabirds could be responding to broad scale climatic events, and that the less exposed waters of PWS provide refugia during winter.

Large Scale Movements

Knowledge of the key influences on seabird movements outside the breeding season is limited, making it difficult to explain changes in distribution for a species, both within and between years. Common Murre, the most numerous PWS seabird during winter, rarely exceeds 15,000 birds during summer, whereas winter numbers can range as high as 157,000 (McKnight *et al.* 2006), thus birds from multiple Common Murre breeding populations may be present in PWS in winter. In contrast, the Marbled Murrelet is the most abundant seabird in PWS during summer, with more than three times the estimated winter (March) population size (McKnight *et al*. 2006), indicating that most of the PWS breeding population winters elsewhere. Our results also suggest that the surveys conducted across PWS in March (as in McKnight *et al*. 2006) have missed the peak in winter murrelet numbers, thus underestimating the importance of PWS as their winter habitat, especially during the worst of winter conditions.

Our study indicates that the nonbreeding season cannot be characterised as a single time period when describing seabird distribution. We found that densities of Black-legged Kittiwake, Common Murre, Marbled Murrelet and large gulls (Glaucous-winged and Herring) all varied greatly between November and March in PWS, suggesting that multiple surveys are required to quantify wintering populations and understand changes in seabird distribution. Although trends differed by species, we found consistent patterns in movements between years for each species, which suggests that it is possible to predict relative population sizes at different periods of the nonbreeding season. The implications of these findings extend beyond local relevance. Our study species' distributions range from the North Pacific (Marbled Murrelet) to the entire northern hemisphere for (Common Murre and Black-legged Kittiwake). Our results, revealing substantial temporal variation in wintering habitat, may also apply to other seabird species with coastal distributions during winter.

Temporal changes in distribution are likely to depend upon the different feeding strategies of each species or species group, and reactions to changing conditions were found to vary, particularly for kittiwakes. Kittiwakes have previously been recorded as abundant at the end of winter in March (McKnight *et al*. 2006) but little is known about population trends in the preceding months. Kittiwakes are medium-sized surface feeders and their movements likely reflect the availability of surface prey in PWS. Iin our study, numbers of kittiwakes declined after early winter, corresponding to a period when zooplankton abundance declines and diel vertical migrations of fish and euphausiids to surface waters are reduced (Cooney *et al*. 2001). The disappearance of kittiwakes, and possibly other surface feeders during winter, may be due to their dispersal in search of food at this time of year, when many forage fish species of PWS move deeper in the water column (eg. Norcross *et al*. 2001). In Europe, kittiwakes' dependence on fisheries discards increases during winter (Camphuysen *et al*. 1995), but there are no corresponding winter fisheries in PWS that would provide sufficient supplemental feeding to meet the energetic needs of surface feeders. Kittiwakes were also absent in the GOA during winter surveys (Day 2006), suggesting that kittiwakes may have to range farther to find available surface food at this time. Recently, A. McKnight (USFWS, unpubl. data) and R. Orben (University of California Santa Cruz; unpubl. data) used geolocation dataloggers to document kittiwake movements from the GOA and the Bering Sea to the subarctic region of the North Pacific during winter months, which is consistent with their absence in PWS during most of our surveys.

We suggest that Common Murre distribution was driven by winter climate more than by habitat proxies for prey availability, based on the stronger association between murres and

habitat type (protected vs exposed). During winter, PWS provides far more sheltered waters than the adjacent Gulf of Alaska (GOA) and we observed relatively high densities of Common Murre in mid winter in both years. Furthermore, within PWS the density of Common Murres was relatively high in more protected waters during January in both years of our study. Winter wrecks of Common Murre have been recorded in the GOA (Piatt and Van Pelt 1997) and rough seas have been documented to negatively impact foraging behaviour for Common Murre in other areas (Finney et al. 1999). Winter storms in the GOA peak from December to February at which time average wind strength is highest, air temperature lowest and wave height greatest (Stabeno *et al*. 2004, NOAA 2010). Close to PWS, Schroeder (2007) found that the strongest winds in the GOA occur near the coast with the prevailing westerly winds at their highest in January and February and colder northerly winds peaking in February.

Informed designation of protected areas or critical habitats will require an understanding of seabird habitat needs during non-breeding months. Notably, the devastating 1989 *Exxon Valdez* oil spill in PWS occurred in late March, during the seasonal transition from nonbreeding to breeding habitats for many birds, and an estimated 250,000 birds were killed directly (Piatt and Ford 1996). The habitats most heavily impacted in the short and long term from this spill were protected bays with little wave action (Peterson *et al.* 2003) – the very habitats favored by many wintering birds, particularly smaller diving species like the Marbled Murrelet. The Marbled Murrelet, one of the species injured by the oil spill (Carter and Kuletz 1995, Kuletz 1996), is an example of a species which has undergone rapid population decline (Piatt *et al*. 2007) and which, with better understanding of habitat associations, could benefit from establishment of dedicated protected areas. Effective marine spatial planning, fisheries management, and designation of meaningful marine protected areas will require improved knowledge, at a range of spatial scales, of seabird habitat selection throughout the seasons.

ACKNOWLEDGEMENTS

The research described in this paper was supported by grant from the Exxon Valdez Oil Spill Trustee Council. The findings and conclusions presented by the authors are their own and do not necessarily reflect the views or position of the Trustee Council. We would like to thank Dave Janka who as skipper of the *MV* Auklet made it possible to survey in PWS in winter, and John Moran and Jeep Rice of National Marine Fisheries Service and Jan Straley of University of Alaska Sitka for allowing us to share their boat time. We are also grateful to additional observers Karen Brenneman and Aaron Lang. Jodi Harney of Coastal and Ocean Resources was very helpful in making data available from the recently completed Shorezone project. Some analyses and visualizations used in this paper were produced with the Giovanni online data system, developed and maintained by the NASA GES DISC.

LITERATURE CITED

Agresti A. 2003. Categorical Data Analysis (Second Edition), John Wiley and Sons, Inc.

Ainley, D.G., R.G. Ford, E.D. Brown, R.M. Suryan and D.B. Irons. 2003. Prey resources, competition, and geographic structure of kittiwake colonies in Prince William Sound. Ecology 84:709–723.

Ainley, D.G., C.A. Ribic, G. Ballard, S. Heath and others. 2004. Geographic structure of Adelie penguin populations: overlap in colony-specific foraging areas. Ecological Monographs 74:159–178.

Ainley, D.G., L.B. Spear, C.T. Tynan, J.A. Barth, S.D. Pierce, R.G. Ford and T.J. Cowles. 2005. Physical and biological variables affecting seabird distributions during the upwelling season of the Northern California current. Deep-Sea Research II 52:123–143.

Alaska Climate Research Center. 2010. Accessed 25 Sept. http://climategialaskaedu/Climate.

Alaska Ocean Observing System. 2010. Accessed 25 Sept. www.aoos.org/

Amorim, P., M. Figueiredo, M. Machete, T. Morato, A. Martins, R. Serrano Santos. 2009. Spatial variability of seabird distribution associated with environmental factors: a case study of marine Important Bird Areas in the Azores. ICES Journal of Marine Science 66:29–40.

Anthony, J.A., D.D. Roby, K.R. Turco. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. J. Experimental Marine Biology and Ecology 248:53-78.

Ashmole, N.P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103b:458-473.

Beck, M.W., K.L. Heck, K.W. Able Jr, D.L. Childers, D.B. Eggleston, B.M. Gillanders, B.S. Halpern, C.G. Hays, K. Hoshino, T.J. Minello, R.J. Orth, P.F. Sheridan, M.P. Weinstein. 2003. The role of nearshore ecosystems as fish and shellfish nurseries. Issues in Ecology 11:1–12.

Bishop, M.A. and S.P. Green. 2001. Predation on Pacific herring (*Clupea pallasi*) spawn by birds in Prince William Sound, Alaska. Fisheries Oceanography 10:149-158.

Bishop, M.A., T. Morgan, K. Kuletz and R. Thorne (In prep.) Seabirds respond to predictable Pacific Herring (*Clupea pallasi)* aggregations during winter in Prince William Sound, Alaska.

Boucher, J.P. and M. Guillén. 2009. A survey on models for panel count data with applications to insurance. Revista de la Real Academia de Ciencias Exactas, Fisicas y Naturales. Serie A. Matematicas, 277-294.

de L Brooke M. 2004. The food consumption of the world's seabirds. Proceedings of the Royal Society of London 271: 246–248.

Burger, A.E. 1991. Maximum diving depths and underwater foraging in alcids and penguins, p 9-15 *In* W.A. Montevecchi and A.J. Gaston (eds), Studies of high-latitude seabirds 1 Behavioral, energetic and oceanographic aspects of seabird feeding ecology Canadian Wildlife Service Occasional Paper 68, Ottawa, Ontario.

Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach 2nd Edition Springer-Verlag, New York, New York, USA.

Cairns, D.K. 1992. Bridging the gap between ornithology and fisheries science: use of seabird data in stock assessment models. Condor 94:811-824.

Camphuysen, C.J., B. Calvo, J. Durinck, K. Ensor, A. Follestad, R.W. Furness, S. Garthe, G. Leaper, H. Skov, M.L. Tasker and C.J.N. Winter. 1995. Consumption of discards by seabirds in the North Sea Final Report EC DG XIV, research contract BIOECO:93: 10 – NIOZ report 1995–5, Netherlands Institute for Sea Research.

Carter, H.R. and K.J. Kuletz. 1995. Mortality of marbled murrelets due to oil pollution in North America p. 261-269. *In* C.J. Ralph, G.L. Hunt, Jr, M.G. Raphael, and J.F. Piatt (eds) Ecology and conservation of the marbled murrelet USDA For Serv Gen Tech Rep PSW-GTR-152.

Cooney, R.T., K.O. Coyle, E. Stockmar and C. Stark. 2001. Seasonality in surface-layer net zooplankton communities in Prince William Sound, Alaska. Fisheries Oceanography 10:97–109.

Daunt, F., V. Afanasyev, J.R.D. Silk and S. Wanless. 2006. Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. Behavioural Ecology and Sociobiology 59:81-388.

Day, R.H. 2006. Seabirds in the northern Gulf of Alaska and adjacent waters, October to May. Western Birds 37:190-214.

Dean, T.A., L. Haldorson, D.R. Laur, S.C. Jewett and A. Blanchard. 2000. The distribution of nearshore fishes in kelp and eelgrass communities in Prince William Sound, Alaska: associations with vegetation and physical habitat characteristics. Environmental Biology of Fishes 57:271–287.

Decker, M.B. and G.L. Hunt, Jr. 1994. Foraging by murres (Uria spp.) at tidal fronts surrounding the Pribilof Islands, Alaska, USA. Mar. Ecol. Prog. Ser. 139: 1–10.

Dunn, E.K. 1973. Changes in fishing ability of terns associated with wind speed and sea surface conditions. Nature 244:520-521.

Fauchald, P., K.E. Erikstad and H. Skarsfjord. 2000. Scale-dependent predator–prey interactions: the hierarchical spatial distribution of seabirds and prey. Ecology 81:773–783.

Fauchald, P. 2009. Spatial interaction between seabirds and prey: review and synthesis. Marine Ecology Progress Series 391:139-151.

Finney, S.K., S. Wanless and M.P. Harris. 1999. The effect of weather conditions on the feeding behaviour of a diving bird, the Common Guillemot *Uria aalge*. Journal of Avian Biology 30:23-30.

Fort, J., W.P. Porter and D. Grémillet. 2009. Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic. Journal of Experimental Biology 212: 2483-2490.

Frederiksen, M., F. Daunt, M.P. Harris and S. Wanless. 2008. The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. Journal of Animal Ecology 77:1020-1029.

Garthe, S. 1997. Influence of hydrography, fishing activity, and colony location on summer seabird distribution in the south-eastern North Sea. ICES Journal of Marine Science 54:566–577.

Garthe, S., N. Markones, O. Hüppop, S. Adler. 2009. Effects of hydrographical and meteorological factors on seasonal seabird abundance in the southern North Sea. Marine Ecology Progress Series 391:243–255.

Gay, S.M. III and S.L. Vaughan. 2001. Physical oceanography of nursery habitats of juvenile Pacific herring. Fisheries Oceanography 10:159-173.

GES DISC (Goddard Earth Sciences Data and Information Services Center). 2009. Accessed Jan 12. http://discscigsfcnasagov/giovanni.

Gremillet, D., I. Tuschy, M. Kierspel. 1998. Body temperature and insulation in diving Great Cormorants and European Shags. Functional Ecology 12:386-394.

Hamilton, J. and B. Konar. 2007. Implications of substrate complexity and kelp variability for south-central Alaskan nearshore fish communities. Fisheries Bulletin 105:189–196.

Harris, M.P. and S. Wanless. 1989. Fall Colony Attendance and Breeding Success in the Common Murre. Condor 91:139-146.

Harris, M.P. and S. Wanless. 1996. Differential responses of Guillemot *Uria aalge* and Shag *Phalacrocorax aristotelis* to a late winter wreck. Bird Study 43:220-230.

Hooker, S.K. and R.L. Gerber. 2004. Marine Reserves as a Tool for Ecosystem-Based Management: The Potential Importance of Megafauna. Bioscience 54:27-39.

Hunt, G.L., F. Mehlum, R.W. Russell, D. Irons, M.B. Decker and P.H. Becker. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. International Ornithological Congress 22: 2040–2056.

Hunt, G.L., G.S. Drew, J. Jahncke and J.F. Piatt. 2005. Prey consumption and energy transfer by marine birds in the Gulf of Alaska. Deep-Sea Research II 52:781-797.

Hyrenbach, K.D., R.R. Veit, H. Weimerskirch, G.L. Hunt. 2006. Seabird associations with mesoscale eddies: the subtropical Indian Ocean. Marine Ecology Progress Series 324:271–279.

IUCN. 2010. IUCN Red List of Threatened Species Version 20103.

Jodice, R.G.R. and M.W. Collopy. 1999. Diving and foraging patterns of marbled murrelets *Brachyramphus marmoratus*: testing predictions from optimal-breathing models. Canadian Journal of Zoology 77:1409-1418.

Johnson, S.W., J.F. Thedinga, K.M. Munk. 2008. Distribution and use of shallow-water habitats by Pacific sand lances in southeastern Alaska. Transactions of the American Fisheries Society 137:1455–1463.

Johnson, S.W., J.F. Thedinga, A.D. Neff, P.M. Harris, M.R. Lindeberg, J.M. Maselko and S.D. Rice. 2010. Fish Assemblages in Nearshore Habitats of Prince William Sound, Alaska. Northwest Science 84:266-280.

Kooyman, G.L., R.L. Gentry, W.P. Bergman and H.T. Hammel. 1976. Heat loss in penguins during immersion and compression. Comparative Biochemistry and Physiology 54:75–80.

Kuletz, K.J., D.B. Irons, B.A. Agler, J.F. Piatt and D.C. Duffy. 1997. Long-term changes in diets and populations of piscivorous birds and mammals in Prince William Sound, Alaska p. 703-706. *In* Proc. Forage fishes in marine ecosystems. Alaska SeaGrant. Univ. Alaska, Fairbanks.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Logerwell, E.A. and N.B. Hargreaves. 1996. The distribution of sea birds relative to their fish prey off Vancouver Island: opposing results at large and small spatial scales. Fisheries Oceanography 5:163–175.

McKnight, A., K.M. Sullivan, D.B. Irons, S.W. Stephensen and S. Howlin. 2006. Marine bird and sea otter population abundance of Prince William Sound, Alaska: trends following the T/V Exxon Valdez Oil Spill, 1989-2005. Exxon Valdez Oil Spill Restoration Project Final Report (Restoration Project 050751) U S Fish and Wildlife Service, Anchorage, Alaska.

Moffitt, S., B. Marston and M. Miller. 2002. Summary of Eulachon Research in the Copper River Delta, 1998-2002, Alaska Department of Fish and Game, unpublished report.

Molnia, B. 2001. Glaciers of Alaska Alaska Geographic vol 28, no2 Alaska Geographic Society, Anchorage, Alaska.

Naslund, N.L. 1993. Why Do Marbled Murrelets Attend Old-Growth Forest Nesting Areas Year-Round? Auk 110:594-602.

Niebauer, H.J., T.C. Royer, T.J. Weingartner. 1994. Circulation of Prince William Sound, Alaska. Journal of Geophysical Research 99:14113 – 14126.

NOAA (National Oceanic and Atmospheric Administration) Fisheries. 2009. Alaska ShoreZone coastal mapping and imagery. Accessed Jan12 2010. http://wwwalaskafisheriesnoaagov/habitat/shorezone/szintrohtm

NOAA (National Oceanic and Atmospheric Administration). 2010. National Data Buoy Center. Accessed Sept 26. http://wwwndbcnoaagov/

Norcross, B.L., E.D. Brown, R.J. Foy, M. Frandsen, S.M. Gay III, T.C. Kline Jr, D.M. Mason, E.V. Patrick, A.J. Paul and K.D.E. Stokesbury. 2001. A synthesis of the life history and ecology of juvenile Pacific herring in Prince William Sound, Alaska. Fisheries Oceanography 10:42–57.

Okes, N.C., P.A.R. Hockey, L. Pichegru, C.D. van der Lingen, R.J.M. Crawford, D. Grémillet. 2009. Competition for shifting resources in the southern Benguela

upwelling: seabirds versus purse-seine fisheries. Biological Conservation 142:2361-2368.
Ouwehand, J., M.F. Leopold, C.J. Camphuysen. 2004. A comparative study of the diet of Guillemots *Uria aalge* and Razorbills *Alca torda* killed during the Tricolor oil incident in the south-eastern North Sea in January 2003. Atlantic Seabirds 6:147-164.
Petersen, M.R., W.W. Larned and D.C. Douglas. 1999. At-sea distribution of spectacled eiders: a 120-year-old mystery resolved. Auk 116:1009-1020.
Peterson, C.H., S.D. Stanley, J.W. Short, D. Esler, J.L. Bodkin, B.E. Ballachey, D.B. Irons. 2003. Long-term ecosystem response to the Exxon Valdez oil spill. Science 302:2082-2086.
Piatt, J.F. and R.G. Ford. 1996. How many seabirds were killed by the Exxon Valdez oil spill?American Fisheries Society Symposium 18:712-19.
Piatt, J.F., K.J. Kuletz, A.E. Burger, S.A. Hatch, V.L. Friesen, T.P. Birt, M.L. Arimitsu, G.S. Drew, A.M.A. Harding and K.S. Bixler. 2007. Status review of the marbled murrelet *Brachyramphus marmoratus* in Alaska and British Columbia U S Geological Survey, Open-File Report 2006-1387.
Piatt, J.F. and T.I. Van Pelt. 1997. Mass-mortality of Guillemots *Uria aalge* in the Gulf of Alaska in 1993. Marine Pollution Bulletin 34:656-662.
Pichegru, L., P.G. Ryan, R.J.M. Crawford, C.D. van der Lingen CD and D. Grémillet. 2010. Behavioural inertia places a top marine predator at risk from environmental change in the Benguela upwelling system. Marine Biology 157:537-544.
Roth, J.E., K.L. Mills and W.J. Sydeman. 2007. Chinook salmon *Oncorhynchus tshawytscha* – seabird covariation off central Califronia and possible forecasting applications. Canadian Journal of Fisheries and Aquatic Science 64:1080-1090.
Sanger, G.A. 1987. Winter diets of Common Murres and Marbled Murrelets in Kachemak Bay, Alaska. Condor 89:426-430.
Shealer, D.A. 2002. Foraging behavior and food of seabirds Pages 137-178 in EA Schreiber and J Burger (eds). Biology of Marine Birds, CRC Press, New York.
Schroeder, I. D. 2007. Annual and interannual variability in the wind field and hydrography along the Seward Line in the northern Gulf of Alaska, Ph.D. dissertation, Old Dominion University, Norfolk, VA.
Skov, H., J. Durinck, M.F. Leopold, M.L. Tasker. 1995. Important Bird Areas for seabirds in the North Sea, including the Channel and Kattegat. BirdLife International, Cambridge.
Skov, H., J. Durinck and P. Andell. 2000. Associations between wintering avian predators and schooling fish in the Skagerrak-Kattegat suggest reliance on predictable aggregations of herring *Clupea harengus*. Journal of Avian Biology 31:135–143.
Stabeno, P.J., N.A. Bond, A.J. Hermann, C.W. Mordy and J.E. Overland. 2004. Meteorology and Oceanography of the Northern Gulf of Alaska. Progress in Oceanography 24:859-897.
Stokesbury, K.D.E., J. Kirsch, E.D. Brown, G.L. Thomas, B.L. Norcross. 2000. Spatial Distributions of Pacific herring and walleye pollock in Prince William Sound, Alaska. Fisheries Bulletin 98:400-409.
Suryan, R.M., D.B. Irons, M. Kaufman, J. Benson, P.G.R. Jodice, D.D. Roby and E.D. Brown. 2002. Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the black-legged kittiwake *Rissa tridactyla*. Marine Ecology Progress Series 236:273–287.
Tasker, M.L., C.J. Camphuysen, J. Cooper, S. Garthe, W.A. Montevecchi, S.J.M. Blaber. 2000. The impacts of fishing on marine birds. ICES Journal of Marine Science 57:531–547.

Taylor, I.R. 1983. Effect of wind on the foraging behavior of Common and Sandwich Terns. Ornis Scandinavica 14:90-96.
Thorne, R.E. and G.L. Thomas. 2008. Herring and the "Exxon Valdez" oil spill: an investigation into historical data conflicts. ICES Journal of Marine Science 65:44–50.
Thorne, R.E. 2010. Trends in adult and juvenile herring distribution and abundance in Prince William Sound Exxon Valdez Oil Spill Restoration Project Final Report, (Restoration Project 070830), Prince William Sound Science Center, Cordova, Alaska.
USFWS. 2007. North Pacific Pelagic Seabird Observer Program Observers Manual, Inshore / small vessel version, November 2007 US Fish and Wildlife Service, Migratory Bird Management Nongame Program, Anchorage, Alaska Unpublished protocol manual.
Vaitkus, G. 2001. Spatial dynamics of regional wintering populations of seabirds in the gradient of winter climatic conditions. Acta Zoologica Lituanica 11: 273-280.
Vaughan, S.L., C.N.K. Mooers and S.M. Gay III. 2001. Physical variability in Prince William Sound during the SEA Study (1994-98). Fisheries Oceanography 10:58-80.
Vlietstra, L.S. 2005. Regional prey abundance affects local spatial associations between marine birds and acoustically determined prey in Monterey Bay, California. Marine Ecology Progress Series 291:275-287.
Wang, J., M. Jin, V. Patrick, J. Allen, D. Eslinger and T. Cooney. 2001. Numerical simulation of the seasonal ocean circulation patterns and thermohaline structure of Prince William Sound, Alaska using freshwater of a line source. Fisheries Oceanography 10:132-148.
Weichler, T., S. Garthe, G. Luna-Jorquera and J. Moraga. 2004. Seabird distribution on the Humboldt Current in northern Chile in relation to hydrography, productivity, and fisheries. ICES Journal of Marine Science 61:148-154.
Weimerskirch, H. 2007. Are seabirds foraging for unpredictable resources? Deep-Sea Research II 54:211–223.
Willette, M., M. Sturdevant and S. Jewett. 1997. Prey resource partitioning among several species of forage fishes in Prince William Sound, Alaska p. 11-29. *In* Proc. Forage fishes in marine ecosystems. Alaska SeaGrant. Univ. Alaska, Fairbanks.
Wood, S.N. 2006. Generalized Additive Models: An Introduction with R Chapman & Hall/CRC.
Yen, P.P.W., W.J. Sydeman and K. Hyrenbach. 2004. Marine bird and cetacean associations with bathymetric habitats and shallowwater topographies: implications for trophic transfer and conservation. Journal of Marine Systems 50:79–99.
Yen, P.P.W., W.J. Sydeman, S.J. Bograd and K.D. Hyrenbach. 2006. Spring-time distributions of migratory marine birds in the southern California Current: oceanic eddy associations and coastal habitat hotspots over 17 years. Deep Sea Research II 53:399–418.
Zuur, A.F., E.N. Ieno, N. Walker, A.A. Saveliev and G.M. Smith. 2009. Mixed effects models and extensions in ecology. R Springer.
Zuur, A.F., E.N. Ieno and C.S. Elphick. 2010. A protocol for data exploration avoiding common statistical problems. Methods in Ecology and Evolution 10:204-210.
Zuur, A.F., N.M. Dawson, M.A. Bishop, K.J. Kuletz, A.A. Saveliev and E.N. Ieno (in press). Zero inflated Common Murre density data. *In* Zuur A.F., Saveliev A.A., Ieno E.N. (eds) Analysing Ecological Data - Practical Solutions When Things Get Complicated.

CHAPTER 1 TABLES

Table 1-1. Continuous explanatory variables included in analyses.

Variable	Range	Mean
Depth (m)	0 – 748	138 (± 3)
Distance to shore (m)	8 – 9952	1558 (± 28)
Distance to eelgrass bed (m)	28 – 13,509	2295 (± 44)
Distance to kelp bed (m)	34 – 70,921	23,649 (± 404)
Sea surface temperature (C^o)	-1 - +8	4 (± 0.1)
Slope (^{o})	0 – 28	3 (± 0.1)

Table 1-2. Pre-selected models for Common Murre, large gulls (Glaucous-winged Gull and Herring Gull) and Marbled Murrelet. Hypotheses leading to model selection are shown with models for each species in Appendix 1. Year = winter 2007/08 or winter 2008/09; SST = sea surface temperature.

Model	Common Murre	Large Gulls	Marbled Murrelet
M1.	Month/year	Month/year	Month/year
M2.	SST	SST	Depth
M3.	Marine habitat and month/year (with interaction)	SST and distance to shore	SST and distance to shore (with interaction)
M4.	Marine habitat, slope and month/year	SST and year	Marine habitat and month/year (with interaction)
M5.	Month/year and exposure (with interaction)	Marine habitat and month/year (with interaction)	Distance to shore and month/year (with interaction)
M6.	Distance to shore and month/year (with interaction)	Distance to shore	Distance to shore, slope and substrate (with interaction between shore and substrate)
M7.	Exposure, Distance to shore and year (with interaction between exposure and year)	Distance to shore and month/year (with interaction)	Marine habitat, slope and month/year (with interaction between marine habitat and Month/year)
M8.	Latitude, longitude and month/year (with interactions)	Distance to shore, slope and substrate	month/year and exposure (with interaction)
M9.	Latitude, longitude, marine habitat and SST (with interaction between Marine habitat and SST)	Marine habitat, slope and month/year	SST, distance to shore, exposure and marine habitat (with interaction between SST and exposure, exposure and marine habitat)
M10.	Distance to eelgrass and SST	month/year and exposure (with interaction)	Latitude, longitude and month/year (with interactions)
M11.	SST and exposure (with interaction)	Exposure, distance to shore and year (with interaction between exposure and year)	Latitude, longitude marine habitat and SST (with interaction between marine habitat and SST)
M12.	SST and year	Latitude, longitude and month/year (with interactions)	Distance to eelgrass and SST
M13.	SST and distance to shore (with interaction)	Latitude, longitude, marine habitat and SST (with interaction between SST and marine habitat)	Marine habitat and depth (with interaction)
M14.	Slope and substrate	Distance to eelgrass	Distance to eelgrass,

	(with interaction)	and SST	substrate and month/year (with interaction between eelgrass and month/year and substrate and month/year)
M15.	Marine habitat and depth (with interaction)	Distance to kelp, depth and month/year (with interaction between kelp and month/year and depth and month/year)	Marine habitat, depth, distance to shore, substrate and month/year (with interaction between marine habitat and depth, marine habitat and distance to shore, marine habitat and substrate, substrate and month/year)
M16.	Distance to shore, slope and substrate (with interaction between distance to shore and substrate)	Marine habitat and depth (with interaction)	

Table 1-3. Mean (± SE) densities (birds • km^{-2}) of three seabird species and one species group in Prince William Sound during two consecutive winters. Large Gulls included Glaucous-winged Gull and small numbers of Herring Gull.

Species	Winter	Nov	Jan	Mar
Common Murre	2007/08	1.71 (0.3)	11.66 (2.16)	19.39 (2.81)
	2008/09	3.88 (0.51)	14.87 (3.17)	11.26 (2.98)
Marbled Murrelet	2007/08	2.03 (0.39)	4.43 (2.29)	2.42 (0.34)
	2008/09	3.03 (0.50)	5.50 (1.71)	0.77 (0.13)
Black-legged Kittiwake	2007/08	0.56 (0.17)	0.04 (0.02)	2.35 (0.45)
	2008/09	1.90 (0.61)	0.01 (0.01)	0.11 (0.04)
Large Gulls	2007/08	1.79 (0.25)	16.45 (5.22)	1.32 (0.36)
	2008/09	3.70 (0.73)	2.88 (0.50)	1.80 (0.43)

Table 1-4. Results and selection of hurdle models for Common Murre. Selected models are in bold italics. Akaike's information criterion (AIC_c), AIC differences (ΔAIC), and Akaike weights (ω_i) are presented for both presence-absence and presence-only data. The names M1 to M16 refer to the 16 models presented in Table 2. A "B" in the model name refers to the model with the interaction. Hence, M3B contains marine habitat and time as main terms and the interaction between marine habitat and time. If a model did not converge no AIC information is presented.

	Presence-absence			Presence-only		
Model	AIC_c	ΔAIC	Akaike weights(ω_i)	AIC_c	ΔAIC	Akaike weights(ω_i)
M1	***10762.1***	***4.4***	***0.065***	2741.8	202.2	0
M2	***10757.7***	***0.0***	***0.592***	2710.3	170.7	0
M3	10780.6	22.8	0.000	2716.9	177.4	0
M3B	10822.4	64.7	0.000	2853.4	313.8	0
M4	10790.8	33.1	0.000	2736.9	197.3	0
M5	10767.0	9.3	0.006	2694.2	154.6	0
M5B	10820.2	62.4	0.000	***2539.6***	***0.0***	***1***
M6	10847.9	90.2	0.000	2595.1	55.5	0
M7	10821.2	63.4	0.000	2580.3	40.7	0
M7B	10826.0	68.3	0.000	2574.3	34.7	0
M8	10807.9	50.3	0.000	2727.3	187.7	0
M8B	10880.5	122.8	0.000	2702.3	162.7	0
M10	10784.2	26.5	0.000	2581.3	41.7	0
M11	***10763.0***	***5.3***	***0.042***	2736.5	196.9	0
M11B	10785.6	27.9	0.000	2583.3	43.7	0
M12	***10759.1***	***1.4***	***0.290***	2594.4	54.8	0
M13	10818.9	61.3	0.000	2724.4	184.8	0
M13B	10831.0	73.3	0.000	2614.6	74.9	0
M14	10766.9	9.2	0.006	2724.6	184.9	0
M15	10967.6	209.8	0.000	2641.7	102.1	0
M15B	10967.6	209.8	0.000	2722.9	183.4	0
M16				2674.8	135.2	0
M16B				2730.6	190.9	0

Table 1-5. Results and selection of hurdle models for large gulls (primarily Glaucous-winged Gull and small numbers of Herring Gull). Selected models are in bold italics. Akaike's information criterion (AIC_c), AIC differences (ΔAIC), and Akaike weights (ω_i) are presented for both presence-absence and presence-only data. The names M1 to M16 refer to the 16 models presented in Table 2. A "B" in the model name refers to the model with the interaction. Hence, M3B contains marine habitat and month/year as main terms and the interaction between marine habitat and time. If a model did not converge no AIC information is presented.

	Presence-absence			Presence-only		
Model	AIC_c	ΔAIC	Akaike weights(ω_i)	AIC_c	ΔAIC	Akaike weights(ω_i)
M1	***10883.6***	***0.3***	***0.442***	1743.9	42.2	0.000
M2	10947.4	64.2	0.000	1715.5	13.7	0.001
M3	10973.7	90.4	0.000	1725.1	23.3	0.000
M5	10910.6	27.4	0.000	1741.3	39.6	0.000
M5B	10952.8	69.6	0.000	1800.8	98.9	0.000
M6	***10883.2***	***0.0***	***0.515***	1774.5	72.7	0.000
M7	10899.8	16.6	0.000	1720.4	18.6	0.000
M7B	10965.7	82.5	0.000	1763.1	61.3	0.000
M8	10893.1	9.8	0.004	1760.0	58.2	0.000
M9	10914.3	31.0	0.000	1718.2	16.4	0.000
M10	10894.9	11.7	0.001	1779.8	78.0	0.000
M10B	10990.6	107.4	0.000	1754.8	52.9	0.000
M11	10888.5	5.3	0.037	1712.2	10.4	0.003
M11B	10918.4	35.2	0.000	1721.7	19.9	0.000
M12	10908.7	25.4	0.000	***1701.8***	***0.0***	***0.526***
M13	10989.9	106.7	0.000	1734.4	32.6	0.000
M14	10996.3	113.0	0.000	1721.7	19.9	0.000
M15	10901.4	18.2	0.000	1734.2	32.4	0.000
M15B				***1702.6***	***0.8***	***0.355***
M16	10897.1	13.8	0.001	1712.2	10.4	0.003
M16B	10936.2	52.9	0.000	***1704.9***	***3.1***	***0.112***

Table 1-6. Results and selection of hurdle models for Marbled Murrelet. Selected models are in bold italics. Akaike's information criterion (AICc), AIC differences (ΔAIC), and Akaike weights (ωi) are presented for both presence-absence and presence-only data. The names M1 to M16 refer to the 16 models presented in Table 2. A "B" in the model name refers to the model with the interaction. Hence, M3B contains marine habitat and month/year as main terms and the interaction between marine habitat and month/year. If a model did not converge no AIC information is presented.

	Presence-absence			Presence-only		
Model	AIC_c	ΔAIC	Akaike weights(ω_i)	AIC_c	ΔAIC	Akaike weights(ω_i)
M1	11765.1	27.3	0	1253.8	225.7	0
M2	11867.1	129.3	0	1232.3	204.2	0
M3	11765.6	27.8	0	1199.5	171.4	0
M3B	11763.6	25.8	0	1197.5	169.4	0
M4	11776.5	38.7	0	1262.9	234.9	0
M4B	11860.5	122.7	0	1146.4	118.3	0
M5	11803.2	65.4	0	1223.5	195.4	0
M5B	11950.7	212.9	0			
M6	11787.5	49.7	0	1183.8	155.7	0
M6B	11810.1	72.3	0	1173.0	144.9	0
M7	11786.5	48.7	0	1227.9	199.9	0
M7B	11871.7	133.9	0	1122.5	94.4	0
M8	11774.9	37.2	0	1256.8	228.7	0
M8B	11804.6	66.8	0	1277.0	248.9	0
M9	11775.8	37.9	0	1196.5	168.4	0
M10				1286.2	258.1	0
M10B	12017.2	279.4	0	1284.2	256.1	0
M11	***11737.8***	***0.0***	***1***	1271.8	243.7	0
M11B				1300.1	271.9	0
M12	11782.8	45.1	0	1196.4	168.3	0
M13	11873.4	135.6	0	1232.6	204.5	0
M13B	11937.2	199.4	0	1137.7	109.7	0
M14	11824.6	86.8	0	1200.5	172.4	0
M14B				1137.9	109.9	0
M15	11932.5	194.7	0	1202.6	174.6	0

CHAPTER 1 FIGURES

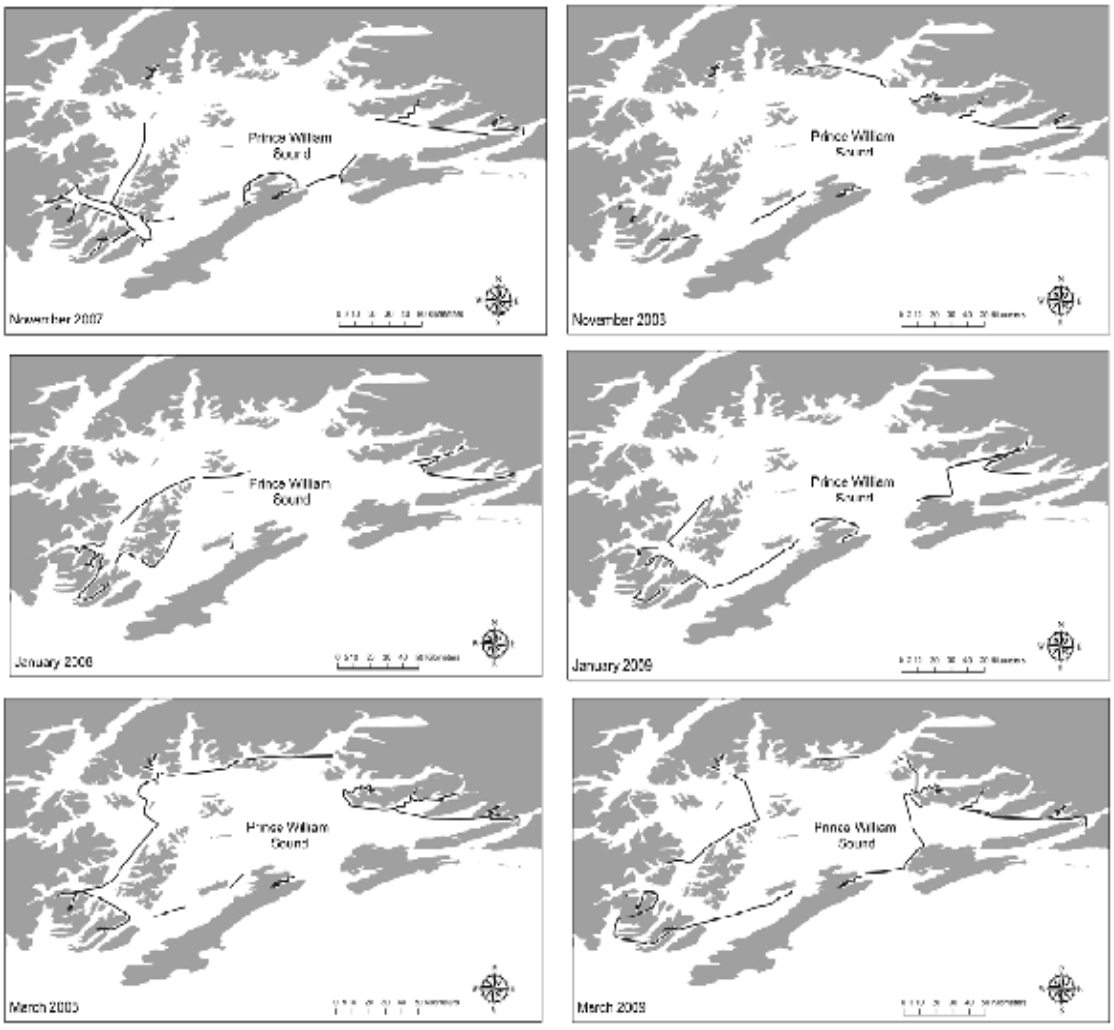

Figure 1-1. Map of Prince William Sound with survey tracks by month shown as dotted lines, November 2007- March 2009.

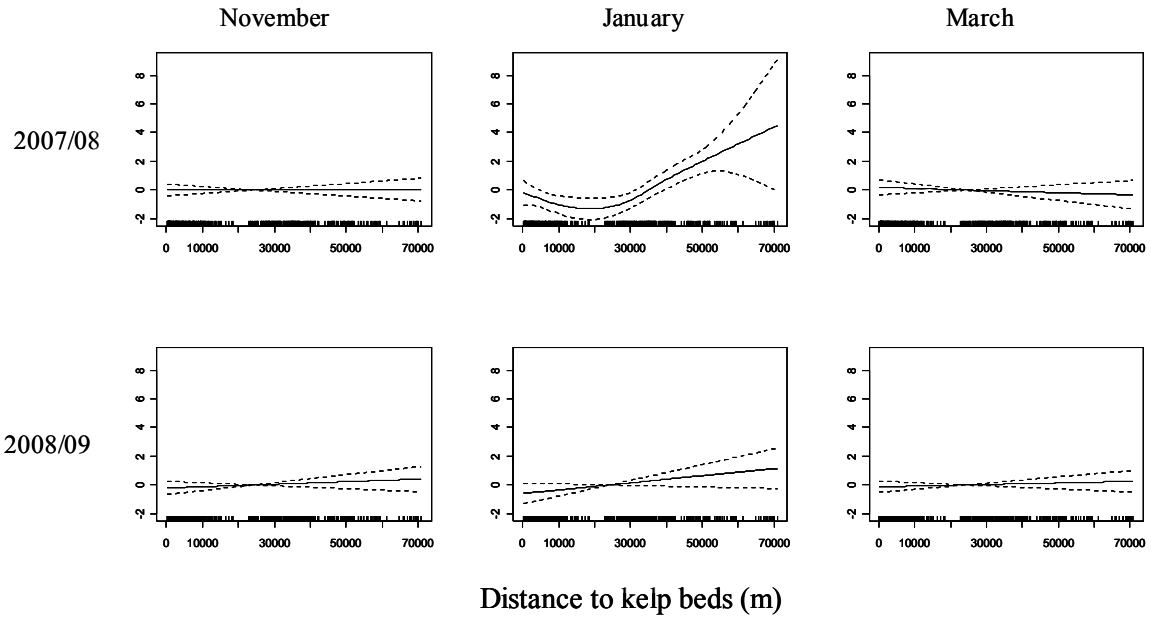

Figure 1-2. Density of large gulls relative to distance to kelp beds for each time period. The x-axis shows the gradient of each variable. The solid line represents the contribution of the smoothing terms to the fitted values in the overall model, showing a measure of preference for proximity to kelp beds. The dashed lines represent 95% confidence intervals.

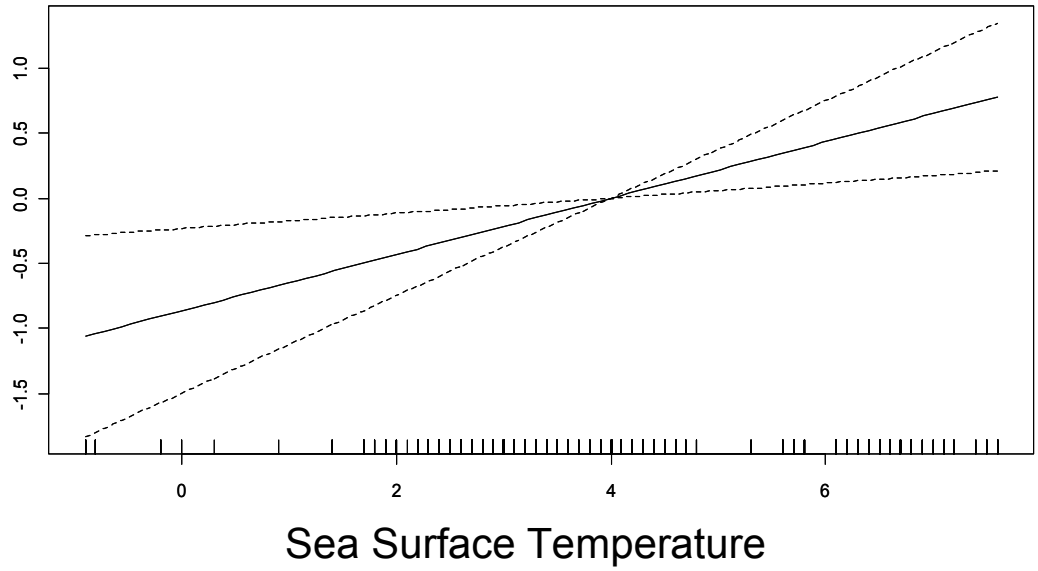

Figure 1-3. Marbled Murrelet occurrence relative to sea surface temperature (SST). The x-axis shows the gradient of SST. The solid line represents the contribution of the smoothing terms to the fitted values in the overall model, showing a measure of preference for warmer SSTs. Dashed lines represent 95% confidence intervals.

.

Appendix 1-1. Hypotheses for *a-priori* selected models for a) Common Murre, b) large gulls (Glaucous-winged and Herring Gulls) and c) Marbled Murrelet

a)

Model	Hypothesis	Models for Common Murre
M1.	Distribution varies randomly with time period	Month/year
2.	Birds avoid colder waters	SST
3.	Distinct habitat types selected at different times	Marine habitat and month/year (with interaction)
4.	Prey made available by seabed slope within habitat	Marine habitat, slope and month/year
5.	Storms influence at specific times	Month/year and exposure (with interaction)
6.	Birds move inshore at specific times for feeding opportunities	Distance to shore and month/year (with interaction)
7.	Movement inshore related to weather	Exposure, Distance to shore and year (with interaction between exposure and year)
8.	Geographical bias in distribution	Latitude, longitude and month/year (with interactions)
9.	Specific hotspot selected for prey mediated by temperature and habitat	Latitude, longitude, marine habitat and SST (with interaction between Marine habitat and SST)
10.	Prey found around eelgrass and warmer water	Distance to eelgrass and SST
11.	Cold and exposed waters avoided	SST and exposure (with interaction)
12.	Colder water avoided only at specific times	SST and year
13.	Birds tied to coast but select warmer water	SST and distance to shore (with interaction)
14.	Prey availability higher with slopes and certain substrate type	Slope and substrate (with interaction)
15.	Prey availability for Murres related to depth and habitat type	Marine habitat and depth (with interaction)
16.	Murres find more food inshore near bathymetry types and gradients.	Distance to shore, slope and substrate (with interaction between distance to shore and substrate)

b)

Model	Hypothesis	Models for large gulls
M1.	Distribution varies randomly with time period	Month/year
M2.	Birds avoid colder waters	SST
M3.	Birds remain closer to shore when lower SST	SST and distance to shore
M4.	SST affects distribution	SST and year
M5.	Birds use specific habitat at certain times of year	Marine habitat and month/year (with interaction)
M6.	Birds restricted to inshore waters in winter	Distance to shore
M7.	Movement inshore at specific period during winter	Distance to shore and month/year (with interaction)
M8.	Birds congregate at predictable feeding sites due to bathymetry	Distance to shore, slope and substrate
M9.	Gulls move to specific habitat for feeding at certain point in winter	Marine habitat, slope and month/year
M10.	Gulls avoid exposed waters at certain times during winter	Month/year and exposure (with interaction)
M11.	Birds move inshore avoiding exposed waters only in strormier years	Exposure, distance to shore and year (with interaction between exposure and year)
M12.	Geographical bias in distribution	Latitude, longitude and month/year (with interactions)
M13.	Specific hotspot selected for prey mediated by temperature and habitat	Latitude, longitude, marine habitat and SST (with interaction between SST and marine habitat)
M14.	Gulls drawn to feeding opportunities through warmer water and eelgrass beds	Distance to eelgrass and SST
M15.	Kelp beds and water depth provide feeding opportunities at certain times	Distance to kelp, depth and month/year (with interaction between kelp and month/year and depth and month/year)
M16.	Gulls select shallower bays for higher surface food availability in winter	Marine habitat and depth (with interaction)

c)

Model	Hypothesis	Models for Marbled Murrelet
M1.	Distribution varies randomly with time period	Month/year
M2.	Murrelets inhabit shallower waters	Depth
M3.	Murrelets inhabit warmer inshore waters	SST and distance to shore (with interaction)
M4.	Murrelets select specific habitat at certain point of winter	Marine habitat and month/year (with interaction)
M5.	Murrelets move inshore at certain point in winter	Distance to shore and month/year (with interaction)
M6.	Birds move inshore to areas with feeding opportunities based on bathymetry	Distance to shore, slope and substrate (with interaction between shore and substrate)
M7.	Murrelets move to specific habitat for feeding at certain point in winter	Marine habitat, slope and month/year (with interaction between marine habitat and Month/year)
M8.	Murrelets avoid exposed waters when seas stormiest in midwinter	Month/year and exposure (with interaction)
M9.	Murrelets select warmer less exposed waters close to shore within specific habitat	SST, distance to shore, exposure and marine habitat (with interaction between SST and exposure, exposure and marine habitat)
M10.	Geographical bias in distribution	Latitude, longitude and month/year (with interactions)
M11.	Favored areas relate to habitat and water temp	Latitude, longitude marine habitat and SST (with interaction between marine habitat and SST)
M12.	Water temp and eelgrass beds provide foraging opportunites	Distance to eelgrass and SST
M13.	Murrelets select specific depth of water for diving within habitat type	Marine habitat and depth (with interaction)
M14.	Murrelets favour areas with predictable prey based on substrate and eelgrass at certain point in winter	Distance to eelgrass, substrate and month/year (with interaction between eelgrass and month/year and substrate and month/year)
M15.	Murrelets have specific habitat preference feeding close to shore in specific substrate and depth	Marine habitat, depth, distance to shore, substrate and month/year (with interaction between marine habitat and depth, marine habitat and distance to shore, marine habitat and substrate, substrate and month/year)

CHAPTER 2. PACIFIC HERRING CONSUMPTION BY MARINE BIRDS DURING WINTER IN PRINCE WILLIAM SOUND, ALASKA

Mary Anne Bishop[1], Jordan Watson[1], Tawna Morgan[1], and Kathy Kuletz[2]

[1] Prince William Sound Science Centre, Cordova, Alaska USA 99574
[2] U.S. Fish and Wildlife Service, Migratory Bird Management, 1011 East Tudor Road, Anchorage, Alaska USA 99503

ABSTRACT

Following the 1989 *M.V. Exxon Valdez* oil spill (EVOS) and subsequent herring population collapse in Alaska's Prince William Sound (PWS), the Pacific Herring (*Clupea pallassii*) fishery was closed. In the two decades since EVOS the PWS herring population has failed to reach pre-spill populations levels and the fishery remains closed today. Assessment of age-structured herring mortality is necessary for developing stock recruitment models and evaluating continued pressures on herring recovery. In this study we estimated the biomass of juvenile and adult herring consumed by marine birds in PWS during 10 winters between 1989 and 2007. We also assessed the potential relationship between avian herring consumption and available herring biomass at 0 – 5 year time scales. As a group marine birds consumed an average of 2.8 – 10.2% of the total adult herring biomass (up to 5,013 t) in a given winter, indicating that avian consumption may represent a substantial and highly variable source of adult herring mortality. Total juvenile herring biomass is unknown, however, on average the avian consumption of juvenile herring was estimated at 1,572 $\pm$ 569 t. Common Murre (*Uria aalge*) consumed the greatest quantity of herring in all years (max = 4,055 t) and like most other species investigated, they depredated a greater portion of juvenile herring than adult herring. Analyses of model parameters showed the model was more sensitive to perturbations in the proportions of herring in the diet and the avian assimilation rate than other model parameters such as bird population size and bird body mass. A model incorporating time lag analysis of 1-5 years showed that consumption of adult herring negatively impacted the amount of spawn observed in the following year but such effects were not observed more than 2 years after consumption. Herring consumption by marine birds in PWS during the winter may account for a major source of mortality, especially during years in which herring recruitment is low or during which bird populations are particularly large.

INTRODUCTION

Globally, seabirds consume nearly an equivalent amount of fish biomass as the commercial fishing industry (Brooke 2004). The largest proportion of fish consumption by seabirds occurs at high latitudes in regions with limited or no commercial fishing industry (*op. cit.*), thus not directly competing with fisheries as an economic resource. In areas where fishing and seabirds overlap there may be competition for resources and the need to accurately assess stocks is magnified (Wanless 1998, Brooke 2004). At times, creative, conservative fisheries management and attention to native predators may be necessary for population recovery of endangered or at risk fish species (Goodrich and Buskirk 1995).

Herring (*Clupea spp.*) are abundant, schooling fish that are the target of major commercial fisheries in both the North Pacific Ocean and the North Atlantic Ocean. Herring are

also a key forage fish for breeding and wintering seabirds in those same areas (Skov et al. 2000, Kuletz 2005, Overholtz and Link 2007). Atlantic Puffins (*Fratercula arctica)* along the east coast of the Norwegian Sea are estimated to consume more than 160,000 t of age 0+ Atlantic herring (*C. harengus*) during the breeding season (Anker-Nilssen and Øyan 1995 cited in Barrett et al. 2002). In the Gulf of Maine, seabirds consumed an estimated 9000 t of Atlantic herring in 2002 (Overholtz and Link 2007). Along the Pacific Coast of Vancouver Island, common murre (*Uria aalge*) and shearwaters (*Puffinus spp.*) consumed on average 16% of the annual juvenile Pacific herring *(C. pallasii*) biomass (Logerwell and Hargreaves 1996).

In Alaska's Prince William Sound (PWS) Pacific herring was historically an important fishery with an annual harvest up to 20,000 metric tons (Lewis et al. 2008). In addition to its economic significance, herring is a critical component of the PWS ecosystem. With its high lipid content (Anthony et al. 2000, Iverson et al. 2002) herring is the principal forage fish for nearshore PWS seabirds (Duffy 2000, Irons et al. 1992, Kuletz 2005). During the breeding season, Marbled Murrelet (*Brachyramphus marmoratus*) and Black-legged Kittiwake (*Rissa tridactyla*) will select herring over other forage fish, even during times of low availability (Suryan et al. 2002, Ostrand et al. 2004). In winter, some 18 marine bird species are known or suspected to forage on juvenile and or adult herring (Bishop et al., chapter 2, this report) while in spring herring spawn provides an important food resource for a variety of birds, including gulls, sea ducks, and migrant shorebirds (Bishop and Green 2001).

In March 1989 the *MV Exxon Valdez* oil spill (EVOS) occurred in PWS releasing 42 million litres of crude oil. Subsequently, the PWS herring population collapsed (Thorne and Thomas 2011) and has yet to recover (EVOS Trustee Council 2010). The post-EVOS herring crash in PWS has been implicated in the decline of several marine bird species. Kuletz (2005) concluded that juvenile herring were critical to the Marbled Murrelet and suggested that the population decline in PWS murrelets was linked to the concurrent herring decline. Similarly, Irons and others (2000) determined that the effects of EVOS on several marine birds lasted longer than expected and may be the result of reduced forage fish abundance. In addition, they found that the most persistent declines were associated with seabirds that over-winter in PWS, while birds that migrated south for the winter recovered more quickly.

Although herring is considered more resilient than other marine fish because it matures early in life and is fished with highly selective gear (Hutchings 2000), herring population declines may take decades to recover. In PWS, a critical bottleneck for herring recruitment is juvenile abundance and the condition of young-of the-year during the October to March winter months, a period when zero or negative growth rates occur (Paul and Paul 1998). Mortality rates for juvenile herring are highest during winter (Stokesbury et. al. 2002), which strongly influences stock recruitment in subsequent years (Brown 2003). Sea surface temperature, ocean currents, disease, competition and predation can all influence stock recruitment by affecting first year survivorship (Schweigert 1995, Ware 1995; Williams and Quinn 2000a, 2000b; Marty et al. 2010). Brown (2003) suggested that abundance of 1+ juvenile herring should be directly correlated with adult recruitment two or three years later unless the local population is under intense predation pressure. Furthermore, she suggested that stable or increasing predator populations in PWS could constrain or further reduce herring recruitment when the juvenile herring population is increasingly composed of smaller and fewer schools over a reduced geographic range.

Herring population recovery and successful management of herring in PWS requires detailed knowledge of age-specific mortality and significant pressures on population growth. In this study we use a bioenergetics simulation model to estimate consumption of Pacific herring by marine birds wintering in PWS. The objectives of this study were to: (1) estimate the biomass of juvenile and adult herring consumed by marine birds during the winter months; and, (2) compare our consumption estimates with the adult herring biomass available during the same time period. Our results are designed to inform herring stock recruitment models by improving the mortality estimate.

METHODS

Study Area

Prince William Sound (PWS) is located on the coast of southcentral Alaska, primarily between 60° and 61°N. The Sound is separated from the adjacent Gulf of Alaska by large, mountainous islands. The coastline is rugged and extensive, with many islands, fjords and bays. Water depths in fjords and bays range from <50 m to >400 m; outside of the bays and fjords are many basins and passages of varying depths up to 700 m. Annual precipitation can be as much as 5.4 m. Sea surface temperatures can be as low as 1° C in late winter, with some inner bays and fjords blocked with ice (Gay and Vaughan 2001).

Consumption Estimation Model

We estimated herring biomass consumption for 18 piscivorous bird species that reside in the marine waters of PWS during winter and consume herring on a regular basis (Fig. 1, Table 1). For each winter, a species' herring consumption (C) is determined by the equation:

$$C = \sum_{d=1}^{D} \sum_{a=1}^{A} (N * E_a) / K_a$$

Where D is the number of days between 15 November and 15 March a species resides in Prince William Sound, N is the bird species population size, A is the number of herring age classes consumed (juvenile or adult), E_a is the daily energy requirement (kJ day^{-1}) from herring of age class a, and K_a is the energy content (kJ g^{-1}) of an individual fish of age class a. We defined juvenile herring as age 0+ to 2+ and adults as all herring 3+ and over.

For this study, we utilized species population estimates and relevant unidentified species group (e.g., "unidentified gull", "unidentified loon") population estimates from ten US Fish and Wildlife Service (USFWS) surveys conducted in March over a period of 18 years: 1990, 1991, 1993, 1994, 1996, 1998, 2000, 2004, 2005, and 2007 (McKnight et. al. 2008; Appendix 1). We assumed that all birds resided in PWS from 15 November to 15 March (n = 120 d) except Black-legged Kittiwake. Because Black-legged Kittiwake are absent from PWS during mid winter (see Cpt. 1), we adjusted residency time to 60 d.

Diet composition in winter is not readily available for marine birds in Alaska. Therefore, we used a composite of information obtained from published literature and unpublished data (Table 1) to estimate for each species a proportion of herring in the daily diet. Small marine birds such as Red-necked Grebe, Horned Grebe, Mew Gull, Black-legged Kittiwake, Marbled

Murrelet, and Pigeon Guillemot cannot effectively consume most adult herring, so the mean proportion of adult herring consumed was assumed to be 0. Other species such as large loons can forage deep in the water column and target primarily larger adult herring. Estimated proportions reflect the amounts of daily kJ acquired from juvenile and/or adult herring.

In order to calculate $E_{a,}$ the daily energy requirement (kJ day^{-1}) from herring age class *a*, we first determined the total daily energetic expenditure (field metabolic rate) *F* (kJ d^{-1}) for an individual bird using allometric equations formulated by Birt-Friesen et al. (1989). For gulls and kittiwakes, we used the equation for seabirds using flapping flight in cold waters: $\log F = 3.24 + (0.727 * \log x)$. For the remaining species we used the equation for seabirds in cold waters: $\log F = 3.13 + (0.646 * \log x)$ where for both equations *F* is in kJ d^{-1} and *x* is body mass (kg). We obtained body mass data for each species (Table 1) from records within Alaska and PWS when available. Otherwise, body mass data were obtained from Dunning (2007) and the respective Birds of North America species account. We then calculated E_a, daily energy requirement (kJ day^{-1}) from herring of age class *a* as:

$$E_a = (F / 0.75) * (H * P_a)$$

Where F is the total daily energy requirement, 0.75 is the assumed assimilation rate (Furness and Tasker 1977), H is the proportion of herring in the diet and P_a is the proportion of each age class of herring.

Depending on the age of a herring, energy density declines over winter (Foy and Paul 1999). We used the following linear equations to calculate the energy density (kJ g^{-1}) of an adult ($K_{a;}$ R. Hientz, unpub. data) and juvenile ($K_{j;}$ T. Kline, unpub. data) herring on a given day:

$$K_{a,} = (9.64 - 0.0199 * d)$$

$$K_j = (5.67 - 0.0108 * d)$$

Where for adult herring, d = days since 15 September and for juvenile herring d = days since 15 November.

To account for uncertainty in our parameter estimates, we used a Monte Carlo simulation approach and performed all analyses using R (R version 2.12.2). One thousand model simulations were run for each species and for each survey year (Fig. 1). Input parameters for population size, proportion of herring in the diet, and marine bird body mass were assigned uniform input distributions. The distribution bounds for each species population and body mass (kg) parameter were set as the mean plus or minus one standard deviation (sd). To accommodate the high uncertainty about the actual amounts of herring in winter diets, the distributions of: a) proportion of herring; and, b) proportion of adult herring in the diet were set at the input value ± 0.25 and were bounded between 0 and 1. However, if the proportion of adult herring was set at 0 (e.g. Mew Gull, Black-legged Kittiwake, Marbled Murrelet, Pigeon Guillemot, and grebes), the proportion was fixed at 0 and not sampled from a distribution. For all species, proportion of juvenile herring was then calculated as the remainder of herring in the diet.

For unidentified loons, grebes, mergansers, murres and murrelets, we used the model inputs for the most common species in that group. For example, Thick-billed Murre (*Uria lomvia*) and Kittlitz's Murrelet (*Brachyramphus brevirostris*) are rare in PWS during winter, therefore unidentified murres and murrelets were assigned to Common Murre and Marbled

Murrelet input distributions, respectively. For gulls, we assigned 1/3 of each survey's unidentified gulls to input distributions for Glaucous-winged Gulls (1/3), Mew Gull (1/3), and Black-legged Kittiwake (1/3).

Sensitivity Analysis

We measured the sensitivity of our herring consumption model parameters using a Monte Carlo error analysis method (Bartell et al. 1986; Hunsicker and Esssington 2008). Our consumption model was run a total of 10,000 times and a parameter's influence on the model was assessed using relative partial sums of squares (RPSS). In this method, consumption of juvenile and adult herring are each regressed against all model parameters (the full model) and the total sum of squares partitioned by comparison with successive regression models, each omitting a single model parameter (Rose et al. 1991). Each parameter is assigned a nominal value equal to the mean of that parameter across all species and drawn randomly from either a uniform distribution or a normal distribution (for those parameters with more robust error estimates). The parameter estimates drawn from a uniform distribution (nominal values provided in parentheses) include population ($\mu = 6039$), bird mass ($\mu = 1.185$g), proportion of herring in diet ($\mu = 0.32$), proportion of adult herring in diet ($\mu = 0.26$), and daily energy requirement for seabirds in cold waters ($\log \mu = 3.13 + (0.646 * \log \text{mass})$ while the remaining parameters were drawn from a normal distribution: assimilation rate ($\mu = 0.75$), juvenile herring energy content (5.67-0.0108*(number of days since November 15)) and adult herring energy content (8.4261-0.0199*(number of days since September 15)). Model sensitivity was examined with coefficients of variation (CV) of 2%, 10% and 20% for juvenile and adult herring consumption.

Lag Analysis

We investigated the potential impact that marine bird consumption in one year may have on herring populations 1 to 5 years later, using linear regression models. Due to the relatively low number of data points in this analysis, correlations were expected to be highly subject to outliers. In 1993 for example, extremely high numbers of Common Murre were present, resulting in much higher consumption in that year. Thus we also performed the lag analysis while excluding 1993.

We examined the roles of marine bird consumption of both juvenile and adult herring by looking at several different metrics for herring abundance (Table 2): miles of spawn and mile days of spawn were based on Alaska Department of Fish and Game (ADFG) aerial surveys (Botz et al. 2010; ADFG unpubl. data 2011) and are indicative of spawning biomass. Estimates of adult herring biomass are taken from acoustic surveys in fall (1992 and 1993) or spring (1995-2010; Thorne and Thomas 2008, Thorne 2010, ADFG unpubl. data) and represent a direct measure of spawning biomass.

RESULTS

Total herring consumption by marine birds averaged 2387 ± 675 tons (t) for the 10 winters (1989-1990 through 2006-2007). Consumption varied inter-annually with a maximum of 5013 ± 1549 t in 1992-93 winter and a minimum of 841 ± 158 t in 1989-90, the first winter

following EVOS (Fig. 2). Consumption was driven by high population numbers of Common Murre during 1992-93, 1997-98, and 2004-05 winters and Glaucous-winged Gulls during winter 1993-94. Common Murre (including unidentified murre) was the largest consumer of adult herring in 8 of the 10 winters ($\bar{x}$ = 507 $\pm$ 341 t) with Pelagic Cormorant and Common Loon the largest consumers during 1989-90 and 1999-2000, respectively (Figs. 3, 4; Appendix 1). Common Murre was also the largest consumer of juvenile herring ($\bar{x}$ = 719 t $\pm$ 483) and Glaucous-winged Gull the second largest consumer during all winters (Fig. 3, 4). Marine birds consumed more juvenile ($\bar{x}$ = 1572 ± 569 t) than adult ($\bar{x}$ =814 ± 362 t) herring in all winters (paired t-test, $P < 0.001$; Fig. 2). The greatest difference between juvenile and adult herring consumption (1286 t) occurred during the 1992-93 winter when Common Murre made up the greatest proportion of the population (76%) compared to other years (10%-52%), and Glaucous-winged Gull made up the smallest proportion of the population (5%) compared to other years (8% - 26%).

Marine bird consumption of adult herring averaged 5.6% $\pm$2.5 of the available adult herring biomass. During two winters, 1992-93 and 1999-2000, over 10.1 and 10.2%, respectively of the available adult herring biomass was consumed. We were not able to estimate the proportion of juvenile herring removed as there was no data for total available juvenile herring.

Sensitivity analysis

The full models for juvenile and adult herring consumption revealed decreasing r^2 values as the CVs were increased from 2% to 20%, indicating an increasing degree of non-linearity with increasing CV (Table 3). Among the top five ranked model parameters for each of the scenarios evaluated, the CV value (2%, 10% or 20%) did not change the parameter rank order. For juvenile herring, the proportion of herring in the diet and the assimilation rate were the most important parameters, while adult herring consumption was dominated first by the proportion of adult herring in the diet and then by the proportion of herring in the diet followed by the assimilation rate.

Lag analysis

One to four years after consumption, lag analyses revealed significant correlations between marine bird herring consumption and spawning biomass. However, when 1993 was excluded from these analyses, most results were not significant ($p > 0.1$). Several significant correlations did still exist however, suggesting that marine bird consumption of adult herring may have a negative impact on miles of spawn ($r^2 = 0.594$, $p = 0.015$) and mile days of spawn ($r^2 = 0.42$, $p = 0.036$) in the year following consumption and mile days of spawn ($r^2 = 0.536$, $p = 0.015$) two years after consumption. Marine bird consumption of juvenile herring showed a negative impact on miles of spawn ($r^2 = 0.43$, $p = 0.046$) the year after juvenile herring were consumed.

DISCUSSION

Herring are the most abundant forage fish in PWS during winter. Multiple factors may be complicating the recovery of herring populations including disease, predation, and poor recruitment (EVOS Trustee Council 2010). Our study demonstrates the importance of marine bird consumption as a source of herring mortality. Our model showed that in winters with relatively low adult herring biomass, such as 1999-2000, or with relatively high numbers of

marine birds, such as 1992-93, more than 10% (1896 t) of the adult biomass and 3117 t of juvenile herring can be removed. This is especially important because PWS herring populations have remained low for two decades (EVOS Trustee Council 2010). While other Pacific herring populations along the west coast of the United States and Canada have occasionally yielded large recruitment events from low levels of spawning biomass, PWS herring populations have historically not exhibited such patterns (Funk 2007). This underscores the potentially large effect that intermediate to high levels of predation could have on a population with low levels of recruitment (Bakun 2006).

Common Murre, the most numerous marine bird during winter, consumed more herring than any other marine bird species in PWS in all winters. The variable amount of herring biomass consumed by murre reflects large but stochastic bird populations. For example, high overall herring consumption during the 1992-93 winter is largely due to elevated numbers (~221,000 birds) of Common Murre. Many of these birds had moved from the Gulf of Alaska in response to reduced food availability associated with an El Nino-Southern Oscillation event (Piatt and Van Pelt 1997). However, that same winter also coincided with high adult herring biomass, thereby mitigating the potential impact on herring populations. Increased predation could have catastrophic consequences on herring populations if such events coincided with low adult herring biomass. Bakun (2006) has postulated that predation on low fish populations can create a "predator pit" whereby predation prevents population recovery. Such effects could be even more intensified for populations susceptible to disease outbreaks or other major perturbations, including oil spills.

Marine birds consumed more juvenile herring than adult herring; however the percentage of juvenile herring consumed is difficult to determine without estimates of total juvenile biomass in PWS. Avian predation on juvenile herring may exacerbate low juvenile survival, however, the impact of juvenile consumption on adult recruitment is difficult to quantify. Our results did suggest that we may be observing a top-down effect of seabirds on adult herring populations one-year after the consumption of adults. This result is consistent with the expected impact of removing individuals from a spawning population thereby potentially reducing miles of spawn. The significant negative correlation between juvenile herring consumption and miles of spawn the following year is likely due to a high degree of correlation between adult and juvenile herring consumption. Three to five years later, however, so many extrinsic factors have acted upon herring populations that the effect of either adult or juvenile herring consumption in year-0 is not evident. The age-structured-analyses (ASA) model in use by ADFG illustrates this idea through its effort to incorporate the complicated population dynamics of PWS herring and the nonlinear relationships among many of the population parameters. For example, the model survival parameter for each age class and each year is a non-linear function that partitions mortality into disease prevalence and other natural mortality (e.g. predation, starvation; Hulson et al. 2007). Thus, we would not expect to see a linear relationship between consumption in year 0 and herring biomass several years later.

Model Uncertainty and Future Directions

Our sensitivity analyses showed that the three most important parameters for estimating juvenile and adult herring consumption are assimilation rate and the proportions of total and adult herring in the diet. Assimilation rate – while shown to be important – is generally believed to vary only a small amount and our nominal value was consistent with the literature. Our results underscore the importance of improving our estimates for the proportions of adult and juvenile

herring in seabird diets. Because most marine birds swallow their prey while under water, most diet information on marine birds is from the summer months, when birds are more easily observed feeding their young at the colony. Diet composition in winter has not been studied for marine birds in Prince William Sound and almost nothing is known outside of PWS. At two areas west of PWS, winter diets of Common Murre and Marbled Murrelet were studied in the late 1970's (Krasnow and Sanger 1982, Sanger 1987). However, this time period coincided with the beginning of a major regime shift in the Gulf of Alaska from a cold to warm-regime community structure (Anderson and Piatt 1999). In PWS, Marbled Murrelet diets in summer were documented over several decades. Murrelet diets changed from being dominated by Pacific Sand lance (*Ammodytes hexapterus*) in the 1970's to being dominated by Pacific Sand lance and Walleye Pollock (*Theragra chalcogramma*) in the late 1980's (Kuletz et al. 1997) and in the 1990's by Sand lance and Pacific Herring *(*Kuletz 2005). While our Monte Carlo and sensitivity analyses examined as much as 20% variability in the diet proportions, zooplankton or other prey dynamics could potentially result in even higher degrees of variability in the case of environmental anomalies, inter-decadal climate oscillations or catastrophic events (eg., oil spills).

The sensitivity analyses also suggest that the model is relatively insensitive to large standard deviations around our population and mass parameters. However, occasional anomalies in bird populations were far greater than the maximum investigated CV of 20%. For example, in 1993, the Common Murre population was nearly 3.5 times greater than the median population of Common Murre in PWS during the winter. While from the statistical sense a year like 1993 may be viewed as an outlier, we should not ignore the implications that such a year may have on herring populations and their potential recovery in PWS. In this case, Common Murre consumed in excess of 4,000 tons of herring, more than double their consumption in any other year. This observation implies that the RPSS parameter rank orders may serve as a guideline for understanding our model, but they should not be viewed in isolation of the broader ecology of the highly dynamic PWS ecosystem. Meanwhile, in a year with so many birds, it is also likely that an even greater variability may occur among the proportions of herring in bird diets, once again highlighting the benefit of improved diet studies on our model parameters. Furthermore, any diet sampling would also allow for data collection on winter weights of local birds, thereby refining the mass parameter estimate.

Except for Black-legged Kittiwake, the bird population estimates in our model do not reflect within-season variability. All population data came from March surveys. In some instances, however, higher numbers of birds such as the Marbled Murrelet occur early in winter, and decline by March while the opposite trend of higher numbers in March than November have been observed for Common Murre. For Glaucous-winged Gull, March populations have varied dramatically with lower numbers associated with birds departing PWS for the Copper River Delta to forage on spring-spawning Pacific eulachon (Thaleichthys pacificus; Dawson et al. in review).

Our model is based on three key assumptions. First, it assigns all juveniles (age 0+ to 2+) an energetic equation associated with juveniles of age 0+, a time of reduced energetic condition. In addition, our model assumes a) that all individuals have equal access to herring; and b) prey consumption is not density dependent. Although it is necessary to keep models simple, both of these assumptions are likely to result in higher estimated consumption than actually occurs.

Herring concentrate in localized regions within PWS and schools vary in density both seasonally and spatially. Juvenile herring (0, 1, and 2 year olds) over-winter at depths <30m in several bays and inlets that are distinct from adult overwintering areas (Stokesbury et al. 2000; Norcross et al. 2001, Thorne 2010). Given the localized nature of herring schools, only a proportion of the marine bird population is able to feed on herring at any given time. An individual's ability to feed on herring is limited by its ability to locate adequate herring densities, intraspecific competition and foraging ability. The decision to target a particular prey species and success in acquiring prey is at least partially a function of prey density (Enstipp et.al. 2007, Axelson et. al. 2001). Marine birds use a diverse set of foraging strategies to meet energy demands. The extent to which marine birds and their co-predators in PWS switch target species when alternative prey are more available is not well documented, but these relationships would undoubtedly affect the biomass of herring consumed.

Summary

We have examined 18 marine bird species that currently forage on herring during winter. Some of these species, for example the Marbled Murrelet, are currently experiencing population lows. In the case of murrelets, an increase in population numbers would likely increase consumption of juvenile herring since their herring consumption is comprised almost exclusively of juveniles. While marine birds may consume a proportion of the herring population they represent only one group of predators in PWS. Predatory fish such as the abundant Pacific cod (*Gadus macrocephalus*) forage on herring among a range of sizes (Bishop and Powers unpub. data). Steller sea lion (*Eumetopias jubatus*) and humpback whale feed extensively on Pacific Herring (Thomas and Thorne 2001; Moran and ??) and the humpback whale population has been increasing by as much as 5-7% per year (need citation). In addition to consuming large quantities of Pacific Herring, humpback whales and other marine mammals can facilitate forage flocks and marine bird foraging efficiency (Obst and Hunt 1990, Pitman and Balance 1992, Thomas and Thorne 2001). A better understanding of levels of predation by these multiple groups of predator will help to refine or improve mortality estimates within herring population models used in fishery management.

ACKNOWLEDGEMENTS

The research described in this paper was supported by grant from the Exxon Valdez Oil Spill Trustee Council. The findings and conclusions presented by the authors are their own and do not necessarily reflect the views or position of the Trustee Council. We thank Neil Dawson for his ideas and contributions to this study.

LITERATURE CITED

Bakun, A. 2006. Wasp-waist populations and marine ecosystem dynamics: navigating the "predator pit" topographies. Progress in Oceanography 68: 271-288.

Barrett, R.T., T. Anker-Nilssen, G.W. Gabrielsen, and G. Chapdelaine. 2002. Food consumption by seabirds in Norwegian waters. ICES Journal of Marine Science 59:43–57.

Bartell, S.M., Breck, J.E., Gardner, R.H. and Brenkert, A.L. (1986) Individual parameter perturbation and error analysis of fish bioenergetics models. Can. J. Fish. Aquat. Sci. 43:160–168.

Bax, N.J. 1991. A comparison of the fish biomass flow to fish, fisheries and mammals in six marine ecosystems. ICES Marie Science Symposia 193:198-208.

Birt-Friesen, V.L., W.A. Montevecchi, D.K. Cairns, and S.A. Macko. 1989. Activity-specific metabolic rates of free-living Northern Gannets and other seabirds. Ecology 70:357-367.

Bishop, M.A. and S.P. Green. 2001. Predation on Pacific herring (*Clupea pallasi*) spawn by birds in Prince William Sound, Alaska. Fisheries Oceanography 10 (Suppl.1): 149-158.

Botz, J. G. Hollowell, J. Bell, R. Brenner, and S. Moffitt. 2010. 2009 Prince William Sound area finfish management report. Alaska Department of Fish and Game, Fishery Management Report No. 10-55, Anchorage.

Brooke, M. de L. 2004. The food consumption of the world's seabirds. Proc. Royal Society B. 271:246-248.

Brown, E.D. 2003. Stock structure and environmental effects on year class formation and population trends of Pacific Herring (*Clupea pallasii*), in Prince William Sound, Alaska. Dissertation. University of Alaska Fairbanks.

Causey, D. 2002. Red-faced Cormorant (Phalacrocorax urile). In the Birds of North America, No. 617 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, PA.

Dunning, J.B. 2007. CRC Handbook of Avian Body Masses, 2nd Edition. Purdue University, West Lafayette, Indiana.

Ellis, H.I. and G.W. Gabrielsen. 2002. Energetics of free-ranging seabirds. Pages 359-407 in E.A. Schreiber and J. Burger. Biology of marine birds. CRC Press: boca Raton, FL

Enstipp, M.R., D. Gremillet, and D.R. Jones. 2007. Investigation of the functional link between prey abundance and seabird predatory performance. Marine Ecology Progress Series 331: 267-279.

Evans, D.R., P.M. Cavanagh, T.W. French, B.G. Blodget. 1995. Identifying the Sex of Massachusetts Herring Gulls by Linear Measurements J, Field Ornithology 66: 128-132

Evers, D. C., J.D. Paruk, J.W. Mcintyre and J.F. Barr. 2010. Common Loon (*Gavia immer*). The Birds of North America (A. Poole, ed.). Ithaca: Cornell Lab Ornithology.

Exxon Valdez Oil Spill Trustee Council. 2010. *Exxon Valdez* Oil Spill Restoration Plan: Update of injured resources and services. May 2010. Exxon Valdez Oil Spill Trustee Council, Anchorage, Alaska. 48pp.

Foy, R.J. and A.J. Paul. 1999. Winter feeding and changes in somatic energy content for age-0 Pacific Herring in Prince William Sound. Transactions American Fisheries Society. 128:1193-1200.

Funk, F. Is recent Pacific herring recruitment in Prince William Sound, Alaska, unusually low compared to recruitment elsewhere on the West Coast of North America? In: S.D. Rice and M.G. Carls. 2007. Prince William Sound Herring: An updated synthesis of population declines and lack of recovery, *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 050794), NOAA, NMFS, Auke Bay Laboratory, Juneau, Alaska.

Furness, R.W. and M.L. Tasker. 1997. Seabird consumption in sand lance MSVPA models for the North Sea, and the impact of industrial fishing on seabird population dynamics. Pages 147–169 in Proc. International Symposium on the Role of Forage Fishes in Marine Ecosystems. Fairbanks: Sea Grant, University of Alaska Fairbanks,.

Gay, S.M. III., and S.L. Vaughan. 2001. Physical oceanography of nursery habitats of juvenile Pacific herring. Fisheries Oceanography 10 (Suppl. 1):159-173.

Hatch, J.J. and D.V. Weseloh. 1999. Double-creseted Cormorant (Phalacrocorax auritus). In The Birds of North America, NO. 441 (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadephia. PA.

Hobson, K.A. 1997. Pelagic Cormorant (*Phalacrocorax pelagicus*), The Birds of North America Online (A. Poole, ed.). Ithaca: Cornell Lab Ornithology.

Hulson, P.J.F., Miller, S. E., Quinn, T. J. II, Marty, G. D., Moffitt, S. D., and Funk, F. 2008. Data conflicts in fishery models: incorporatinghydroacoustic data into the Prince William Sound Pacific herring assessment model. – ICES Journal of Marine Science, 65: 25–4

Hunsicker, M.E. and T.E. Essington. 2008. Evaluating the potential for trophodynamic control of fish by the longin inshore squid (Loligo pealeii) in the Northwest Atlantic Ocean. Can. J. Fish. Aquat.Sci. 65:2524-2535.

Hutchings, J.A. 2000. Collapse and recovery of marine fishes. Nature 406: 882-885.

Irons, D.B., S.J. Kendall, W.P. Erickson, L.L. McDonald and B.K. Lance. 2000. Nine years after the EXXON VALDEZ oil spill: effects on marine bird populations in Prince William Sound, Alaska. Condor 102:723-737.

Isleib, M.E., B. Kessel. 1973. Birds of the North Gulf Coast – Prince William Sound Region, Alaska. Biological Papers Univ. Alaska. No. 14. 149pp.

Krasnow, L.D., and G.A. Sanger. 1982. Feeding ecology of marine birds in the nearshore waters of Kodiak Island: Anchorage, Alaska, USFWS, National Fishery Research Center, Migratory Bird Section, Final Report to the Outer Continental Shelf Environmental Assessment Program (OCSEAP), Research Unit 45, p. 505-630.

Kuletz, K.J. 2005. Foraging behavior and productivity of a non-colonial seabird, the Marbled Murrelet (*Brachyramphus marmoratus*), relative to prey and habitat. Ph.D. Dissertation, Univ. Victoria, British Columbia. 195pp.

Lewis, B., J. Botz, R. Brenner, G. Hollowell, and S. Moffitt. 2008. 2007 Prince William Sound Area Finfish Management Report. Alaska Dept. Fish Game, Fishery Mgmt. Rept. No. 08-53.

Logerwell, E. A. and N.B. Hargreaves. 1996. The distribution of seabirds relative to their fish prey off Vancouver Island: opposing results at large and small spatial scales. Fisheries Oceanography 5:163-175.

Mallory, M. and K. Metz. 1999. Common Merganser (*Mergus merganser*). The Birds of North America (A. Poole, Ed.). Ithaca: Cornell Lab Ornithology.

Marty GD, P.J.F. Hulson, S.E. Miller, T.J. Quinn II, S.D. Moffitt, R.A. Merizon. 2010. Failure of population recovery in relation to disease in Pacific herring. Diseases Aquatic Organisms 90:1-14.

McKnight, A., K.M. Sullivan, D.B. Irons, S.W. Stephensen, and S. Howlin. 2008. Marine bird and sea otter population abundance of Prince William sound, Alaska: trends following the *T/V Exxon Valdez* oil spill, 1989-2005. *Exxon Valdez* Oil Spill Restoration Project Final Rept.

Nelson, K.S. 1997. Marbled Murrelet (*Brachyramphus marmoratus*). The Birds of North America (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology.

Obst, B.S., and G.L. Hunt Jr. 1990. Marine birds feed at Gray Whale mud plumes in the Bering Sea. Auk 107:678-688.

Ostrand, W.D., S. Howlin, and T.A. Gotthardt. 2004. Fish school selection by Marbled Murrelets in Prince William Sound, Alaska: responses to changes in availability. Marine Ornithology 32:69-76.

Overholtz, W.J and J.S. Link. 2007. Consumption impacts by marine mammal, fish and seabirds on the Gulf of Maine – Georges Bank Atlantic Herring (*Clupea harengus*) complex during the years 1977 – 2002. ICES Journal of Marine Science 64:83-96.

Paul, A.J, and J.M. Paul. 1998. Comparisons of whole body energy content of captive fasting age zero Alaskan Pacific Herring (*Clupea pallasii valenciennes*) and cohorts over-wintering in nature. J. Experimental Marine Biology Ecology 226:75-86.

Piatt, J.F. and T.I. Van Pelt. 1997. Mass-mortality of Guillemots *Uria aalge* in the Gulf of Alaska in 1993. Marine Pollution Bulletin 34:656-662.

Pierotti, R.J., and T.P. Good. 1994. Herring gull (Larus argentatus). In the Birds of North America, No. 124 (A. Poole and F. Gill, eds.). the Birds of North America, Inc., Philadelphia, PA.

Pitman, R.L. and L.T. Balance. 1992. Parkinson's Petrel distribution and foraging ecology in the Eastern Pacific: Aspects of an exclusive feeding relationship with dolphins. Condor 94: 825-835.

Roby, D.D., K.R. Turco, J.A. Anthony. 1998. Diet composition, reproductive energetics, and productivity of seabirds damaged by the *Exxon Valdez* Oil Spill. *Exxon Valdez* Oil Spill Restoration Project Annual Report Restoration Project 97163 G.

Rose, K. A., E. P. Smith, R. H. Gardner, A. L. Brenkert, S. M. Bartell. 1991. Parameter Sensitivities, Monte Carlo Filtering and model forecasting under uncertainty. Journal of Forecasting 10:117-133.

Russell, R.W. 2002. Pacific Loon (*Gavia pacifica*). The Birds of North America (A. Poole, Ed.). Ithaca: Cornell Lab Ornithology.

Sanger, G.A. 1987. Winter diets of Common Murres and Marbled Murrelets in Kachemak Bay, Alaska. Condor 89:426-430.

Saulitis, E.L., C.O. Matkin, L. Barrett-Lennard, K. Heise and G. Ellis. 2000. Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska. Marine Mammal Science 16:94-109.

Schweigert, J.F. 1995. Environmental effects on long-term population dynamics and recruitment to Pacific herring (*Clupea pallasi*) populations in southern British Columbia. Pages 569-583 *in* R. J. Beamish, ed., Climate Change and Northern Fish Populations, Canadian Special Pub. Fisheries Aquatic Science No 121.

Stokesbury, K.D.E., J.E. Kirsch, V. Patrick, and B.L. Norcross. 2000. Natural mortality estimates of juvenile Pacific herring (*Clupea pallasii*) in Prince William Sound, Alaska. Canadian J. Fisheries Aquatic Science 59:416-423.

Suryan R.M., D.B. Irons, M. Kaufman, J. Benson, P.G. Jodice, D.D. Roby, D.E. Brown. 2002. Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the black-legged kittiwake *Rissa tridactyla.* Marine Ecology Progress Series Vol. 236: 273–287.

Thomas, G.L. and R. E. Thorne. 2001. Night time predation by Steller Sea Lions. Nature 411:1013.

Thomas, G.L. and R.E. Thorne. 2003. Acoustical-optical assessment of Pacific herring and their predator assemblage in Prince William Sound, Alaska. Aquatic Living Resources 16:247–253

Thorne, R.E. 2010. Trends in adult and juvenile herring distribution and abundance in Prince William Sound. *Exxon Valdez* Oil Spill Restoration Project Final Rept. Project No. 070830.

Thorne, R. E., and G.L. Thomas. 2008. Herring and the "Exxon Valdez" oil spill: an investigation into historical data conflicts. ICES Journal Marine Science, 65:44-50.

Thorne, R.E. and G.L. Thomas 2011. The Role of Fishery Independent Data, Chapter 12, In, Janice S. Intilli (ed) Fisheries Management. Nova Science Publishers, ISBN 978-1-61209-682-7 (In Press-Publication date 2nd Quarter 2011

Ware, D.M. 1995. The link between ocean climate and herring recruitment. Page 133 *in* D. E. Hay and P. B. McCarter, editors, Proceedings of the Seventh Pacific Coast Herring Workshop, Vancouver, B.C., Canadian Manuscript Report of Fisheries and Aquatic Science, No. 2060.

Williams, E. H., and. T. J. Quinn, II. 2000a. Pacific herring, *Clupea pallasii*, recruitment in the Bering Sea and north-east Pacific Ocean, I: relationships among different populations. Fisheries Oceanography 9:285-299.

Williams, E. H., and. T. J. Quinn, II. 2000b. Pacific herring, *Clupea pallasii*, recruitment in the Bering Sea and northeast Pacific Ocean, II: relationships to environmental variables and implications for forecasting. Fisheries Oceanography 9:300-315.

Woodby, D., D. Carlile, S. Siddeek, F. Funk, J.H. Clark and L. Hulbert. 2005. Commercial Fisheries of Alaska. Alaska Dept. Fish Game. Spec. Pub. No. 05-09. Anchorage, Alaska.

CHAPTER 2 TABLES

Table 2-1. Table of model input mean values for body mass (kg), proportion of herring in diet, and proportion of herring by age class (adult or juvenile). Unidentified (Unid.) loons, grebes, mergansers, murres and murrelets are assigned model inputs for the most common species in their respective genera.

Species	Body Mass (kg) ± sd	Prop. Herring	Prop. Adult Herring	Prop. Juvenile Herring	Body Source**
Common Loon, *Gavia immer*	4.98 (1.0)	0.5	0.7	0.3	2, 3
Yellow-billed Loon, *G. adamsii*	4.00 (1.2) ǂ	0.5	0.7	0.3	2
Red-throated Loon, *G. stellata*	1.52 (0.1)	0.5	0.7	0.3	2
Pacific Loon, *G. pacifica*	1.67 (0.1)	0.5	0.7	0.3	2, 10
Unid. Loon, *Gavia spp.*	1.67 (0.5)	0.5	0.7	0.3	
Red-necked Grebe, *Podiceps grisegena*	1.22 (0.2)	0.25	0	1.0	2,12,
Horned Grebe, *P.auritus*	0.45 (0.04)	0.25	0	1.0	2, 11
Unid. Grebe, *Podiceps spp.*	0.45 (0.04)	0.25	0	1.0	
Double-crested Cormorant, *Phalacrocorax auritus*	1.83 (0.1)	0.25	0.5	0.5	14
Red-faced Cormorant, *P.urile*	1.85 (0.1)	0.25	0.5	0.5	5
Pelagic Cormorant, *P. pelagicus*	1.8 (0.5)	0.25	0.5	0.5	2, 4
Unid. Cormorant, *Phalacrocorax spp.*	1.8 (0.5)	0.25	0.5	0.5	
Common Merganser, *Mergus merganser*	1.4 (0.5)	0.3	0.1	0.9	2,7
Red-breasted Merganser, *M. serrator*	0.9 (0.1)	0.3	0.1	0.9	2,13
Unid. Merganser, *Mergus spp.*	0.9 (0.1)	0.3	0.1	0.9	
Herring Gull, *Larus argentatus*	1.02 (0.1)	0.1	0.2	0.8	16
Glaucous-winged Gull, *L. glaucescens*	1.33 (0.5)	0.2	0.2	0.8	1
Mew Gull, *L. canus*	0.45 (0.2)	0.1	0	1.0	1
Black-legged Kittiwake, *Rissa tridactyla*	0.43 (0.1)	0.2	0	1.0	2, 9
Unid. Gull*	1.33 (0.5)	0.2	0.2	0.8	
Unid. Gull*	0.45 (0.2)	0.1	0	1.0	
Unid. Gull*	0.43 (0.1)	0.2	0	1.0	
Common Murre, *Uria aalge*	0.99 (0.1)	0.5	0.5	0.5	2
Unid. Murre, *Uria spp.*	0.99 (0.1)	0.5	0.5	0.5	
Marbled Murrelet, *Brachyramphus marmoratus*	0.22 (0.04)	0.5	0	1.0	2,6,8
Unid. Murrelet, *Brachyramphus spp.*	0.22 (0.04)	0.5	0	1.0	
Pigeon Guillemot, *Cepphus columba*	0.49 (0.1)	0.2	0	1.0	2

*For each survey year, unidentified gull population estimates were divided by three, with each population estimate assigned body mass and diet inputs corresponding to Glaucous-winged Gull (1/3 of all unidentified gulls), or Mew Gull (1/3) or Black-legged Kittiwake (1/3)

**Data sources for mass: [1]Bishop and Green 2001; [2]Dunning 2007; [3] Evers et. al. 2010; [4]Hobson 1997; [5]Causey 2002; [6]Kuletz 2005; [7]Mallory and Metz 1999; [8]Nelson 1997; [9]Roby et. al. 1998; [10]Russell 2002; [11]Stedman 1999, [12]Stout and Nuechterlein 1999; [13]Titman 1999, [14] Hatch and Weseloh 1999; [15] Evans et al. 1995

ǂStandard deviation was calculated using only four published maximum and minimum values for the mass ranges of males and females

Table 2-2. Metrics used for lag analysis to indicate spawning biomass of adult herring.

Year	Miles of Spawn (aerial survey)	Mile Days of Spawn (aerial survey)	Adult Herring (tons) (acoustic estimate)
1990	94.1	164.4	ND
1991	58	71.5	ND
1992	74.7	119.8	ND
1993	20.4	50.3	18812
1994	14.6	23.1	12555
1995	20.4	28.8	12070
1996	27.2	37.3	23203
1997	42.7	64.3	37400
1998	38.7	62	17655
1999	25.4	40.7	17301
2000	19.5	31.7	7280
2001	16	14.8	6330
2002	21.5	23.6	10700
2003	25.2	26.1	23200
2004	29.7	30.4	12700
2005	29.9	31.7	20100
2006	19.9	21.7	13000
2007	NA	18.3	20400
2008	NA	45.4	17900
2009	NA	29.8	20400
2010	NA	30.81	17500

Table 2-3. Relative partial sums of squares (RPSS) values for model parameters with rank order at three coefficients of variation (CV). PerHer = Proportion of herring in diet. Assim = Assimilation rate. PerAd = proportion of adult herring in diet; population = number of birds; DKJ = daily energy budget; KJJ = juvenile herring condition index; mass = bird mass (g); KJA = adult herring condition index.

	Juvenile Herring CV			Adult Herring CV		
	2%	10%	20%	2%	10%	20%
r^2	0.999	0.962	0.633	0.998	0.951	0.555
Rank						
1	PerHer (0.462)	PerHer (0.423)	PerHer (0.262)	PerAd (0.430)	PerAd (0.408)	PerAd (0.226)
2	Assim (0.249)	Assim (0.258)	Assim (0.214)	PerHer (0.288)	PerHer (0.267)	PerHer (0.146)
3	PerAd (0.085)	PerAd (0.078)	PerAd (0.05)	Assim (0.155)	Assim (0.167)	Assim (0.118)
4	Population (0.047)	Population (0.045)	Population (0.028)	Population (0.030)	Population (0.028)	Population (0.017)
5	DKJ (0.046)	DKJ (0.042)	DKJ (0.027)	DKJ (0.029)	DKJ (0.027)	DKJ (0.015)
6	KJJ (< 0.001)	Mass (< 0.001)	KJA (< 0.001)	KJA (< 0.001)	KJA (< 0.001)	KJA (< 0.001)
7	Mass (< 0.001)	KJA (< 0.001)	KJJ (< 0.001)	KJJ (< 0.001)	Mass (< 0.001)	Mass (< 0.001)
8	KJA (< 0.001)	KJJ (< 0.001)	Mass (< 0.001)	Mass (< 0.001)	KJJ (< 0.001)	KJJ (< 0.001)

CHAPTER 2 FIGURES

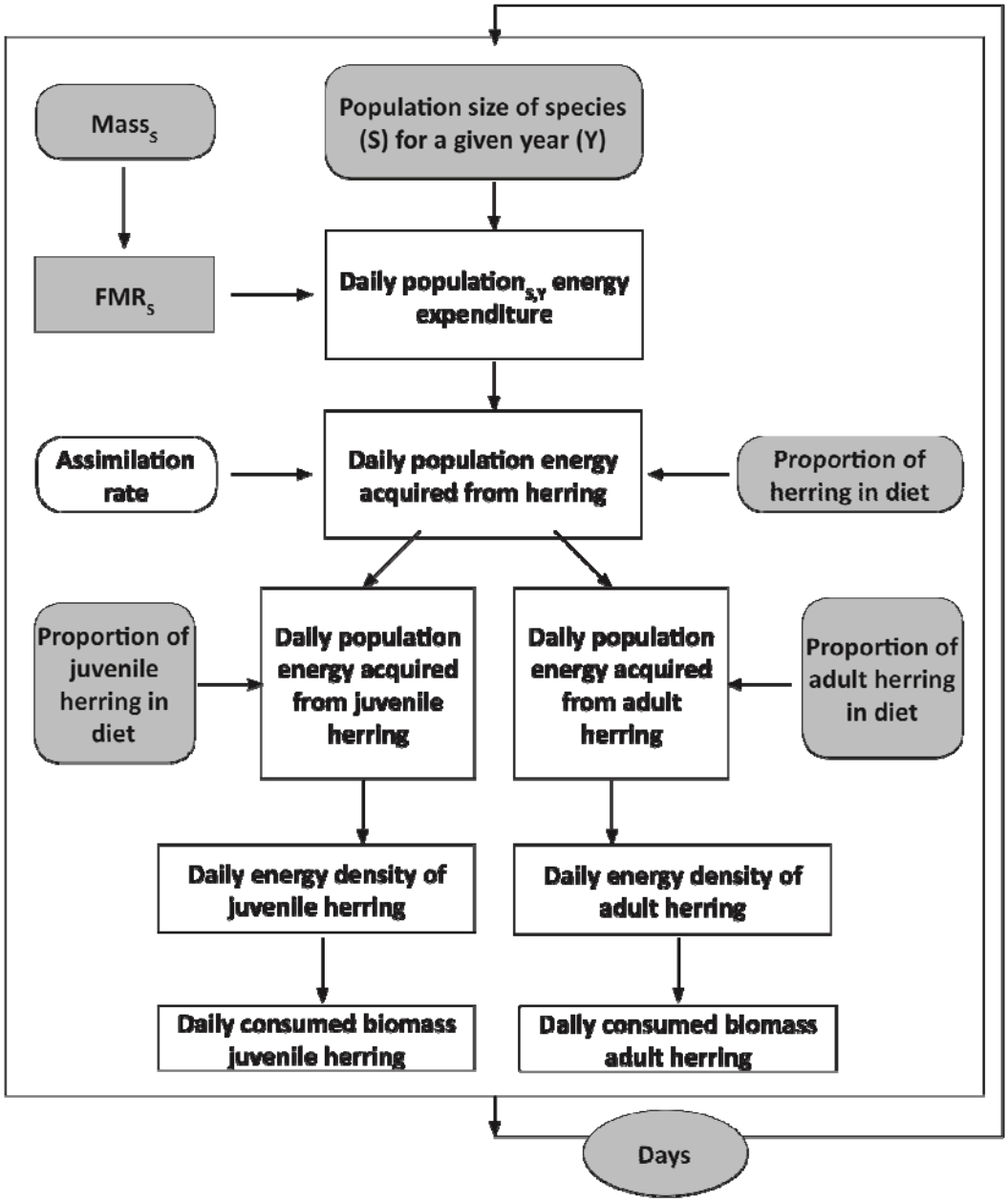

Figure 2-1. . Model schematic for winter Pacific herring consumption by 18 marine bird species in Prince William Sound. Round-cornered rectangles indicate inputs sampled from a distribution. Shaded boxes indicate species specific model inputs. All values within the box were iterated for each day.

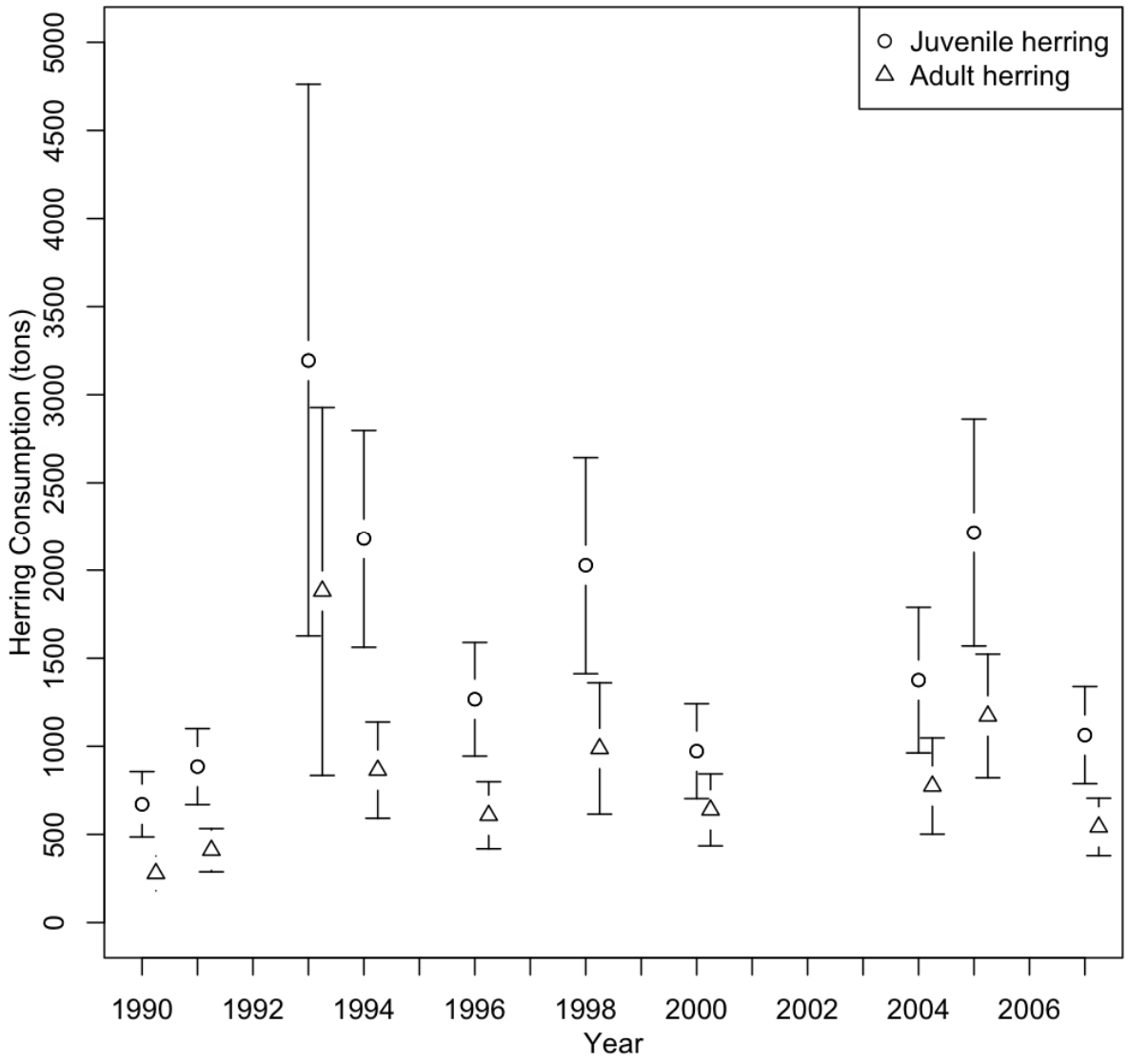

Figure 2-2. Annual marine bird winter consumption of herring from Monte Carlo simulations. Circles = mean juvenile herring consumption; triangles = mean adult herring consumption. Error bars = $\pm$ 1 sd. Year on the x-axis corresponds to the previous-present year's winter (e.g., 1994 refers to winter 1993 – 1994). All time periods are the same for juvenile and adult consumption but slight offset in x-axis is provided for ease of illustration**.**

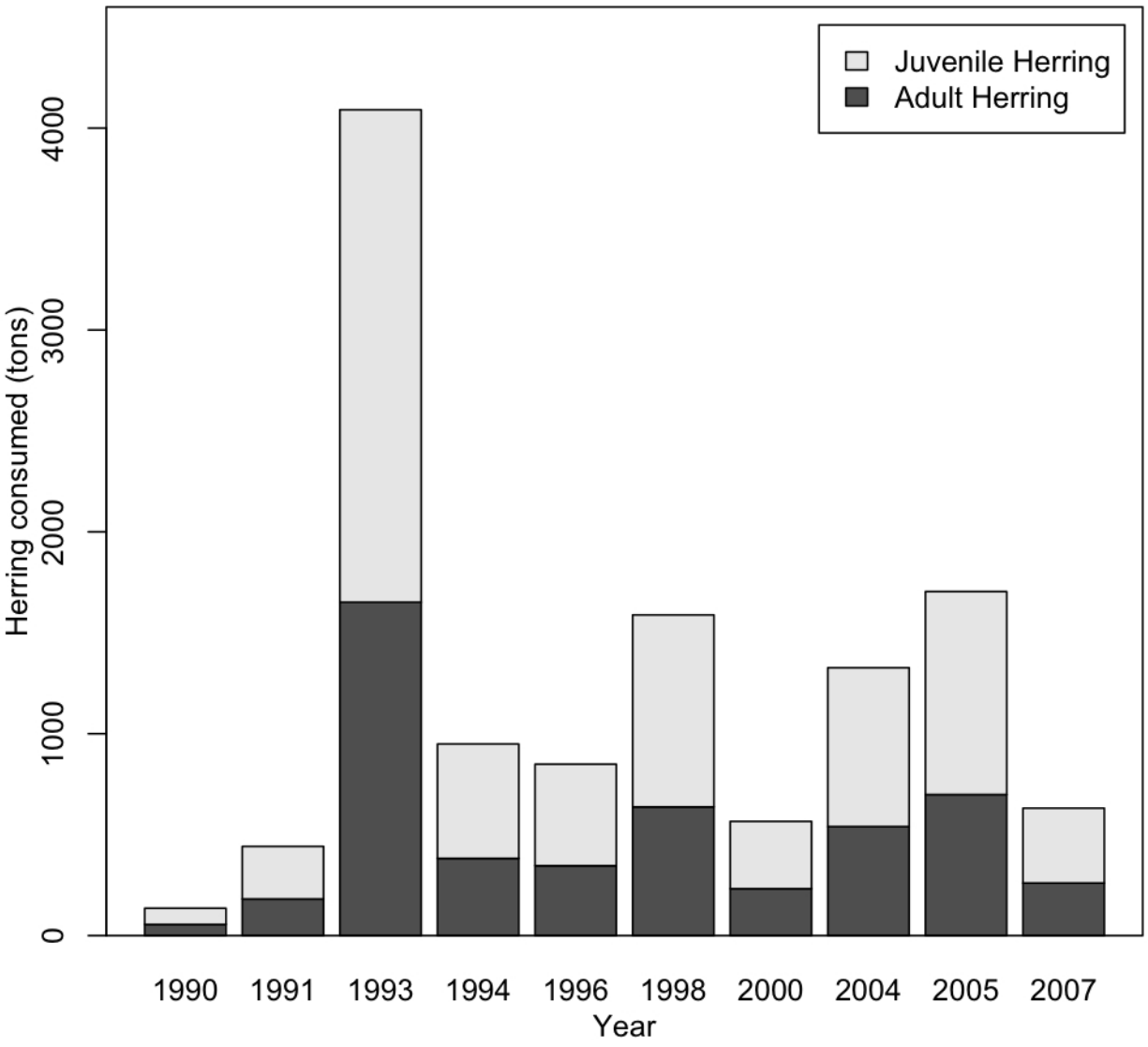

Figure 2-3. Pacific Herring consumption (t) by Common Murre in Prince William Sound during winter (15 November through 15 March). Consumption estimates are for 10 winters. Year on the x-axis corresponds to the previous-present year's winter (e.g., 1994 refers to winter 1993 – 1994). Light gray illustrates juvenile herring consumed and dark gray depicts adult herring consumed. No population estimates are available for 1992, 1995, 1997, 1999, 2001-2003, and 2006.

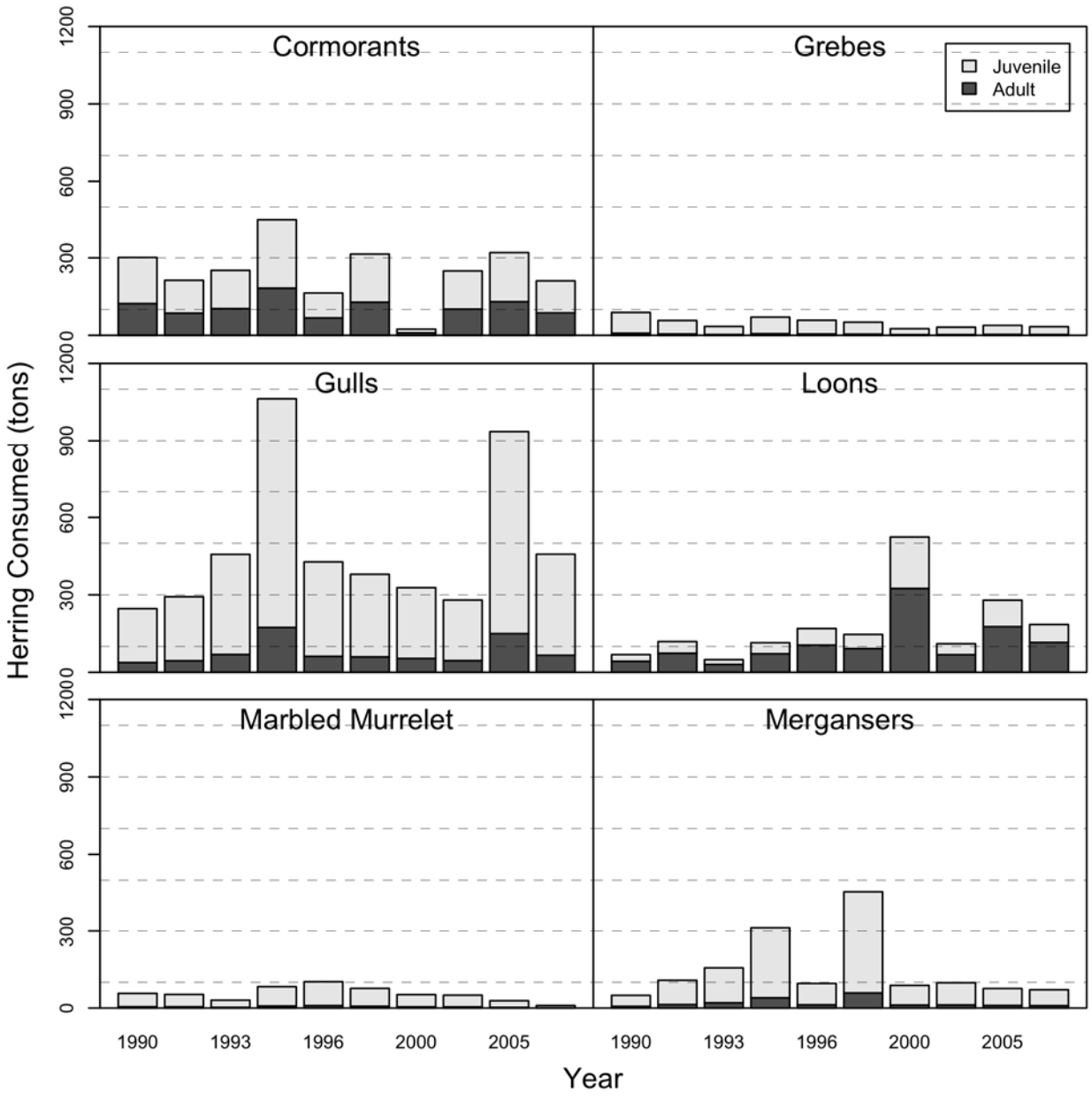

Figure 2-4. Pacific Herring consumption (t) by major marine bird species or species groups in Prince William Sound during winter (15 November through 15 March). Consumption estimates are for 10 winters. Year on the x-axis corresponds to the previous-present year's winter (e.g., 1994 refers to winter 1993 – 1994). Light gray illustrates juvenile herring consumed and dark gray depicts adult herring consumed. No population estimates are available for 1992, 1995, 1997, 1999, 2001-2003, and 2006.

Appendix 2-1. Population estimates (± SD) of marine bird species as determined from March surveys conducted by U.S. Fish and Wildlife Surveys in Prince William Sound. Taken from McKnight et al. 2008.

	Year									
Species	1990	1991	1993	1994	1996	1998	2000	2004	2005	2007
Yellow-billed Loon, *G. adamsii*	23 (31)	47 (69)	23 (25)	140 (173)	90 (123)	94 (158)	206 (368)	28 (25)	27 (24)	52 (64)
Red-throated Loon, *G. stellata*	8 (14)	90 (164)	89 (125)	0	0	12 (16)	0	0	0	7 (14)
Common Loon, *Gavia immer*	227 (120)	386 (196)	67 (24)	353 (106)	636 (209)	514 (122)	2390 (1642)	330 (118)	1234 (331)	580 (609)
Pacific Loon, *G. pacifica*	64 (117)	0	0	206 (202)	242 (303)	713 (1034)	200 (328)	195 (193)	323 (266)	1437 (2534)
Unid. Loon, *Gavia spp.*	543 (314)	1110 (1118)	871 (636)	826 (901)	967 (963)	433 (384)	1618 (1030)	1064 (1209)	762 (570)	357 (285)
Red-necked Grebe, *Podiceps grisegena*	2571 (812)	1565 (251)	681 (160)	1878 (368)	1719 (277)	1430 (379)	572 (131)	859 (169)	1054 (407)	941 (516)
Horned Grebe, *P.auritus*	3863 (1516)	2255 (1588)	400 (322)	3698 (2181)	2636 (947)	2401 (1042)	2452 (905)	2075 (652)	2203 (782)	1813 (744)
Unid. Grebe, *Podiceps spp.*	609 (295)	1775 (1357)	4209 (2105)	1184 (531)	653 (253)	820 (764)	400 (195)	135 (62)	166 (203)	240 (230)
Double-crested Cormorant, *Phalacrocorax auritus*	269 (230)	124 (108)	1041 (1046)	131 (106)	367 (227)	1009 (1056)	476 (405)	802 (469)	155 (139)	271 (292)
Red-faced Cormorant, *P.urile*	32 (31)	458 (449)	81 (77)	81 (138)	0	34 (32)	0	6 (9)	8 (14)	0
Pelagic Cormorant, *P. pelagicus*	8527 (2521)	5431 (2237)	8050 (3140)	10958 (2765)	590 (545)	728 (582)	297 (317)	7279 (1947)	10649 (2575)	8535 (2656)
Unid. Cormorant, *Phalacrocorax spp.*	351 (353)	3477 (1286)	2774 (1591)	277 (209)	12431 (3961)	6455 (2300)	8437 (2845)	1801 (639)	3392 (1514)	4453 (2170)
Common Merganser, *Mergus merganser*	1171 (211)	4466 (1146)	5954 (1538)	7460 (1798)	2721 (670)	20641 (9045)	2779 (847)	4243 (1717)	3009 (779)	2913 (1017)
Red-breasted Merganser, *M. serrator*	1476 (469)	231 (157)	464 (403)	7824 (11113)	2423 (1382)	2261 (2195)	1217 (845)	998 (436)	962 (467)	790 (540)
Unid. Merganser, *Mergus spp.*	863 (536)	1226 (1620)	2825 (3071)	6463 (5460)	1364 (1228)	162 (117)	1791 (1740)	348 (234)	328 (195)	80 (59)
Herring Gull, *Larus argentatus*	154 (170)	96 (131)	858 (541)	1987 (2020)	60 (71)	676 (783)	306 (242)	910 (588)	2031 (813)	307 (180)
Glaucous-winged Gull *L. glaucescens*	8442 (1870)	10225 (3645)	10053 (4596)	42479 (18514)	13935 (5373)	14623 (7316)	12757 (4834)	9385 (3573)	35363 (8851)	12874 (4080)
Mew Gull, *L. canus*	2542 (1276)	9784 (3296)	9068 (9913)	12590 (3289)	20324 (11553)	6817 (3341)	3105 (1688)	1761 (814)	8925 (3497)	29712 (33862)
Black-legged Kittiwake, *Rissa tridactyla*	157 (119)	843 (449)	3292 (2884)	4451 (2159)	5278 (2102)	12598 (6061)	6200 (2933)	9567 (11659)	15903 (5416)	949 (4154)
Unid. Gull*	4225 (4689)	1440 (960)	18546 (11823)	3932 (2166)	1391 (1440)	546 (396)	1492 (994)	3719 (1662)	4660 (1327)	2450 (703)
Common Murre, *Uria aalge*	4863 (2058)	11735 (6553)	157176 (140665)	47340 (17856)	44855 (19348)	87287 (48710)	26989 (12157)	62231 (23157)	90902 (23191)	31280 (10343)
Unid. Murre, *Uria spp.*	2575 (1899)	12367 (6810)	63528 (37553)	4386 (1836)	1223 (649)	426 (360)	4071 (1756)	8703 (3712)	1874 (983)	3160 (1069)
Marbled Murrelet, *Brachyramphus marmoratus*	13687 (5831)	7717 (4537)	7360 (4040)	23260 (15347)	25801 (8917)	29193 (11245)	17404 (10256)	19740 (15967)	9432 (3292)	3144 (1904)
Unid. Murrelet, *Brachyramphus spp.*	11245 (6801)	15328 (7196)	6176 (3228)	13058 (4906)	18351 (6671)	4623 (2739)	5839 (2061)	2117 (1192)	3209 (1242)	1309 (1044)
Pigeon Guillemot, *Cepphus columba*	810 (171)	2842 (1075)	1640 (452)	1276 (326)	2541 (521)	907 (353)	1127 (545)	946 (259)	1486 (448)	1946 (1952)

Appendix 2-2. Consumption (t) + SD of juvenile and adult herring by marine bird species and winter. Winter corresponds to the previous-present year's winter (e.g., 1994 refers to winter 1993 – 1994).

	Winter									
Species	1990	1991	1993	1994	1996	1998	2000	2004	2005	2007
Yellow-billed Loon, *G. adamsii*	3.6 (2.2)	7.9 (4.8)	3.3 (2)	21.3 (13.2)	14 (8.5)	17.3 (10.8)	39.4 (23.9)	3.7 (2.1)	3.8 (2.1)	7.9 (4.7)
Red-throated Loon, *G. stellata*	0.3 (0.2)	4.1 (2.2)	3.4 (1.9)	0 (0)	0 (0)	0.4 (0.2)	0 (0)	0 (0)	0 (0)	0.3 (0.2)
Common Loon, *Gavia immer*	42.6 (18.1)	72.8 (30.3)	12.7 (4.8)	66.7 (25.2)	122.4 (45.4)	97.8 (35)	459.9 (216.6)	61.5 (23.8)	232.9 (83)	115.3 (66.4)
Pacific Loon, *G. pacifica*	3.4 (2)	0 (0)	0 (0)	7.6 (4.5)	10.1 (5.9)	32 (19.1)	10 (6)	7.1 (4.3)	12 (6.7)	73.4 (44.4)
Unid. Loon, *Gavia spp.*	20 (9.3)	41.4 (24.9)	33.1 (16.8)	31.4 (18.5)	37 (21.6)	15.7 (8.7)	61.3 (29.5)	43.7 (25.9)	28.6 (14.6)	14 (7.4)
Red-necked Grebe, *Podiceps grisegena*	76.6 (29.8)	46.9 (15.6)	19.8 (7.3)	54.9 (19)	51.1 (17.5)	42.9 (15.6)	17.1 (6)	24.9 (8.5)	31.5 (12.5)	28.3 (13.3)
Horned Grebe, *P.auritus*	12.9 (8.4)	7.6 (5.8)	1.3 (1.1)	12.3 (8.8)	9.1 (5.6)	8.1 (5.3)	8.3 (5.2)	6.9 (4.3)	7.3 (4.5)	5.9 (3.8)
Unid. Grebe, *Podiceps spp.*	2 (1.4)	5.9 (4.6)	13.9 (9.2)	4 (2.6)	2.2 (1.4)	2.9 (2.5)	1.3 (0.9)	0.5 (0.3)	0.6 (0.5)	0.8 (0.7)
Double-crested Cormorant, *Phalacrocorax auritus*	5.9 (3.9)	2.9 (1.8)	24.2 (16.7)	2.8 (1.8)	8.3 (4.9)	23.2 (15.7)	10.9 (7.2)	18.6 (10.6)	3.5 (2.3)	6.1 (4.3)
Red-faced Cormorant, *P.urile*	0.7 (0.5)	10.6 (7.1)	1.9 (1.3)	2.6 (1.8)	0 (0)	0.8 (0.5)	0 (0)	0.2 (0.1)	0.2 (0.2)	0 (0)
Pelagic Cormorant, *P. pelagicus*	187.9 (99.7)	121.9 (67)	172 (94.9)	245 (135.9)	12.5 (8.8)	16.1 (10.8)	7.1 (5.2)	166.7 (89.2)	241 (127.8)	196.8 (105.7)
Unid. Cormorant, *Phalacrocorax spp.*	7.7 (5.9)	78.2 (44.3)	58.6 (36.2)	6.3 (4)	271.7 (154.7)	141.4 (78.9)	192.2 (102.1)	39.8 (22.2)	76.4 (43.4)	101.5 (60.3)
Common Merganser, *Mergus merganser*	25.2 (13.4)	92.5 (52.8)	122.9 (67.8)	153.7 (88.3)	56.5 (31.9)	420.5 (244.7)	54.8 (30.2)	88.6 (53.8)	61.1 (33.7)	60.7 (34.1)
Red-breasted Merganser, *M. serrator*	15.6 (7.9)	2.4 (1.4)	4.9 (3.3)	102.5 (76)	26.3 (14.6)	24.3 (17.2)	12.8 (7.8)	10.7 (5.5)	10.2 (5.2)	8.7 (5.2)
Unid. Merganser, *Mergus spp.*	9.1 (5.3)	14.5 (10.6)	31.4 (22.8)	69.4 (46.8)	14.9 (10.2)	1.7 (1)	19.8 (13.8)	3.7 (2.2)	3.5 (2)	0.9 (0.5)
Herring Gull, *Larus argentatus*	1.8 (1.2)	1.2 (0.9)	9.7 (5.3)	21.6 (15.1)	0.7 (0.5)	7.9 (5.4)	3.4 (2.1)	10 (5.4)	22.5 (10.3)	3.4 (1.8)
Glaucous-winged Gull *L. glaucescens*	183 (106)	213.3 (127.2)	214.3 (131.7)	921.4 (578.7)	299.5 (189.3)	324.7 (223.2)	276.4 (168.6)	207.2 (119.8)	781.9 (450.7)	287.4 (168.4)
Mew Gull, *L. canus*	8.1 (5.6)	29.7 (19)	28.3 (25.4)	39.6 (25.2)	61.7 (45.8)	21.4 (14.2)	9.8 (6.9)	5.5 (3.7)	27.1 (17.4)	98.8 (87.3)
Black-legged Kittiwake, *Rissa tridactyla*	0.3 (0.2)	1.6 (0.9)	6.5 (4.8)	8.4 (4.9)	9.9 (5.3)	24.7 (13.6)	11.8 (6.8)	19.6 (15.8)	31.1 (16.4)	4.7 (3.8)
Unid. Gull*	30.3 (16.9)	10.7 (5.9)	127.3 (72.6)	27.7 (15.5)	10.1 (5.7)	4.1 (2.3)	10.8 (6.1)	26.8 (15)	34 (18.7)	17.7 (10)
	4.3 (2.6)	1.4 (0.8)	19.2 (11.4)	3.9 (2.3)	1.4 (0.9)	0.6 (0.3)	1.5 (0.9)	3.6 (2.2)	4.7 (2.8)	2.5 (1.5)
	2.6 (1.2)	0.9 (0.4)	11.7 (5.7)	2.4 (1.2)	0.9 (0.4)	0.3 (0.2)	0.9 (0.4)	2.3 (1.1)	3 (1.4)	1.5 (0.7)
Common Murre, *Uria aalge*	88.2 (31.6)	211.3 (84.9)	2882.7 (1478.8)	868.3 (302.9)	812.3 (299.5)	1614.7 (648.5)	501.7 (180.9)	1142.7 (391.5)	1671.5 (531.2)	574.2 (197.8)
Unid. Murre, *Uria spp.*	47 (20.9)	224.1 (87.2)	1171.8 (477.9)	82.5 (29.8)	22.5 (8.6)	8 (3.9)	74.4 (27.2)	160.8 (59.2)	34.1 (13.2)	59.3 (20.3)
Marbled Murrelet, *Brachyramphus marmoratus*	33 (13.8)	18.4 (8.9)	17.3 (8.3)	56.2 (29.3)	60 (23.7)	69.8 (29.1)	40.8 (20.2)	46.4 (28.2)	22 (8.6)	7.4 (3.7)
Unid. Murrelet, *Brachyramphus spp.*	26.6 (13.8)	36.6 (16.2)	15.1 (6.7)	31.1 (12.4)	43.4 (17)	11 (5.6)	13.8 (5.4)	5 (2.4)	7.7 (3.1)	3.1 (1.8)
Pigeon Guillemot, *Cepphus columba*	3.1 (1.5)	10.8 (5.6)	6.1 (3)	4.9 (2.4)	9.6 (4.7)	3.4 (1.8)	4.2 (2.4)	3.6 (1.8)	5.6 (2.8)	7.1 (5.8)

CHAPTER 3. SEABIRDS RESPOND TO PREDICTABLE PACIFIC HERRING (*Clupea pallasii*) AGGREGATIONS DURING WINTER IN PRINCE WILLIAM SOUND, ALASKA

Tawna Morgan[1], Mary Anne Bishop[1], Kathy Kuletz[2] and Richard Thorne[1]

[1] Prince William Sound Science Centre, Cordova, Alaska USA 99574, [2]U. S. Fish and Wildlife Service, Migratory Bird Management, 1011 East Tudor Road, Anchorage, Alaska USA 99503

ABSTRACT

We used seabird surveys conducted over two winters (2007/008 and 2008/2009) in conjunction with the hydroacoustic herring surveys in bays throughout Prince William Sound in order to compare Pacific herring abundance spatially and temporally relative to the distribution and abundance of piscivorous birds. Analysis of presence/ absence of the most prevalent seabirds in PWS in winter revealed that at a 1 km^2 scale in the bays that we surveyed, fish predictability and bathymetric features were important to foraging seabirds. We found that the presence of Common Murre, Glaucous-winged Gull, Pelagic Cormorant and grebes were positively associated with the predictability of fish at depths >23m while Marbled Murrelet and mergansers were negatively associated with water depth . The association between presence of seabirds and predictable fish aggregations at the scale of 1 km^2 suggests a searching ability of seabirds to locate seasonally predictable resources among the bays of PWS. Among the piscivorous birds we recorded, Glaucous-winged Gull, the most common surface feeder in PWS during winter, demonstrated a strong, interspecific association with Black-legged Kittiwake and loons. Pelagic Cormorants showed the greatest association with the most species while grebes showed the least interspecific association. Of the pursuit divers, Common Murre, Pelagic Cormorant and loons were associated with one another.

INTRODUCTION

Seabird winter survivorship is a function of locating and competing for resources. Interspecific competition in the form of exploitation (Birt et. al. 1987), active interference (Piatt 1990) or passive interference (Lewis et. al 2001, Ainley et. al. 2003) can lead to differences in foraging strategies, resource selection and distribution. Similar species can reduce localized competition by targeting fish schools of different densities (Piatt 1990), size classes and spatial distribution (Sanger 1987) or through species avoidance and habitat segregation (Burger et. al. 2008). Throughout the year seabirds show tendencies to aggregate at food resources (Skov et. al. 2000), possibly benefiting from foraging with conspecifics (Chilton and Sealy 1987). Aggregations around a resource increase the opportunity for mutually beneficial foraging associations between species as well as competition among species.

Forage fish represent a valuable, yet stochastic food resource for piscivorous seabirds. Along the eastern Pacific coast, Pacific Herring (*Clupea pallasii*) is an important forage fish for seabird species (Logerwell and Hargreaves 1997, Agler et al. 1999; Irons et al. 2000), and their high lipid content (Anthony and Roby 1997, Iverson et al. 2002) make them a valuable resource during times of high energy demands. Following the 1989 *Exxon Valdez* oil spill in Prince William Sound (PWS), Alaska, the Pacific Herring population underwent a significant

population decline and since then has failed to reach pre-spill population numbers (Thorne and Thomas 2008). Concurrent with the decline in the herring population, Glaucous-winged Gull (*Larus glaucescens*), Pigeon Guillemot (*Cepphus columba), Brachyramphus* murrelets, and merganser populations also experienced population declines (Lance et. al. 2001). The most persistent declines documented were associated with seabirds that overwinter in PWS (Irons et. al. 2000) and in part have been attributed to the reduced abundance of Pacific Herring (Irons et. al. 2000, Kuletz 2005).

Several bays in PWS hold large aggregations of either adult or juvenile herring (Thorne 2010, Stokesbury et. al. 2000). These bays appear to offer seasonally predictable sources of prey for piscivorous seabirds during the winter in PWS. Juvenile herring (age-0, age-1, age-2 year classes) over-winter in several bays and inlets primarily in east-northeast and west-southwest areas of PWS that are distinct from adult over-wintering areas (Stokesbury et al. 2000; Norcross et al. 2001). Juvenile herring occur at more shallow depths than adult herring (<30 m), making them potentially more readily available to diving seabirds. Within bays, herring may also school in consistent areas dependent on geographic and oceanographic features (Stokesbury et al. 2000). Over small spatial scales, tidal interactions with geography may concentrate herring in a temporally predictable manner (Zamon 2000).

The objectives of this study were twofold: 1) compare Pacific herring abundance, spatially and temporally, relative to the distribution and abundance of wintering piscivorous birds in Prince William Sound; and 2) characterize key habitats and characteristics of fish schools where seabirds were present. We hypothesized that species directly competing with one another would show greater differences in spatial distribution. Black-legged Kittiwake (*Rissa tridactyla*), Glaucous-winged Gulls, Mew Gull (*L. canus*), Common Murre, Marbled Murrelet (*Brachyramphus marmoratus*), Common Loon (*Gavia immer*), Pacific Loon (*G. pacifica*), Pelagic Cormorant (*Phalacrocorax pelagicus*), Red-breasted Merganser (*Mergus serrator*), Common Merganser (*M. merganser*), Horned Grebe (*Podiceps auritus*) and Red-necked Grebe (*P. grisegena*) are numerous in PWS for most of the winter (McKnight et al. 2007). Because these seabird species are known to forage at least partially on herring, they are likely to be influenced by the distribution and availability of herring overwintering in PWS.

STUDY

Prince William Sound (PWS) is a large fjord-type embayment (~ 10,000 km^2) in south-central Alaska, primarily between 60 and 61N, and is separated from the northern Gulf of Alaska (GOA) by large, mountainous islands. The Sound is surrounded by the Kenai Mountains on the west and the Chugach Mountains on the north and east, with a rugged and extensive coastline that includes many islands, deep fjords and shallow bays. There are several large icefields with > 20 tidewater glaciers (Molnia 2001). Abundant rain, snow and glacial melt result in a strong cyclonic circulation that generally runs east to west (Neibauer et al. 1994). During summer the waters of PWS are highly stratified, but during winter months they are more mixed, with GOA surface waters pulsing into PWS via the Alaska Coastal Current (ACC; Niebauer et al. 1994). The northern half of PWS is strongly influenced by fjord waters and tend to be colder and fresher relative to the ACC-influenced waters that are warmer and more saline (Wang et al. 2001).

METHODS

We conducted a pilot study in March 2007 to test methods for concurrently conducting fish hydroacoustic and seabird surveys. Data collected during the March 2007 cruise is not included in the current analysis, but informed our methodology and identified the target bays used in subsequent years. For this study we conducted four cruises in PWS (Fig. 1) over two winters during November 2007 and March 2008, and November 2008 and March 2009. Surveys focused on known and likely bays where herring over-winter (Norcross et al. 2001, Thorne 2005). We surveyed eight bays. Due to inclement weather, two bays were surveyed during three cruises, while the remaining six bays were surveyed during all four cruises. Surveylines ranged in length from 4 km (West Whale Bay) to 24 km (Port Gravina; Table 1, Fig 1). For all surveys we used the same, 17 m charter vessel.

Herring Abundance and Distribution

For each survey, our vessel followed a zigzag track at a speed of approximately 5 knots. Two surveys were conducted in each bay, one diurnal, followed later by a nocturnal survey that repeated the same GPS-generated track line. Fish biomass was recorded using a BioSonics 70 kHz DTX digital echosounder with a single beam (7º), down-looking transducer. Hydroacoustic data were integrated in one-min intervals and in 5-m depth intervals from 1 to 101m (reference the transducer depth, which was typically 2 m below surface). We used a threshold of -70 dB to eliminate plankton scattering.

We used a generalized acoustic cross-section of 0.0006 to estimate biomass (Kg) except when age 0 herring were specifically identified, in which case we used 0.00095 for the age 0 scattering (Thomas et al. 2002). During the day, some herring are found on the ocean floor and not detected by the acoustics. However, virtually all herring are pelagic at night (Thomas and Thorne 2003; Thorne and Thomas 2008), and often age-stratified by depth. Using the nocturnal surveys, in most cases, but not all, we were able to identify and separate age 0 and adult herring based on patterns associated with historic net catches (McClatchie et al. 2000). Other juvenile herring were more difficult to identify from the echo traces, and such identification was only accomplished on occasion. Where separation was possible, we calculated an average juvenile (primarily age 0+) and adult (age 3+) herring biomass (kg/m^2) for each bay.

Seabird Abundance and Distribution

We conducted seabird surveys concurrent with daytime hydroacoustic herring surveys onboard the same vessel. Seabird observations were conducted using established U.S. Fish and Wildlife Service protocols adapted for GPS-integrated data entry programs (USFWS 2007). One observer using 10x binoculars recorded number and behavior (in transit, in air, on water, foraging) of birds and marine mammals occurring within a strip transect width of 300 m (150 m both sides and ahead of the boat). All birds and mammals within the strip were counted continuously. The observer recorded observations into a laptop computer integrated with a global positioning system (GPS) using the program Dlog (Ford Consulting, Inc., Portland OR). The GPS-integrated program provided location data at 20-sec intervals and for every entered observation.

Data Analyses

We used generalized linear models (GLM) to test whether there were seasonal (November, March) and location (8 bays) differences in seabird density. We calculated density (birds/km^2) based on the number of birds observed and the total km surveyed (Table 3-1). We used linear mixed effects models (LME) to detect seasonal and location differences in the average juvenile herring (primarily age 0+), adult herring (age 3+) and total fish biomass (kg/m^2) for each bay. Both seabird density and fish biomass were log transformed.

We used a a binomial generalised additive mixed model (GAMM) to determine whether fish biomass, fish biomass predictability and bathymetry were related to the presence and absence of seabirds on transect. For birds, we calculated a density for each species based on the number of birds observed on a 1 km segment (birds/km2). Birds in flight and determined to be in transit were omitted from analysis. Observations of loons, mergansers and grebes were infrequent, therefore for this analysis, species were pooled and analyzed at the level of genus. We used the nocturnal hydroacoustic survey data to calculate fish biomass. For each 1 km transect segment we calculated the total fish biomass and the average fish biomass (kg/m^2, log transformed) in < 23 m and ≥ 23 m water depth. Depth (in meters) was obtained from the Alaska Ocean Observing System (2010) grid of bathymetry for PWS that is modelled to a resolution of 500 m.

We used LME to analyze the influence of bathymetry on biomass and predictability within depth category. For all models, fish predictability was treated as a categorical variable. We calculated between-year fish predictability for each transect as the proportion of times fish were detected on each transect, within a depth category, out of the total number of times a transect was surveyed in either fall or spring. Predictability across years, within seasons was used instead of overall predictability since adult fish move seasonally (Brown et al. 2002) and overwinter mortality in juvenile fish is high (Foy and Paul 1999). We used the hydroacoustic data from all four surveys as well as the March 2007 pilot study to make our predictability calculations and assumed that predictability was static across years. For example, if fish biomass was detected in the >23m depth category on transect 1 at Port Gravina on both fall surveys, predictability equaled 1.0 for that transect for both fall surveys. If fish biomass >23m depth category for that same transect was detected on 2 of the 3 spring surveys, predictability equalled 0.66 for that transect for all spring surveys. Since survey lines did not follow the exact same path between surveys, transect midpoints within 400 m of each other were considered repeat transects.

We used linear mixed effects models (LME) to detect differences in seabird density in relation to fish density, using bay as a random term to account for correlation between transects within the same bay. For this analyses we used seabird density and total fish biomass and the average fish biomass (kg/m^2, log transformed) in < 23 m and ≥ 23 m water depth for each 1 km transect segment.

We investigated seabird flocking behaviour during winter. For this analyses, we defined a flocks as >10 birds, single or mixed species, and occurring within a 1 km segment. We examined the degree of spatial clumping of seabird species using variance to mean ratios. Interspecific associations between seabird species were determined using Spearman Rank

correlation for all 1 km transect segments. We used analysis of covariance (ANCOVA) to detect differences in vertical fish distribution at identified forage flock locations.

All statistical analyses were performed using R version 2.8.1. Significance was accepted at $P = 0.05$, although for additive models, P values close to 0.05 were considered with caution.

RESULTS

Distribution of Fish Schools

Adult herring and total fish did not differ by season ($P > 0.15$ for all models) or between bays ($P > 0.2$ for all models (Figure 3-2). Juvenile herring biomass was higher during November surveys compared to March surveys (df = 2, $F = 4.36$, $P = 0.05$). Between bays, there was a trend for higher densities of age 0 herring to be found in Simpson, Whale and Eaglek Bays, although the difference was not significant (df = 7, $F = 1.4$ $P = 0.24$).

Peak fish biomass occurred 2.2 - 9.3 km from the head of bays. Fish biomass and fish predictability on transects in the <23 m depth category was not influenced by bathymetry (0.009 ± 0.008, df = 367, $t = 1.08$, $P = 0.28$; and 0.0007 ± 0.0004 df = 326 $t = 1.62$ $P = 0.10$ respectively). On transect segments >23 m depth, both fish biomass and fish predictability were significantly influenced by bathymetry (0.024 ± 0.009, df = 367, $t = 2.87$, $P < 0.01$; and -0.002 ± 0.0006, df = 326, $t = -2.52$ $P = 0.01$ respectively. Between the two depth categories, biomass was positively correlated but the relationship was weak ($r = 0.58$, $P < 0.01$, Fig. 3-3). Fish biomass for either depth category also did not vary between bays or seasonally (top 23 m: $F_{8,19} = 0.6$, $P = 0.77$; below 23 m: $F_{8,19} = 0.49$, $P = 0.85$

Seabird Response to Fish Density

Seabird density were significantly higher in March compared with November for Common Murre ($P < 0.01$) and Pelagic Cormorant ($P < 0.04$), however, we detected no seasonal differences for other species ($P > 0.10$). Seabird density (Table 3-2) did not differ by bay for any species ($P > 0.10$). The presence of Common Murre, Glaucous-winged Gull, Pelagic Cormorant and grebes were positively associated with predictability of herring at depths > 23 m (Table 3-3, Fig 3-4.). Water depth was the only significant term for Marbled Murrelet and mergansers (Table 3-3, Fig. 3-5), both of which were more common in shallow regions.

The density of Common Murre was negatively related to juvenile herring density (-0.84± 0.29, df = 21, $t = -2.93$, $P = 0.01$), but showed no relationship to adult herring (0.3± 0.22, df = 21, $t = 1.35$, $P = 0.19$) or total fish biomass (-0.36± 0.49, df = 21, $t = -0.75$, $P = 0.46$). Grebe density was positively related to juvenile herring density (0.57 ± 0.28, df = 21, t = 2.05, $P = 0.05$), but showed no relationship to adult herring biomass (0.02± 0.21, df = 21, $t = 0.1$, $P = 0.92$) or total fish biomass (0.15± 0.42, df = 21, t = 0.36, $P = 0.72$). All other seabird species showed no significant relationship to herring or total fish biomass ($P > 0.1$ for all models). For herring biomass associated with forage flocks, fish biomass above and below 23m was significantly related (Spearman Rank; r = 0.66, $P < 0.01$), which was significantly different from the correlation between depth categories for all 1 km segments (Fig. 3-3; $r = 0.338$, F = 6.36, $P = 0.01$).

Flocking

All seabirds showed a high degree of intra-specific spatial clumping. Glaucous-winged Gulls, mergansers and Common Murre had the highest variance to mean ratios. Marbled Murrelet and grebes showed the least amount of clumping and were most frequently seen as pairs or in groups of four. Glaucous-winged Gull, the most common surface feeder in PWS during winter, demonstrated a strong, interspecific association with Black-legged Kittiwake and loons. Pelagic Cormorants showed the greatest association with the most species while grebes showed the least interspecific association. Of the pursuit divers, Common Murre, Pelagic Cormorant and loons were associated with one another. Marbled Murrelet, a juvenile herring consumer, was not associated with any other pursuit diver but was positively associated with Black-legged Kittiwakes, which also targets juvenile herring. Mergansers were associated with Mew Gulls and Pelagic Cormorants (Table 3-4).

DISCUSSION

Understanding the distribution of seabirds in relation to prey presents a challenging question to ecology, evolution and management. Generally, seabird distribution is influenced by biotic and abiotic factors, including availability of high energy prey (Piatt 1990, Ostrand et. al. 2004), oceanographic features (Hunt et. al. 1999, Adams et. al. 2010,), predictable forage locations (Skov et. al. 2000), and interspecific interactions (Berger et. al. 2008, Davoren et al. 2003, and others). During the breeding season proximity to the breeding colony is a critical factor (Coulson 2002). During winter, however, seabirds are not constrained by duties at the colony and changes in regional prey species composition may result in alternative spatial distributions of seabirds in relation to food resources.

Analysis of presence/ absence of the most prevalent seabirds in PWS in winter revealed that at a1-km^2 scale, forage predictability and bathymetric features may be more important than herring abundance to foraging seabirds. The association between presence of seabirds and predictable fish aggregations at the scale of 1-km^2 suggests fine tune selection on predictable forage availability by some species. The lack of a significant association between herring biomass and specific bays may reflect the broadscale searching ability of seabirds, and the bird's abilities to locate seasonally predictable resources among the bays of PWS. Within regions harboring suitable resources, tidal flows can work with the underlying topography to aggregate prey in predictable locations (Hunt et. al 1999, Zamon 2003).

Herring distribution in PWS varies temporally and spatially (Brown and Carls 1998). Seasonally, herring separate by age class into bays with high spatial predictability (i.e., among bays; Brown and Carls 1998). Spawning and nursery areas may change over time, but on seasonal temporal scales they remain spatially predictable (Stokesbury et al. 2000), thus offering seasonally predictable resources to seabirds.

Seabirds use a variety of mechanism for locating suitable resources. Visual searching is one mechanism for identifying forage location. For piscivorous seabirds, biomass and fish school characteristics can influence foraging decisions (Axelson et. al. 2001, Ostrand et al. 2004), particularly when detectable from the air. In addition to visual cues, seabirds may target temporally dependable prey locations (Irons 1998). When biomass is moderate or low, but

highly predictable, individuals can reduce energy expenditure by foraging in predictable locations (Gende and Sigler 2006).

The variety of forage behaviors observed across seabird species leads to expected differences in spatial distributions despite high dependence on a few resources. Common Murre, a pursuit diver, tended to flock with other species in both this study and others (Chilton and Sealy 1987). Forage flocks containing Common Murre were associated with low herring biomass compared with other interspecific flocks, indicating that Common Murre may benefit from interspecific interactions when foraging on low density herring schools. When not utilizing cues associated with forage flocks, Common Murre in PWS were found in regions of predictable herring (Fig. 3-4), as has been observed in other studies (Decker and Hunt 1996).

Surface feeders in particular may cue into forage aggregations or fish driven to the surface by diving birds (Ostrand 1999). Gulls foraging near the surface offer a secondary signal to attract other species (Chilton and Sealy 1987). Mixed species associations are likely to develop between highly conspicuous surface feeders and species that target similar resources and their associated predators. Although Glaucous-winged Gulls are surface feeders, their positive association with herring predictability at depths greater than 23 m likely reflects the use of these foraging areas by other diving birds or predatory fish which may stir up resources for surface feeders (Hoffman et al. 1981, Hunt 1988). The presence of zooplankton associated with fish schools may also attract surface feeding birds. Gulls may in turn provide visual and auditory signals to other species, such as loons, of active forage hotspots.

Marbled Murrelets tend to forage in shallower waters (Sanger 1987, Burger et. al. 2008) with smaller herring schools (Ostrand et. al. 2004). Their association with shallow depths (see Fig. 3-6) suggests murrelets may employ a sit and wait search effort (Schneider and Piatt 1986) in locations where tidal upwelling occurs. This sort of strategy is profitable if oceanographic process operate cyclically to produce predictable resources. The lack of association with herring may indicate that areas targeted by Marbled Murrelet may be reliable sources of alternative forage such as zooplankton, which may be a significant source of energy for wintering Marbled Murrelets (Nelson 1997).

Interspecific associations reflect differences in diet, foraging behaviors and habitat preferences. The interspecific association between loons, murrelets, and mergansers and gulls suggest these species may contribute to the formation of forage flocks. Marbled Murrelet and mergansers are unable to dive as deep as Common Murre and loons (Fig.3-7), thus may be limited to shallow regions where fish are forced toward the surface. Marbled Murrelet had a positive association with Black-legged Kittiwake but not Glaucous-winged Gulls. This relationship might be a consequence of diet because Glaucous-winged Gull can eat larger fish. However, Glaucous-winged Gull and other large birds can exclude smaller birds from prey in mixed flocks (Kuletz 2005). Black-legged Kittiwake feed primarily on euphausiids and juvenile fish similar to Marbled Murrelet and may benefit from disoriented or injured euphausiids stirred up from diving alcids (Hunt 1988). Additionally, Marbled Murrelet appear able to locate small, ephemeral fish schools, and by driving the fish to the surface, attract surfacing feeding birds like kittiwakes (Ostrand 1999). In other regions Marbled Murrelets avoid flocking with other alcids (Porter and Sealy 1982, Burger et. al. 2008) possibly to reduce interspecific competition. Where populations overlap, Murrelet typically forage in shallower water (Burger et. al. 2008) than

Common Murre, but frequently forage in mixed flocks with gulls (Mahon et. al. 1992). A lack of association with other diving seabirds would suggest Marbled Murrelet avoid interspecific competition, are limited by dive depths, and are likely to be found in areas separate from Common Murre in PWS.

Pelagic Cormorant foraging success is dependent on high density fish schools (Enstipp et. al. 2007), however, we did not find a direct relationship between herring biomass and presence of Pelagic Cormorant in Prince William Sound. When we assess forage flock composition in relation to herring biomass, flocks containing Pelagic Cormorant were detected in areas with higher biomass than other pursuit diving species.

The differences in herring-seabird relationships observed during this study reflect the variety of foraging techniques employed by seabirds during the winter in PWS. Foraging strategy, diet and competition likely influence bird distributions in relation to herring. Similar to other studies, we found that predictability of herring may contribute to its value as a food resource (Skov 2000). Associations between both surface feeding and diving species indicates that all forage guilds may be influenced by changes in the prey base in PWS, highlighting the need to consider ecosystem level process when making management decisions regarding fish or birds.

ACKNOWLEDGMENTS

The research described in this paper was supported by grant from the Exxon Valdez Oil Spill Trustee Council. The findings and conclusions presented by the authors are their own and do not necessarily reflect the views or position of the Trustee Council. We would like to thank Dave Janka who as skipper of the *MV* Auklet made it possible to survey in PWS in winter and James Thorne who helped with hydroacoustic surveys. We are also grateful to additional seabird observers Karen Brenneman and Aaron Lang.

LITERATURE CITED

Adams, J., Takekawa, J.Y., H.R. Carter, and J. Yee. 2010. Factors influenceing the at-sea distribution of Cassin's Auklets (*Ptychoramphus Aleuticus*) that breed in the Channel Island, California. Au 127(3) 503-513.

Agler, B.A., S.J. Kendall, D.B. Irons and S.P. Klosiewski 1999. Declines in marine bird populations in Prince William Sound, Alaska, coincident with a climatic regime shift, Waterbirds 22:98-103.

Ainley, David G., R. Glenn Ford, Evelyn D. Brown, Robert M. Suryan, and David B. Irons. 2003. Prey resources, competition, and geographic structure of kittiwake colonies in Prince William sSund. Ecology 84:709–723.

Alaska Ocean Observing System. 2010. www.aoos.org/

Anthony, J.A. and D.D. Roby. 1997. Variation in lipid content of forage fishes and its effect on energy provisioning rates to seabird nestlings. Pages 725-729 in Proc. forage fishes in marine ecosystems. Alaska Sea Grant. AK-SG-97-01.

Axelson, B.E., P. Fossom, C. Kvamme, and L. Nottestad. 2001. Pretty patterns but a simple strategy: predator prey interactions between juvenile herring and Atlantic Puffins observed with multibeam sonar. Canadian Journal Zoology 79: 1586-1596.

Brown, E. D. and M.G. Carls. 1998. Pacific Herring *Clupea pallisi.* Restoration Notebook, *Exxon Valdez* Oil Spill Trustee Council, anchorage, Alaska.

Brown, ED, J Seitz, BL Norcross, and HP Huntington. 2002. Ecology of herring and other forage fish as recorded by resource users of Prince William Sound and the outer Kenai Peninsula, Alaska. Alaska Fishery Research Bulletin 9:75-101.

Burger, A.E., C.L. Hitchcock, E. A. Stewart, and G.K. Davoren 2008. Coexistence and spatial distributions of Marbled Murrelets (*Brachyramphus Marmotratus*) and other alcids off Southwest Vancouver Island, British Columbia.

Decker, M.B. and G.L. Hunt, Jr. 1996. Foraging by murres (Uria spp) at tidal fronts surrounding the Pribilof Islands, Alaska USA. Marine Ecology Progress Series 139:1-10.

Enstipp, M.R., D. Gremillet, and D.R. Jones. 2007. Investigation of the functional link between prey abundance and seabird predatory performance. Marine Ecology Progress Series 331: 267-279.

Foy, R.J. and A.J. Paul. 1999. Winter feeding and changes in somatic energy content for age-0 Pacific Herring in Prince William Sound. Transactions American Fisheries Society. 128:1193-1200.

Hunt, G.L. Jr., F. Mehlum, R.W. Russell, D. Irons, M.B. Decker, and P.H. Becker. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. In: N.J. Adams & R.H. Slotow (eds) Proc.22 Int. Ornithol. Congr., Durban.

Hunt, GL Jr, N.M. Harrison, W.M. Hamner and B.S. Obst. 1988. Observations of a mixed-species flock of birds foraging on euphausiids near St. Mathew Island, Bering Sea. Auk 105: 345-349

Irons, D.B., S.J. Kendall, W.P. Erickson, L.L. McDonald and B.K. Lance. 2000. Nine years after the Exxon Valdez oil spill: effects on marine bird populations in Prince William Sound, Alaska. Condor 102:723-737.

Iverson, S.J., K.J. Frost, and S.L.C. Lang. 2002. Fat content and fatty acid composition of forage fish and invertebrates in Prince William Sound, Alaska: factors contributing to among and within species variability. Marine Ecology Progress Series 241: 161–181

Kuletz, K.J. 2005. Foraging behaviour and productivity of a non-colonial seabird, the Marbled Murrelet (*Brachyramphus marmoratus*) relative to prey and habitat. Ph.D. Diss., Univ. Victoria, Victoria, British Columbia.

Lance, B.K., D.B. Irons, S.J. Kendall and L.L. McDonald. 2001. An evaluation fo marine bird population trends following the Exxon Valdez Oil Spill, Prince William Sound, Alaska. Marine Pollution Bulletin 42: 298-309.

Lewis, S. T. N. Sherratt*, K. C. Hamer* & S. Wanless. 2001. Evidence of intra-specific competition for food in a pelagic seabird. Nature: 412:816-819.

Logerwell, E. A. and Hargreaves, N.B. 1996. The distribution of sea birds relative to their fish prey off Vancouver Island: opposing results at large and small spatial scales. Fisheries Oceanography 5: 163-175.

Mahon, T.E., G.W. Kaiser, and A.E. Burger. 1992. The role of Marbled Murrelets in Mixed-Species Feeding Flocks in British Columbia. Wilson Bulletin 104: 738-743.

McClatchie, S., R. Thorne, P. Grimes and S. Hanchet 2000. Ground truth and target identification for fisheries acoustics. Fisheries Research **47**:173-191.

Molnia, B. 2001. Glaciers of Alaska Alaska Geographic vol 28, no2 Alaska Geographic Society, Anchorage, Alaska.

Niebauer, H.J., T.C. Royer, T.J. Weingartner. 1994. Circulation of Prince William Sound, Alaska. Journal of Geophysical Research 99:14113 – 14126.

Norcross, B.L., E.D. Brown, R.J. Foy, M. Frandsen, S.M. Gay, T.C. Kline, D.M. Mason, E.V. Patrick, A.J. Paul and K.D.E. Stokesbury 2001. A synthesis of the life history and ecology of juvenile Pacific herring in Prince William Sound, Alaska. Fisheries Oceanography 10 (supp. 1):42-57.

Ostrand, W.D., S. Howlin, and T.A. Gotthardt. 2004. Fish school selection by Marbled Murrelets in Prince William Sound Alaska: responses to changes in availability. Marine Ornithology 32:69-76

Piatt, J. F. 1990. The aggregative response of Common Murres and Atlantic Puffins to schools of capelin. Studies in Avian Biology 14:36-51.

Porter, J.M. and S.G. Sealy. 1982. Dynamics of seabird multispecies feeding flocks: Age-related feeding behavior. Behavior 81:91:109

Sanger, G.A. 1987. Wintering diets of Common Murres and Marbled Murrelets in Kachemak Bay, Alaska. Condor 89: 426-430.

Schneider, D.C. and J.F. Piatt. 1986 Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. Marine Ecology Progress Series 32: 237-246

Skov, H., J. Durinck, and P. Andell. 2000. Associations between wintering avian predators and schooling fish in the Skagerrak-Kattegat suggest reliance on predictable aggregations of herring *Clupea havengus.* Journal Avian Biology 31: 135-143

Stokesbury, K.D.E., J. Kirsch, E.D. Brown, G.L. Thomas and B.L. Norcross. 2000. Spatial distributions of Pacific herring and walleye pollock in Prince William Sound, Alaska. Fish Bulletin 98:400-409.

Thomas, G.L, J. Kirsch and R.E. Thorne 2002. Ex situ target strength measurements of Pacific herring and Pacific sand lance,. N. Am. J.Fisheries Management **22**:1136-1145.

Thorne R. E. 2005. Monitoring Pacific Herring Abundance with Combined Acoustic and Optical Technologies. *Exxon Valdez* Oil Spill Restoration Project Final Report.

Thorne, R.E. 2010. Trends in Adult and Juvenile Herring Distribution and Abundance in Prince William Sound. *Exxon Valdez* Oil Spill Restoration Project 070830 Final Report.

Thorne, R. E., and G.L. Thomas. 1990. Acoustic observation of gas bubble release by Pacific herring. Canadian Journal Fisheries Aquatic Sciences, 47: 1920–1928

Thomas, G.L. and R.E. Thorne 2003. Acoustical-optical assessment of Pacific herring and their predator assemblage in Prince William Sound, Alaska. Aquatic Living Resources **16**:247-253.

Thorne, R. E., and G.L. Thomas. 2008. Herring and the "Exxon Valdez" oil spill: an investigation into historical data conflicts. ICES Journal Marine Science, 65: 44–50.

US Fish Wildlife Service. 2007. North Pacific Pelagic Seabird Observer Program Observers Manual, Inshore / small vessel version, November 2007. U.S. Fish Wildlife Service, Migratory Bird Management Nongame Program, Anchorage, Alaska. Unpub. protocol manual, 25 pp

Wang, J., M. Jin, V. Patrick, J. Allen, D. Eslinger and T. Cooney. 2001. Numerical simulation of the seasonal ocean circulation patterns and thermohaline structure of Prince William Sound, Alaska using freshwater of a line source. Fisheries Oceanography 10:132-148.

Zamon, J.E. 2003. Mixed species aggregations feeding upon herring and sandlance school in a nearshore archipelago depend on flooding tidal currents: Marine Ecology Progress Series 261: 243-255.

CHAPTER 3 TABLES

Table 3-1. Distance (km) surveyed by bay and cruise, Prince William Sound, Alaska.

Bay	Nov 2007	Mar 2008	Nov 2008	Mar 2009
Simpson	11	11	11	11
Port Fidalgo	NA	23	22	23
Port Gravina	19	24	18	17
Eaglek	18	15	15	15
W. Whale	4	NA	4	3
E. Whale	6	5	6	3
Sawmill	11	11	11	11
Zaikof	16	18	16	15

Table 3-2. Seabird density (birds/km^2 ± S.E.) for bays in PWS, November 2007 and 2008, March 2008 and 2009. Densities determined from 300m width transects of varying lengths.

Species	Simpson *n* = 4	Gravina *n* = 4	Fidalgo *n* = 3	Eaglek *n* = 4	West Whale *n* = 3	East Whale *n* = 4	Sawmill *n* = 4	Zaikof *n* = 4
Common Loon	0.05 ± 0.03	0.03 ± 0.02	0.24 ± 0.15	0.03 ± 0.03	0.09 ± 0.09	0.05 ± 0.05	0.00 ± 0.00	0.26 ± 0.08
Pacific Loon	0.11 ± 0.05	0.44 ± 0.13	0.18 ± 0.08	0.02 ± 0.02	0.45 ± 0.45	0.10 ± 0.10	0.00 ± 0.00	0.74 ± 0.43
Common Merganser	0.09 ± 0.04	0.03 ± 0.02	0.00 ± 0.00	0.11 ± 0.11	0.00 ± 0.00	0.00 ± 0.00	0.09 ± 0.09	0.03 ± 0.02
Red-breasted Merganser	0.30 ± 0.12	0.31 ± 0.16	0.29 ± 0.16	0.08 ± 0.07	0.00 ± 0.00	0.35 ± 0.24	0.00 ± 0.00	0.00 ± 0.00
Pigeon Guillemot	0.11 ± 0.07	0.36 ± 0.09	0.12 ± 0.05	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.12 ± 0.06
Glaucous-winged Gull	0.55 ± 0.21	0.91 ± 0.26	1.1 0± 0.25	0.65 ± 0.21	0.64 ± 0.31	0.10 ± 0.07	0.3 ± 0.09	4.06 ± 1.21
Mew Gull	0.23 ± 0.09	0.1 ± 0.04	0.34 ± 0.12	0.46 ± 0.15	1.27 ± 0.9	0.70 ± 0.35	1.2 ± 0.53	0.15 ± 0.06
Black-legged Kittiwake	1.57 ± 0.8	0.31 ± 0.08	0.78 ± 0.21	0.44 ± 0.16	0.00 ± 0.00	0.10 ± 0.07	0.86 ± 0.47	1.26 ± 0.53
Common Murre	6.64 ± 2.53	7.83 ± 2.60	8.28 ± 1.77	1.32 ± 0.41	0.64 ± 0.39	0.10 ± 0.10	5.57 ± 2.26	1.42 ± 0.31
Marbled Murrelet	2.52 ± 0.50	0.88 ± 0.20	0.21 ± 0.08	0.73 ± 0.18	0.36 ± 0.36	0.00 ± 0.00	0.39 ± 0.18	1.02 ± 0.28
Red-necked Grebe	0.07 ± 0.05	0.1 0± 0.04	0.49 ± 0.26	0.06 ± 0.04	0.27 ± 0.19	0.35 ± 0.21	0.00 ± 0.00	0.06 ± 0.03
Horned Grebe	0.34 ± 0.15	0.03 ± 0.02	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00	0.25 ± 0.12	0.00 ± 0.00	0.18 ± 0.15
Pelagic Cormorant	0.36 ± 0.12	0.12 ± 0.04	2.35 ± 0.93	0.29 ± 0.14	0.64 ± 0.43	1.50 ± 0.85	8.86 ± 4.18	0.28 ± 0.1

Table 3-3. Summary of significant factors influencing the presence and absence of seabirds at the 1 km scale. Explanatory variables were considered significant at $P < 0.05$.

	1 Kilometer Scale				
Species or Species Group	Water Depth	Predictability to 23m	Predictability ≥ 23m	Biomass to 23m	Biomass 23-63m
Glaucous-winged Gulls	No	No	**Yes**	No	No
Common Murre	No	No	**Yes**	No	No
Pelagic Cormorant	No	No	**Yes**	No	No
Marbled Murrelet	**Yes**	No	No	No	No
Loons	No	No	No	No	No
Grebes	No	No	**Yes**	No	No
Mergansers	**Yes**	No	No	No	No

Table 3-4. Spearman Rank correlation coefficients for species densities within 1 km segments. Correlation coefficients are above the blue line, P values are below. Significant values are indicated in bold.

	Black-legged Kittiwake	Glaucous-winged Gull	Mew Gull	Pelagic Cormorant	Marbled Murrelet	Common Murre	Loons	Grebes	Mergansers
Black-legged Kittiwake		**0.31**	0.09	**0.13**	**0.17**	0.07	0.06	0.03	**0.18**
Glaucous-winged Gull	0.00		-0.02	0.01	0.00	0.02	**0.14**	0.00	-0.02
Mew Gull	0.08	0.69		**0.62**	-0.01	0.03	-0.02	-0.01	**0.22**
Pelagic Cormorant	0.01	0.90	0.00		-0.06	**0.15**	**0.19**	0.09	**0.37**
Marbled Murrelet	0.00	0.99	0.78	0.27		-0.08	-0.02	0.07	0.01
Common Murre	0.16	0.67	0.59	0.00	0.12		**0.19**	0.01	0.08
Loons	0.24	0.00	0.75	0.00	0.71	0.00		0.04	**0.13**
Grebes	0.56	0.99	0.86	0.08	0.20	0.91	0.39		0.06
Mergansers	0.00	0.66	0.00	0.00	0.89	0.09	0.01	0.21	

CHAPTER 3 FIGURES

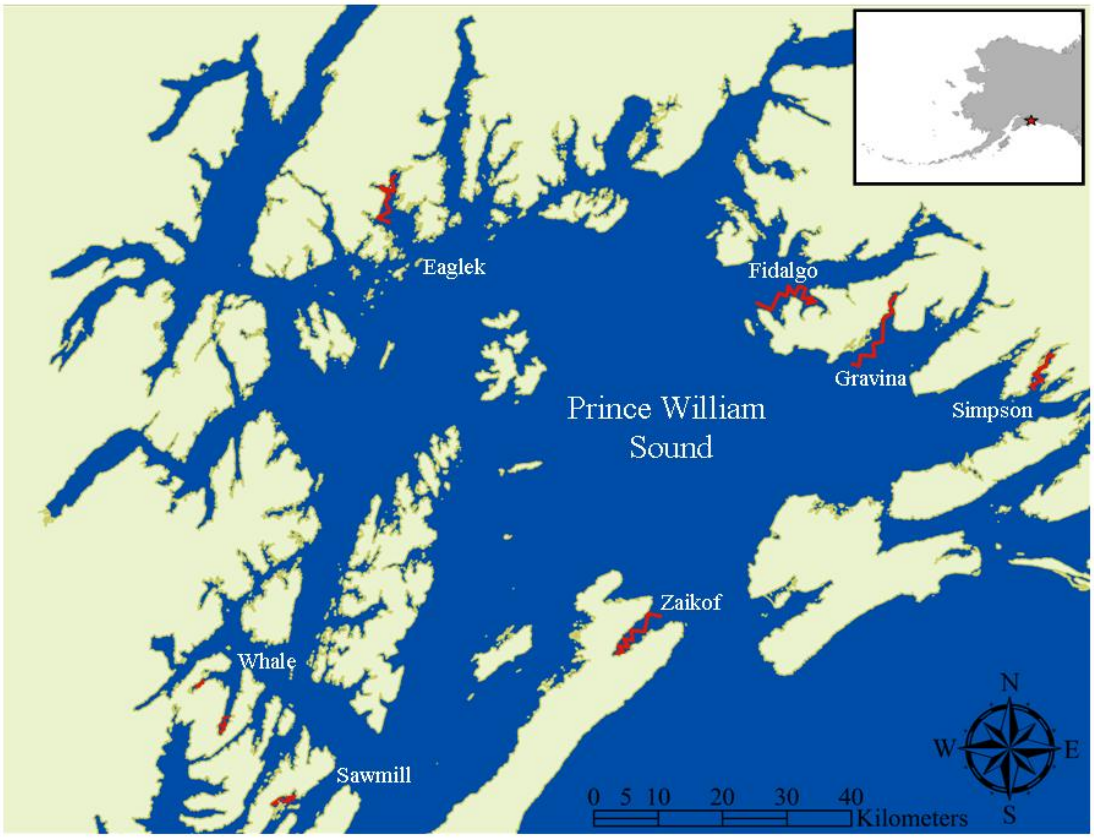

Figure 3-1. Prince William Sound. Red lines indicate approximate location of hydroacoustic and seabird surveys.

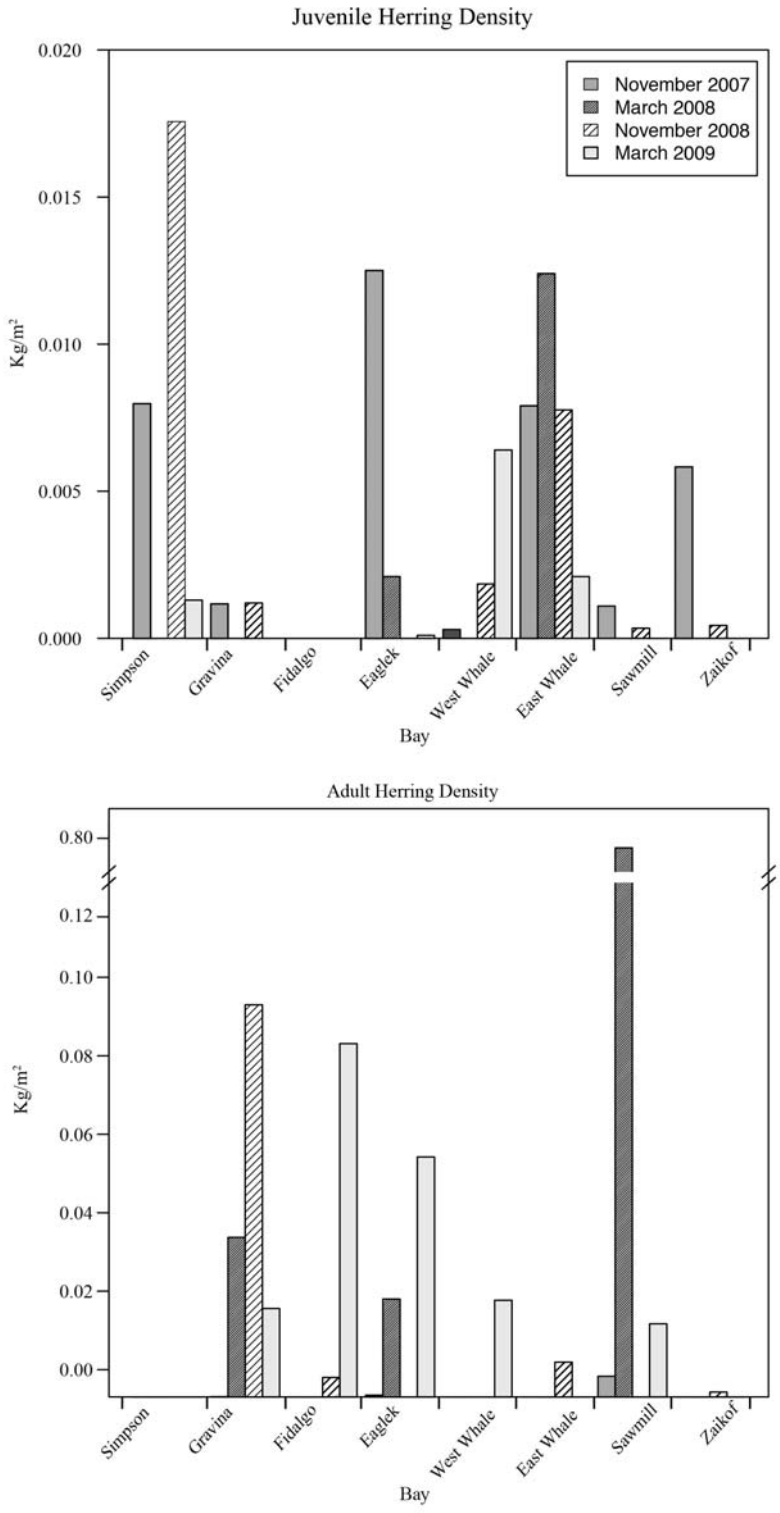

Figure 3-2. Juvenile 0+ herring (top) and adult 3+ herring (bottom) density in bays with concurrent seabird surveys during November and March 2007-2009. Densities determined during nocturnal hydroacoustic surveys. No surveys: Fidalgo in November 2007 and West Whale in March 2008.

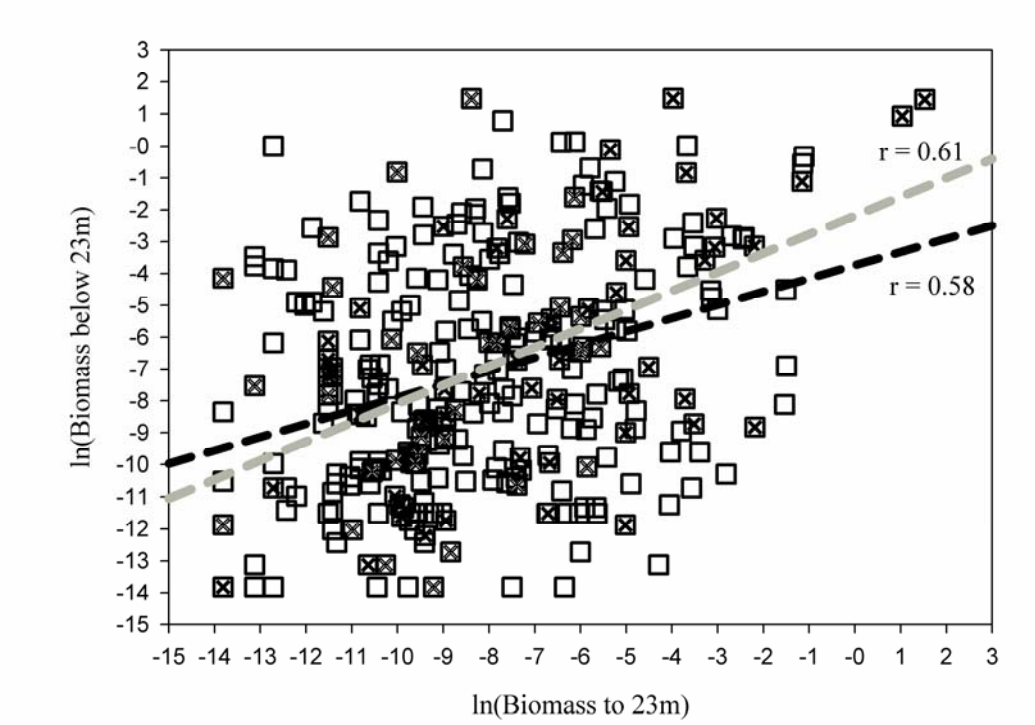

Figure 3-3. The vertical distribution of fish for all transects is shown with open squares. Squares filled with X's represent the vertical distribution of fish on transects with flocks. The black dotted line shows the correlation between biomass above and below 23m for all transects surveyed (n = 379 km) Grey dashed line shows correlation between biomass above and below 23m on transects where flocks occur (n = 316 km).

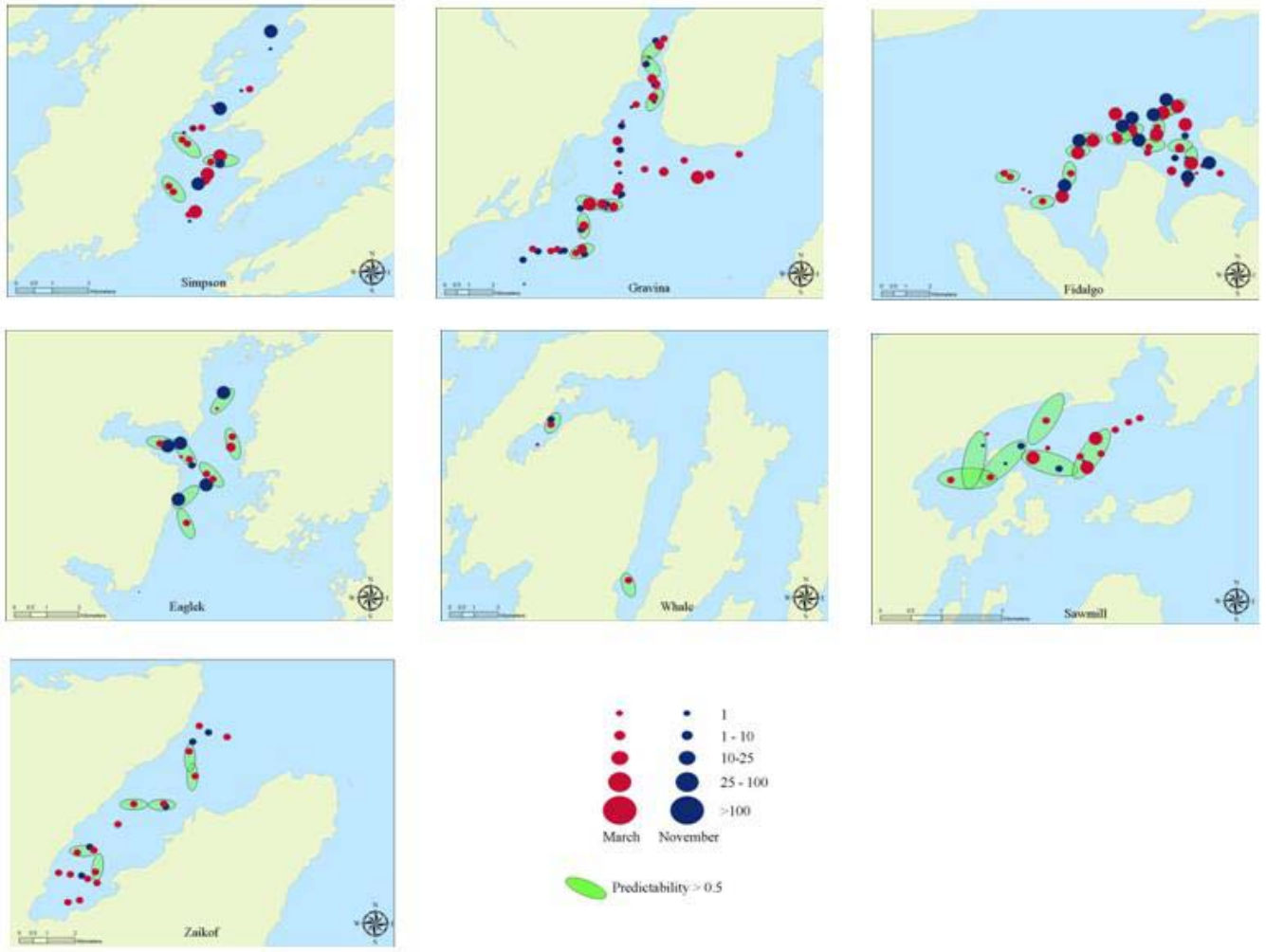

Figure 3-4. Herring predictability in relation to the distribution of Common Murre in PWS in March and November 2007 - 2009

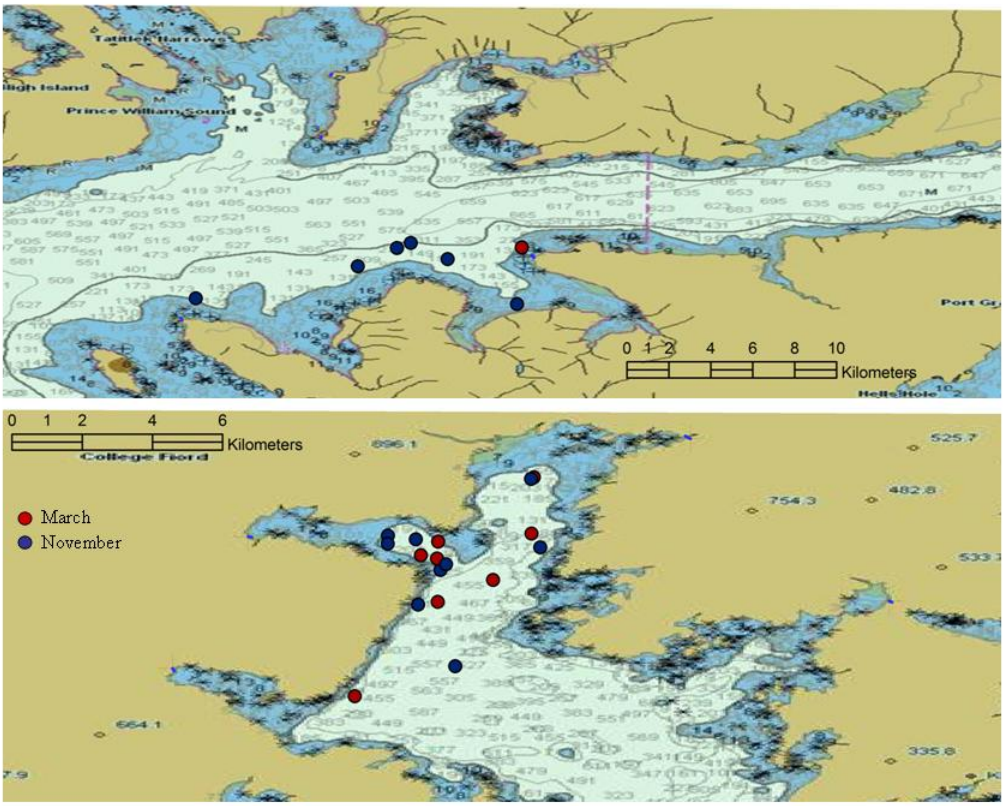

Figure 3-5. Marbled Murrelet observations during March and November cruises for Fidalgo (top) and Eaglek (bottom) bays. Depths noted in feet.

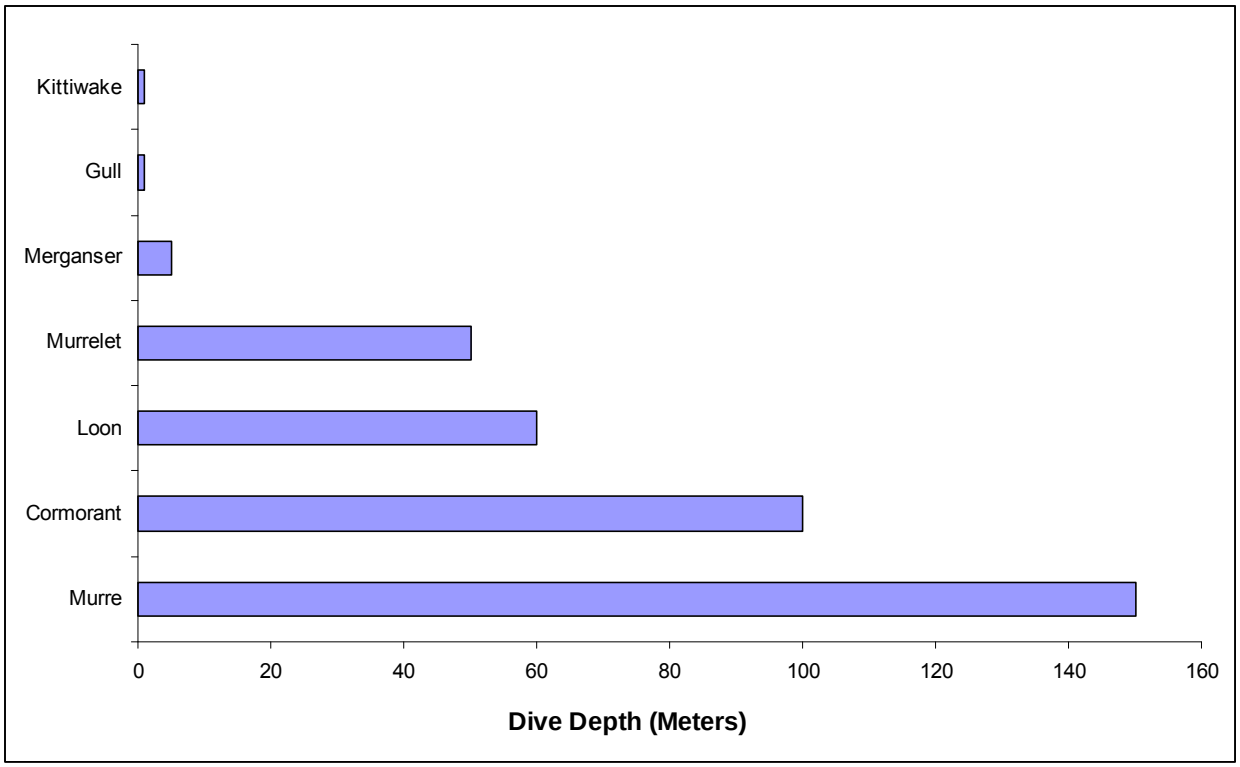

Figure 3-6. Dive depths for common seabirds in Prince William Sound.