ENVIRONMENTAL GRADIENTS AND PREY AVAILABILITY RELATIVE TO GLACIAL FEATURES IN KITTLITZ'S MURRELET FORAGING HABITAT

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ENVIRONMENTAL GRADIENTS AND PREY AVAILABILITY RELATIVE TO GLACIAL FEATURES IN KITTLITZ'S MURRELET FORAGING HABITAT

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

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Fairbanks, Alaska

December 2009

Abstract

The goal of this study was to characterize Kittlitz's murrelet (*Brachyramphus brevirostris*) foraging habitat relative to prey availability and oceanography in Kenai Fjords National Park, a glacial-marine system. I conducted oceanographic, hydroacoustic, trawl, beach seine, and marine bird surveys monthly from June-August in 2007 and 2008. High sediment load from glacial river runoff shaped the marine ecosystem, and this appeared critically important to Kittlitz's murrelets at sea. Submerged moraines influenced inner fjord habitat that was characterized by cool, fresh, stratified, and silt-laden waters. This silty glacial runoff limited light availability to chlorophyll near tidewater glaciers, but zooplankton abundance was enhanced in the surface waters, perhaps due to the absence of a photic cue for vertical migration. Zooplankton community structure was influenced by glacial features and varied along an increasing temperature gradient over the summer. Acoustic measurements suggested that low density aggregations of fish and zooplankton were available in the surface waters near glacial river outflows where murrelets typically forage. Dense fish aggregations moved into the fjords by August. Kittlitz's murrelets were more likely to occur in areas with higher acoustic biomass near glaciers, making these birds more susceptible to climate change than the congeneric marbled murrelet (*B. marmoratus*), which was most associated with shallow, ice-free areas.

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Acknowledgements

I appreciate the guidance and support of my supervisor, Dr. John F. Piatt, my major advisor, Dr. Nicola Hillgruber, and also my committee members Dr. Franz Mueter, and Dr. Tom Weingartner. This project would not have been possible without the help of Erica Madison, who helped with field operations, data management, and moral support throughout. I also wish to thank USGS staff including Shiway Wang, Gary Drew, and Naomi Bargmann for their help in the field. Greg Snedgen and Jon Wetzel, captains of the USGS M/V *Alaskan Gyre*, were also instrumental in field operations. The staff of Kenai Fjords National Park, including the chief of resources, Shelley Hall, and also Meg Hahr, Mark Kansteiner, Caroline Jezierski, Dan Shultz, Mike Tetreau, and the captain and crew of the M/V *Serac,* all provided valuable assistance and support to this project. I also thank Marc Romano (NOAA), Kathy Kuletz (USFWS), Terry Quinn (UAF), Chris Hay-Jahans (UAS), and Martin Renner (USGS), who provided assistance during the planning and analysis phases of the study. Finally, I wish to thank my family for their unending faith in my ability to accomplish what I set out to do.

This project was funded by the U.S. Geological Survey, Alaska Science Center, with supplemental funds from the U.S. Geological Survey Natural Resource Protection Program and with valuable logistic support from Kenai Fjords National Park.

Introduction

Glacial fjord ecosystems are characterized by dynamic oceanographic processes (Royer *et al.*, 1990; Etherington *et al.*, 2007) that influence primary productivity (Keck *et al.*, 1999) and trophic interactions in marine communities (Abookire & Piatt, 2005; Suryan *et al.*, 2006; Piatt & Gende, 2007). Most glaciers throughout coastal Alaska are thinning rapidly (Larsen *et al.*, 2004), particularly since the mid-1990's (VanLooy *et al.*, 2006) which gives some concern about how local marine production will be affected by diminished glacial input into the sea. While linkages between oceanographic characteristics and patterns of faunal abundance and composition have been demonstrated successfully for marine and estuarine systems (Becker *et al.*, 2007; Ehrich *et al.*, 2009), fewer studies have focused on glacial fjord systems. It is these systems, however, which are important for many Arctic and Subarctic species (Kuletz *et al.*, 2003; Mathews & Pendleton, 2006; Arimitsu *et al.*, 2008a) and which may experience dramatic changes in the near future because of global warming.

Variability in physical oceanographic processes influences prey distribution in marine and estuarine systems (Rakocinski *et al.*, 1992; Speckman *et al.*, 2005). In Cook Inlet, Alaska, forage fish community structure aligned with temperature and salinity gradients. For example, juvenile salmonids and osmerids occurred in warmer, fresher habitats, while Pacific sand lance (*Ammodytes hexapterus*) occurred in colder, more saline waters (Abookire & Piatt, 2005). Abundance and distribution of fishes were influenced by oceanography, sediment influx, and upwelling of nutrient rich waters (Robards *et al.*, 1999). Similarly, capelin (*Mallotus villosus*) were associated with areas

characterized by cool temperatures, low salinity, high turbidity, and marine sills in a Southeast Alaska glacial fjord system (Arimitsu *et al.*, 2008a).

Zooplankton community structure in glacial fjord systems is influenced by advective processes in the dynamic shallow waters above submerged moraines, and by diurnal migration patterns within the more stable water masses below the sills (Gorsky *et al.*, 2000; Basedow *et al.*, 2004). Advective processes are affected by tidal motion, freshwater input, and bathymetric features, whereas daily vertical migration of zooplankton is influenced by light penetration and ultraviolet radiation in the surface waters (Digby, 1961; Alonzo *et al.*, 2004). Some zooplankton migrate to the surface waters at night to feed, and occur in deeper waters during the day to avoid predation, although vertical migration patterns vary by species, location, and also under conditions of varying light conditions (Coyle & Pinchuk, 2005; Blachowiak-Samolyk *et al.*, 2006).

Prey availability and environmental gradients may influence the distribution and abundance of marine predators. The Kittlitz's murrelet is a non-colonial, diving seabird that generally forages in marine waters near tidewater glaciers during the summer breeding season (Day *et al.*, 2003; Kuletz *et al.*, 2003). These birds feed on small schooling fishes and macrozooplankton (Hobson *et al.*, 1994; Day & Nigro, 2000). Isotope analysis suggests Kittlitz's murrelets occupy a lower trophic position because they consume more zooplankton in their diets, compared to the congeneric marbled murrelet (Hobson *et al.*, 1994). At-sea surveys in Alaska indicate that Kittlitz's murrelet populations have declined by as much as 84% since the late 1980's at a rate of up to 18% per year (Kuletz *et al.*, 2003; Kissling *et al.*, 2007; Drew & Piatt, 2008; USFWS, 2008).

These rates of decline underscore the need to better understand the dependence of Kittlitz's murrelet on foraging habitat near nesting grounds in glaciated marine systems (Kuletz *et al.*, 2003; Kissling *et al.*, 2007; Drew & Piatt, 2008; USFWS, 2008).

The overall goal of this study was to describe the environmental patterns of Kittlitz's murrelets' marine foraging habitat in relation to glacial ecosystem features in Kenai Fjords National Park, southcentral Alaska. Specifically, I measured ecosystem variables with conductivity-temperature-depth (CTD) casts and water samples, beach seines, pelagic trawls, hydroacoustic transects and seabird surveys in two glacial fjords during summer 2007 and 2008. I identified spatial and temporal changes in oceanographic gradients, chlorophyll *a*, nutrients, zooplankton community structure, and acoustic biomass relative to tidewater glaciers and submerged moraines. I also examined foraging habitat preferences between two congeneric species of murrelets, prey availability and oceanography.

Methods

Field work for this study was conducted during June-August, in 2007 and 2008. Three cruises coincided with the early (June), middle (late June/July), and late (August) breeding season for Kittlitz's murrelets (Table 1). The primary research platform for this study was the U.S. Geological Survey's M/V *Alaskan Gyre*, a 15.2 m purse seiner, and work requiring a smaller vessel was carried out from a 4.8 m rigid-hulled inflatable skiff. In July 2007, I conducted a pilot study using a stratified random sampling approach (Arimitsu *et al.*, 2008b). Results of the pilot study indicated that a greater level of effort was required to better understand spatial and seasonal changes in marine habitat;

consequently, a monthly systematic sampling approach was employed in the summer of 2008.

Table 1. Survey effort during Kittlitz's murrelet (*Brachyramphus brevirostris*) foraging habitat study in Kenai Fjords National Park, Alaska.

Year	Date	Survey Type
2007	06/01-06/09	Early-season bird surveys, oceanography, beach seine
2007	06/25-06/29	Mid-season bird surveys
2007	06/29-07/03	Ecosystem pilot study
2007	07/31-08/04	Late-season bird surveys, oceanography, beach seine
2008	06/04-06/09	Early-season hydroacoustic/bird surveys, zooplankton, oceanography
2008	07/05-07/15	Mid-season hydroacoustic/bird surveys, zooplankton, oceanography, beach seine
2008	08/07-08/12	Late-season hydroacoustic/bird surveys, zooplankton, oceanography

Study Area

Kenai Fjords is a glaciated fjord system located on the southeastern side of the Kenai Peninsula in southcentral Alaska (Fig. 1). The outer fjords are exposed to direct oceanic influence from the Gulf of Alaska, while the inner fjords are more protected and influenced by tidewater glaciers extending from the Harding Icefield. For this study, two fjords were of particular interest because they supported breeding populations of Kittlitz's murrelets: Northwestern Lagoon/ Harris Bay (hereafter referred to as Northwestern Lagoon) and Aialik Bay. Both fjords contain a neoglacial terminal moraine shoal that represents the position of the glacier terminus during the Little Ice Age maximum (Wiles *et al.*, 1995). Glacial retreat in Aialik Bay occurred around the late

1600's, while ice retreat in Northwestern Lagoon began around the late 1800's (Wiles *et al.*, 1995).

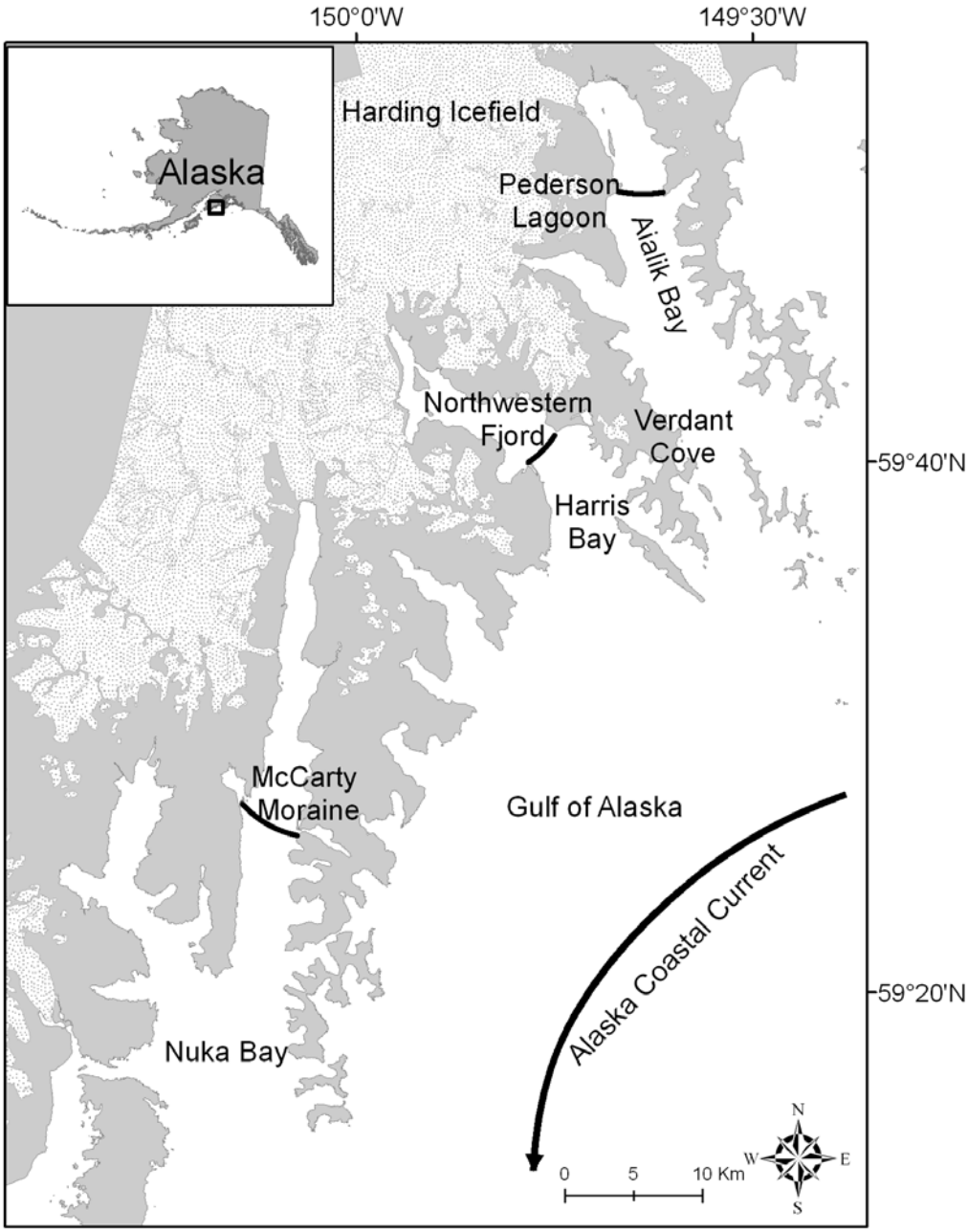

Figure 1. Map of study area in Kenai Fjords National Park, Alaska, including place names and glacial features. Ice cover is indicated in stipple and the position of submerged glacial moraines is indicated by the black lines.

Sample Collection

Oceanographic gradients in the marine environment were measured during oceanography surveys at sampling sites established by Gay and Armato (1999) in Aialik Bay and Northwestern Lagoon (Fig. 2). In 2007, oceanographic surveys were conducted in June and August, and coincided with the timing of bird surveys and beach seine sampling (Table 1). In 2008, oceanographic surveys were conducted either directly before or after the hydroacoustic/bird surveys in each fjord (described below). At each station, I deployed a CTD (SeaBird Electronics® SBE-19) equipped with a fluorometer (WetLabs® WetStar). In June and July 2008, additional sensors were employed, including a dissolved oxygen sensor (SeaBird Electronics® SBE-43), photosynthetically active radiation (PAR) sensor (Biospherical® Quantum Scalar 2300L), and a beam transmissometer (WetLabs® C-STAR) to measure water clarity. In August 2008 all external sensors failed and only CTD data were recorded for that sampling period.

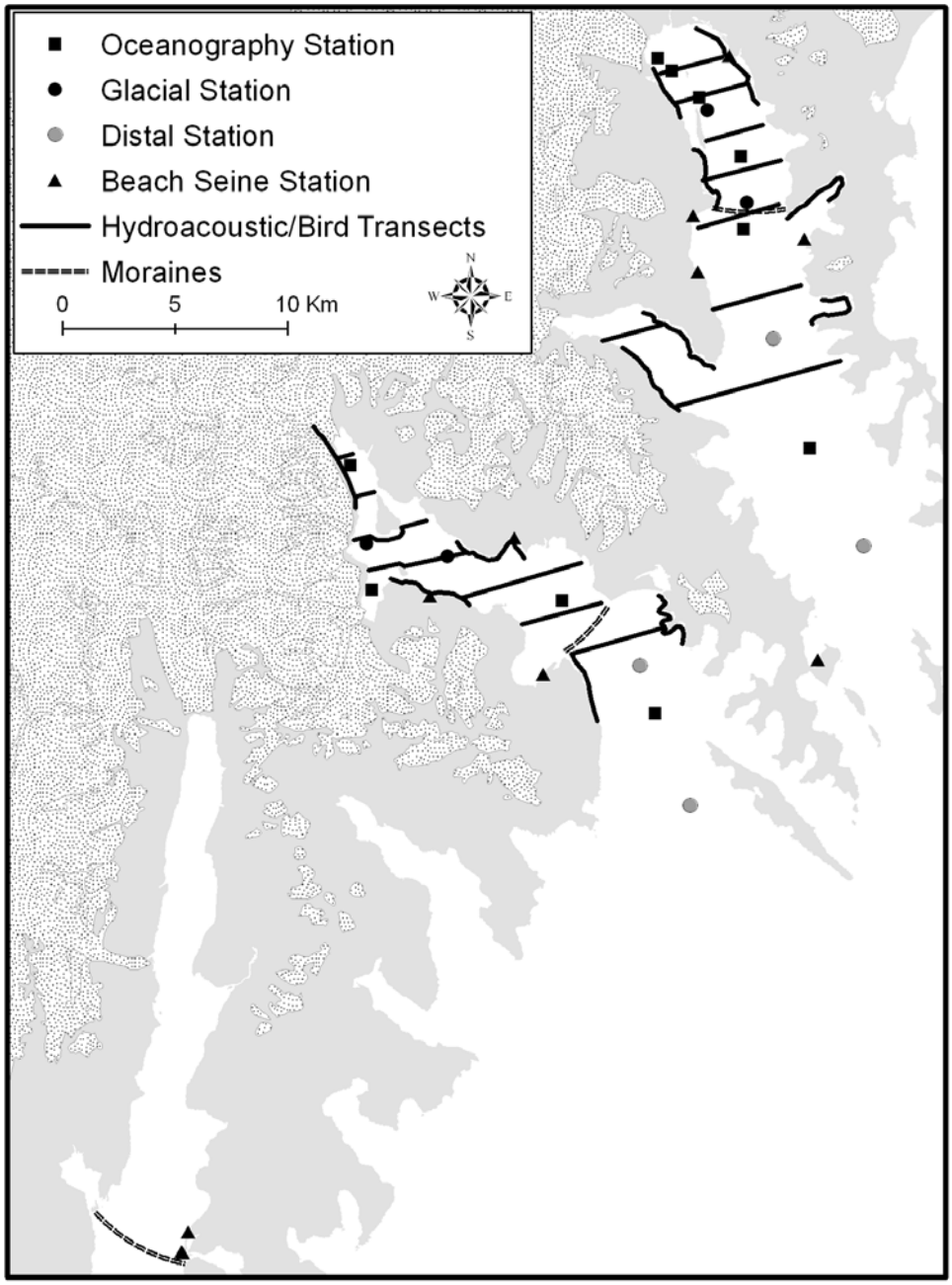

Figure 2. Sample locations during Kittlitz's murrelet (*Brachyramphus brevirostris*) study in Kenai Fjords National Park, 2007-2008.

Environmental and biological parameters were sampled in 2008 at a subset of oceanographic stations including two inner-fjord and two outer fjord stations, hereafter referred to as glacial and distal stations, respectively (Fig. 2). A rosette-style water sampler (Seabird Electronics® SBE 55) was deployed in conjunction with the CTD and discrete depth water samples were collected at 2 m and 10 m depths. In July 2007, nutrient samples were also collected from 10 m depth using a Niskin® bottle at 21 randomly selected stations stratified by distance to glacial features in Aialik Bay and Northwestern Lagoon (Fig. 3). Water samples were frozen in the field and later analyzed for ammonium, phosphate, silicic acid, nitrate, and nitrite concentrations at the Marine Chemistry Lab of the University of Washington, Seattle.

To assess zooplankton community structure, I sampled large zooplankton and small nekton taxa with an Isaacs-Kidd Midwater Trawl (IKMT). In 2007, I deployed a large IKMT at 21 randomly selected stations (Fig. 3). The large IKMT was 6 m long with a 3.05 m depressor bar, 7.68 m^2 mouth opening and 3 mm knotless nylon mesh. The collection cup at the cod end had 1 mm mesh screen. A flowmeter (General Oceanics®) was attached to the mouth of the net to estimate distance towed through the water. Each station was sampled for 30 minutes, for an average transect length ± SD of 2.9 ± 0.38 km. This net was effective at catching ichthyoplankton and macrozooplankton; however, the large depressor bar made the net very difficult to deploy, so a smaller net was used in 2008.

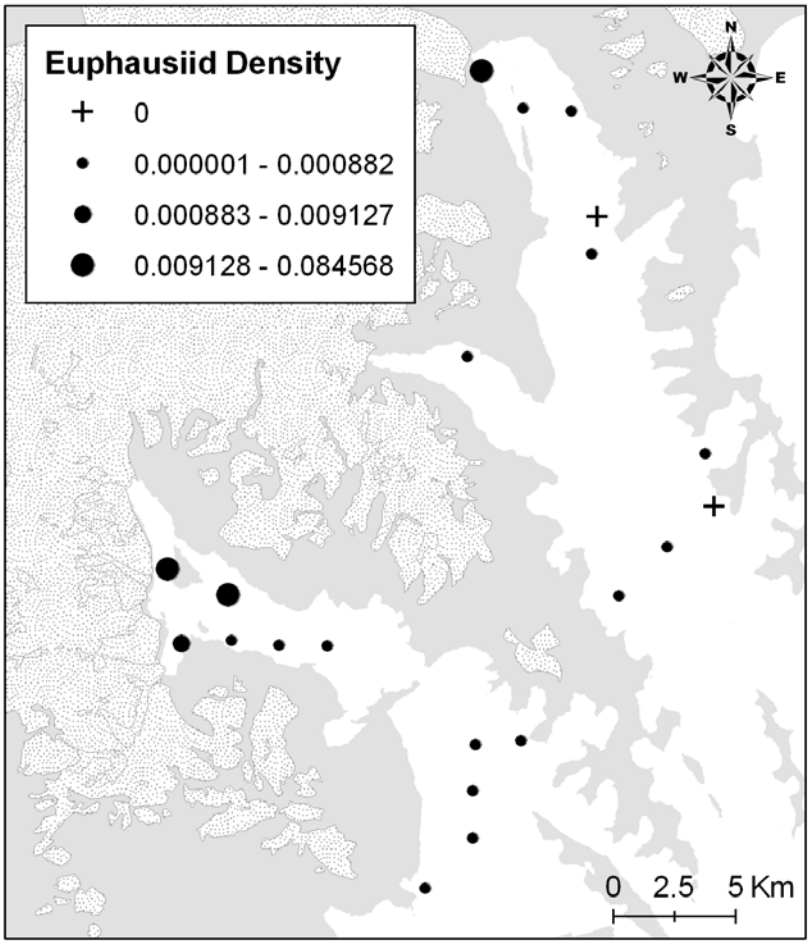

Figure 3. Station location and euphausiid density (organisms m^{-3}) in Isaacs-Kidd midwater trawl catches in Kenai Fjords National Park during July 2007 pilot study. Glaciers are indicated as grey-stipple.

In 2008, macrozooplankton and other small nekton taxa were collected monthly between June and August with a smaller IKMT outfitted with a 1.8 m depressor bar, 3 mm stretched knotless mesh near the mouth, and a 333 µm mesh ring net, which comprised approximately 2/3 of the body including the cod end. A flowmeter was attached to the mouth of the net to estimate distance towed through the water. The net design acted to minimize the pressure wave ahead of the net, potentially capturing larger and faster-swimming organisms; however, it may have allowed smaller planktonic

organisms to escape through the mesh near the mouth. Therefore, the volume of water filtered could not be adequately estimated, and catch per unit effort (CPUE) was expressed as biomass distance towed^{-1}. The net was deployed in an oblique manner and outfitted with a depth sensor (VEMCO® minilog T data logger, or Star Oddi® DST CTD) to assess the maximum depth of collection. Maximum depth towed was 35 m, average ± SD distance towed was 1.2 ± 0.1 km, and speed during the tow was held at approximately 5.5 km h^{-1}. One distal station could not be sampled with the IKMT during the 2008 early-season cruise due to inclement weather.

For each IKMT haul, total catch volume was estimated to the nearest 10 ml after water was drained through a sieve. Gelatinous zooplankton, including ctenophores and cnidarians, were separated and their volume was estimated as above. Individual ctenophores and cnidarians were not identified to species or enumerated owing to damage of individuals during capture. All fishes collected in IKMT hauls were identified to species and fork lengths (FL) were measured to the nearest 1.0 mm. Fishes that could not be identified in the field were preserved in 10% formaldehyde seawater solution and returned to the laboratory for later identification.

IKMT zooplankton sample contents were preserved in a 3-5% buffered formaldehyde seawater solution. Samples were identified to species (or lowest possible taxon) and developmental stage, enumerated, and damp dry weights were measured to the nearest 0.01 mg (or for organisms weighing over 100 mg, to the nearest mg) under contract with the University of Alaska Fairbanks. In the lab, large samples were

subsampled with a Folsom plankton splitter after rare organisms were counted and removed.

To document nearshore fish species occurrence, I deployed a beach seine opportunistically at suitable beaches with no surf, boulder-free substrate, and a shallow incline for skiff access. I conducted a total of 13 beach seine sets at 6 sites in 2007 and 2 beach seine sets at 2 sites in 2008 (Fig. 2). The beach seine was 37 m long with 28 mm stretched mesh at the wings and 5 mm nylon mesh at the center. The seine was set parallel to shore from a skiff and brought into shore by 2-3 people. The catch was sorted by species, enumerated, and fork length was measured for a maximum of 25 individuals for each species.

Relative abundance of forage fish and other nekton taxa was estimated in 2008 during hydroacoustic surveys conducted along established transects in Aialik Bay and Northwestern Lagoon (Fig. 2). I used a single beam, 120 kHz transducer (Biosonics DT-X®) deployed from a hydrodynamic fin and towed along side of the boat at an approximate depth of 2 m below the surface. The vessel generally travelled at speeds between 9-11 km h^{-1}, however, ice obstructions near the head of the fjords forced us to slow the vessel down to 5 km h^{-1} at some times. The instrument had a beam angle of 6.5° and collected data at 2 pings s^{-1} with a pulse length of 0.5 ms. A minimum threshold for data collection was set at -80 db. Field calibration was conducted according to Foote *et al.* (1987) on June 2 and July 11, 2008 using a 33 mm standard calibration sphere of known target strength. During hydroacoustic transects, I used a thermosalinograph

(Seabird Electronics® SBE 45 MicroTSG) to identify surface temperature and salinity conditions.

In 2007, bird surveys were conducted from a 4.8 m skiff using standard U.S. Fish and Wildlife strip survey methodology (Gould & Forsell, 1989). Two observers counted all marine birds sighted within 100 m of either side and 100 m ahead of the boat and recorded observations using a hand-held GPS enabled computer (Recon® Pocket PC). In 2008, outer coast surveys were conducted from a 4.8 m vessel as in 2007, while on inner fjord transects (Fig. 2) seabird density was assessed concurrently with hydroacoustic surveys from a 15.8 m vessel. Identification of murrelets within the genus *Brachyramphus* can be particularly difficult given the similarity in size, shape and plumage of the Kittlitz's murrelet and the marbled murrelet. Survey crews slowed the vessel if needed to confirm identification of murrelets. A behavior code was assigned to all birds and mammals sighted on transect while on the water (swimming on surface), fish-holding (holding fish in bill), and flying. Flying birds were counted continuously. Weather conditions and sea state were constantly monitored and to ensure detection of birds at all times, surveys were not conducted if wave height exceeded 0.5 m in height. Speed during bird surveys conducted concurrently with hydroacoustics was generally held between 9-11 km h^{-1}.

Data Analysis

Raw CTD data were processed through SBE Data Processing modules v. 7.16 (Sea-Bird Electronics Inc., 2007). Spurious salinity spikes and other water parcel misalignments were reduced through alignment of conductivity, temperature, and

fluorescence relative to pressure data. Proper alignment was assessed visually for a single cast from each cruise, and water column profiles were batch processed by cruise using the advance values for each parameter. Photic depth was calculated as the depth at which PAR values dropped to 1% of surface values. Profile data were contoured in MATLAB v. 7.5 (MathWorks Inc., 2007) relative to depth and station distance along a line drawn between the head of the fjord and the outer-most station.

Spatial and temporal differences within abiotic and biotic datasets were tested with two-way or three-way fixed effects ANOVA using JMP® v. 7.0.2 (SAS Institute, 2007) including within fjord (glacial vs. distal), between fjord (Northwestern vs. Aialik), and month factors. Response variables were tested for normality with Shapiro-Wilks tests, and homogeneity of variance was assessed through residual plots and Levene's tests at $\alpha < 0.05$. For multi-factorial tests, additive models were applied when interaction terms were not significant. Nutrients data were fourth-root transformed, and catch data were log (x+1) transformed to induce normality and homoscedasticity, respectively, or a Spearman rank correlation was employed when assumptions of normality were not satisfied. A multiple comparison test (Tukey HSD) was employed to examine differences among months when the null hypothesis for the month factor was rejected.

Prior to trawl catch community structure analysis, I reduced the dataset to include only species that are important in murrelet diets (Day *et al.*, 1999; Piatt *et al.*, 2007). Euphausiids, shrimp, amphipod and gadid species' CPUE were aggregated at the group level due to low abundance by individual species, while copepod species and capelin were analyzed at the species level. Gelatinous zooplankton were also included because

they were likely to have an impact on community structure and negative spatial associations with Kittlitz's murrelets were observed in Glacier Bay (J. Piatt, U.S. Geological Survey, pers. comm.). A log (x+1) transformation was used to reduce the influence of a few very high abundance values. The data spanned several taxa of differing trophic levels; therefore, I standardized the abundances for each species at a given station by the total abundance of the species across all stations in order to reduce the influence of abundant groups.

Multivariate statistical analyses of trawl catch community structure were conducted in PRIMER v6 (PRIMER-E Ltd, 2008). The Bray-Curtis similarity measure was computed on abundance data that were first log (x+1) transformed and standardized. To test for homogeneity of multivariate dispersions in trawl catch species composition between levels of factors, I used the PERMDISP routine. Factors included glacial influence (glacial vs. distal stations), month, and fjord (Aialik vs. Northwestern). Factor levels for which the homogeneity of dispersions assumption was met were included in a 3-way, fixed effects, permutation-based MANOVA to test for differences in trawl catch species composition. A pseudo-F was calculated using type III sums of squares and compared against a random distribution under the null hypothesis of no difference using 999 permutations. When interaction terms were not significant at $\alpha = 0.05$, additive models were applied. Contributions of individual species or groups were examined using the SIMPER routine. Non-metric multidimensional scaling (MDS) was used to obtain an ordination of Bray-Curtis similarities for all samples in two dimensions. Pearson

correlations between MDS axes and environmental variables were computed to test for associations between species composition and environmental variability.

Hydroacoustic data were echointegrated with Sonardata Echoview® software v. 2.10 (Echoview, 2001). Vessel noise was reduced by setting a minimum threshold for integration at -80 db. Sound speed and absorption coefficients were determined from average temperature and salinity data at the nearest oceanographic station. Surface noise and the bottom signal were determined visually by examining the echograms, and these regions were excluded from the analysis. Additionally, the upper 1 m of data was removed to eliminate the effects of collecting data in the near field of the transducer. This resulted in an effective minimum depth of acoustic measurements of 3 m below the surface. The integration output for acoustic backscatter was expressed as nautical area scattering coefficient (NASC), and is used as a relative index of biomass in the water column (Simmonds & MacLennan, 2005). Cell resolution for integration output was 1 m depth by 100 m width; however, I summed NASC over 40 m ($NASC_{40}$) to estimate biomass available within the estimated diving depth of Kittlitz's murrelets (Day *et al.*, 1999). $NASC_{40}$ over the length of each transect was summed and divided by the transect length (sum of $NASC_{40}$ km^{-1}) to standardize by effort. Distance from the midpoint of each acoustic transect to the nearest tidewater glacier was estimated in GIS. A 2-way ANOVA was applied to acoustic data summed by transect to test for differences between fjords and months. I used least-squares linear regression to examine the relationship between the log-transformed sum of $NASC_{40}$ km^{-1} and the transect distance to nearest

tidewater glacier by month and fjord. Normality of the response was tested with a Shapiro Wilks test, and homogeneity of variance was assessed through residual plots.

To assess changes in schooling fish distribution over the course of the 2008 breeding season, I separated dense fish aggregations from more dispersed prey and weaker scattering targets as in Mehlum *et al.* (1996). I integrated dense forage fish aggregations encountered on hydroacoustic surveys by month by visually examining the echograms, identifying regions containing dense aggregations of fish, and integrating aggregations separately from weaker scattering organisms such as zooplankton and dispersed fish. Dense schools of fish were distinct in their shape and target strength characteristics compared to weaker scattering organisms (Simmonds & MacLennan, 2005).

To relate Kittlitz's murrelet distribution in Aialik Bay and Northwestern Lagoon to environmental variables, I used a combination of general linear models (glm) and generalised linear mixed effects models (glmm) using survey data, bathymetry, and concurrent hydroacoustic and thermosalinograph data from July 2008. For comparison, I also examined habitat relationships for the more abundant marbled murrelet. Raw point data, with a resolution between 10-100 m, corresponding to the subset of marine bird and acoustic transects in Aialik Bay and Northwestern Lagoon (Fig. 2) were broken into 200, 400, 800, and 1,600 m segments. Point data were then aggregated by segment and analyzed in R statistical software v. 2.7.2 (R development Core Team, 2008). For each distance class, the response variable was presence/absence of murrelets within each segment, and independent variables were calculated as the mean acoustic backscatter, sea

surface salinity, and bottom depth within each segment. Distance from the midpoint of each transect segment to the nearest tidewater glacier was also included as an explanatory variable. Ice presence/absence, fjord (Aialik Bay or Northwestern Lagoon), and transect type (coastal or offshore) were coded as categorical variables. I first log (x + 0.0001) -transformed mean acoustic backscatter and then normalized continuous predictor variables prior to analysis. Sea surface temperature was not included as an independent variable because it was highly correlated with glacier distance. The presence or absence of murrelets was coded as a binary response (0/1) and the probability of observing murrelets along a given segment was modeled as a function of the predictor variables using a glm with a binomial error distribution and a logit link. The best glm models were chosen on the basis of Akaike's Information Criterion (AIC). Kittlitz's murrelets were never present where ice was absent; modeling of habitat preferences was therefore restricted to those observations where ice was present.

Lack of independence among samples artificially inflates sample size, and may lead to bias in parameter estimates and increased type I error rates (false rejection of the null hypothesis) in statistical modeling (Legendre & Legendre, 1998). To account for spatial autocorrelation between segments on a single transect, I followed the exploration of candidate glm models with glmm models that incorporated spatial autocorrelation within transects and allowed for random differences in the mean response (probability of occurrence) among transects (Dormann *et al.*, 2007). The correlation structure was modeled as an exponential spatial correlation using the following equation:

$$f(d_{ij}) = \left[\exp\left(\frac{-d_{ij}}{p} \right) \right]$$

where d_{ij} is equal to the distance between two observations, and p is the range coefficient. Distances less than p are considered autocorrelated (Legendre & Legendre, 1998). The performance of the final models in predicting presence/absence of murrelets was evaluated based on the proportion of fitted probabilities that resulted in correct classification of the response (presence/absence), whereby a predicted probability of greater than or equal to 0.5 was considered to indicate presence.

Results

Oceanography

Water column profiles show spatial and temporal differences in temperature, salinity, and chlorophyll *a* concentration. Temperature and salinity profiles demonstrate the importance of submerged moraines for the exchange of inner and outer fjord waters. The cool, fresh waters pool behind the moraines in the inner fjord, while warmer, more saline water is held outside of the moraines (Figs. 4-5). The sill in Northwestern Lagoon is shallower and the passage is more constricted than in Aialik Bay, and turbulent mixing of surface waters was observed at the sills in both fjords. Surface freshening in Northwestern Lagoon extended deeper into the water column than in Aialik Bay during all sampling periods of the study, indicating less exchange with outer fjord waters in Northwestern Lagoon.

Relative chlorophyll *a* concentrations were lowest in both fjords during June 2007 (Figs. 6-7). Low photic depth near the glaciers corresponded with lower chlorophyll *a*

concentrations in both fjords. Chlorophyll *a* concentrations were consistently higher in Northwestern Lagoon compared to Aialik Bay, particularly in August 2007.

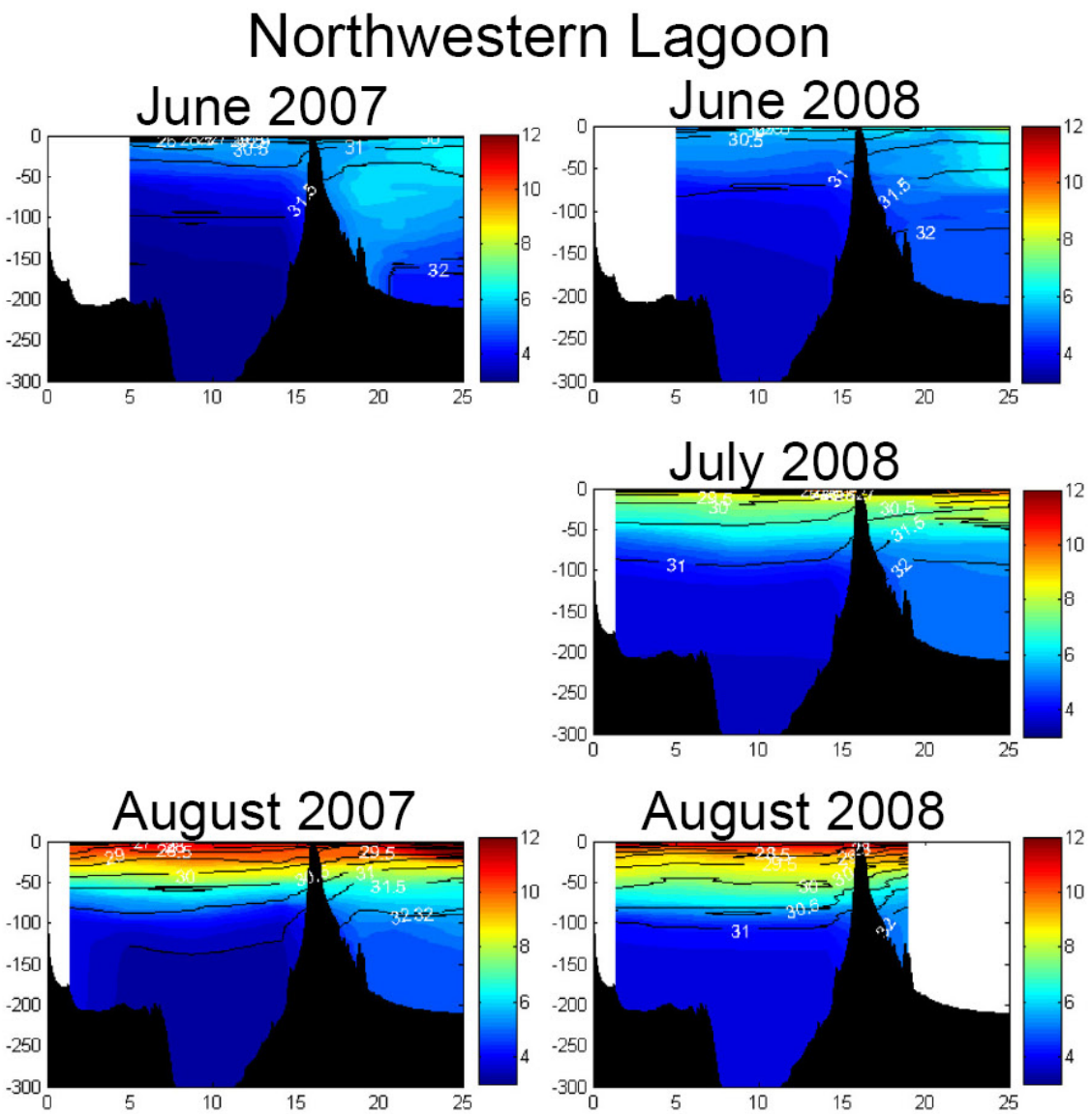

Figure 4. Temperature (color) and salinity (lines) vertical contours relative to bottom depth (m, x-axis), and distance to nearest tidewater glacier (km, y-axis) in Northwestern Lagoon, Kenai Fjords National Park, Alaska. Bathymetry is indicated in black.

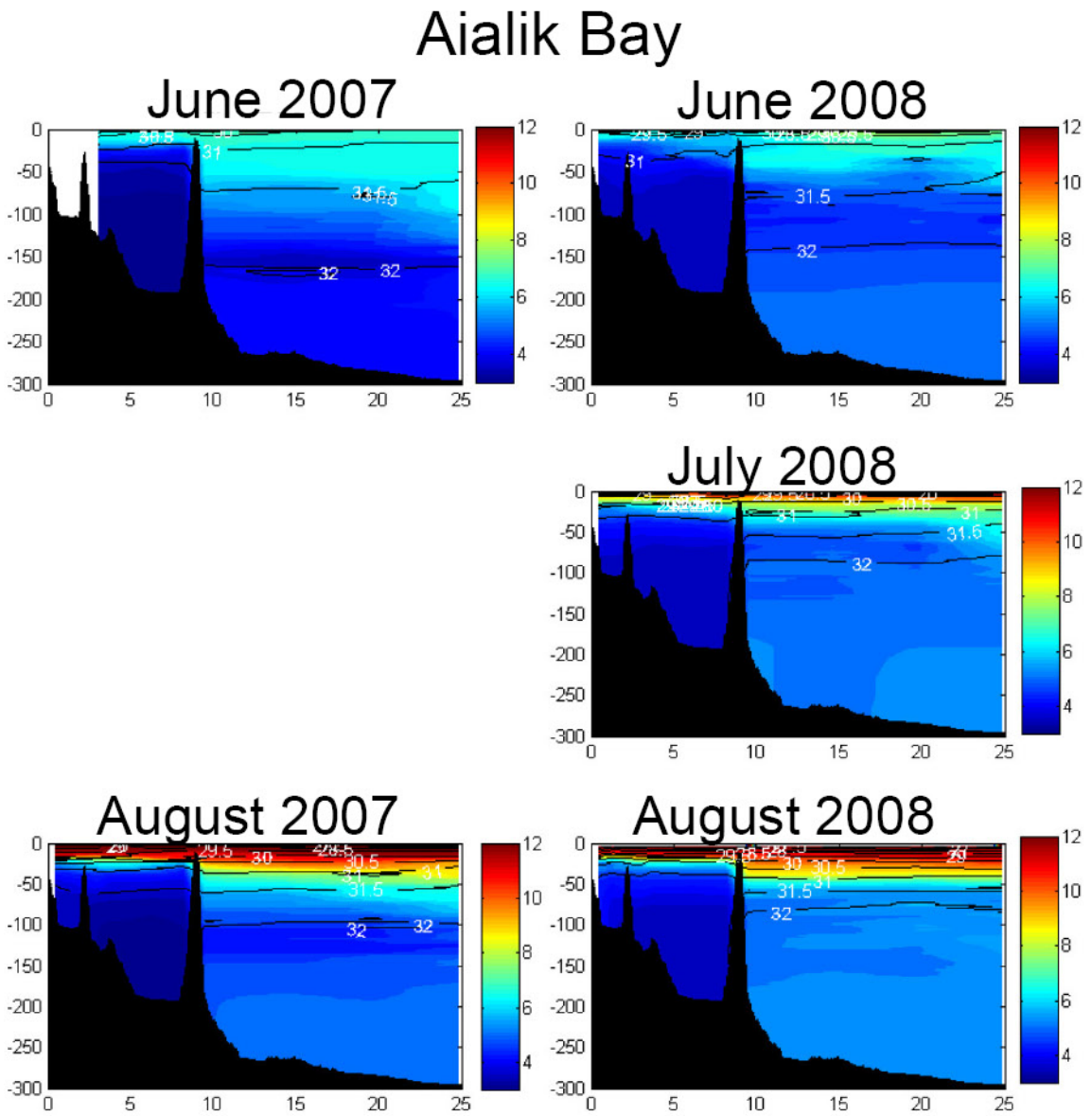

Figure 5. Temperature (color) and salinity (lines) vertical contours relative to depth (m, x-axis) and distance to tidewater glacier (km, x-axis) in Aialik Bay, Kenai Fjords National Park, Alaska. Bathymetry is indicated in black.

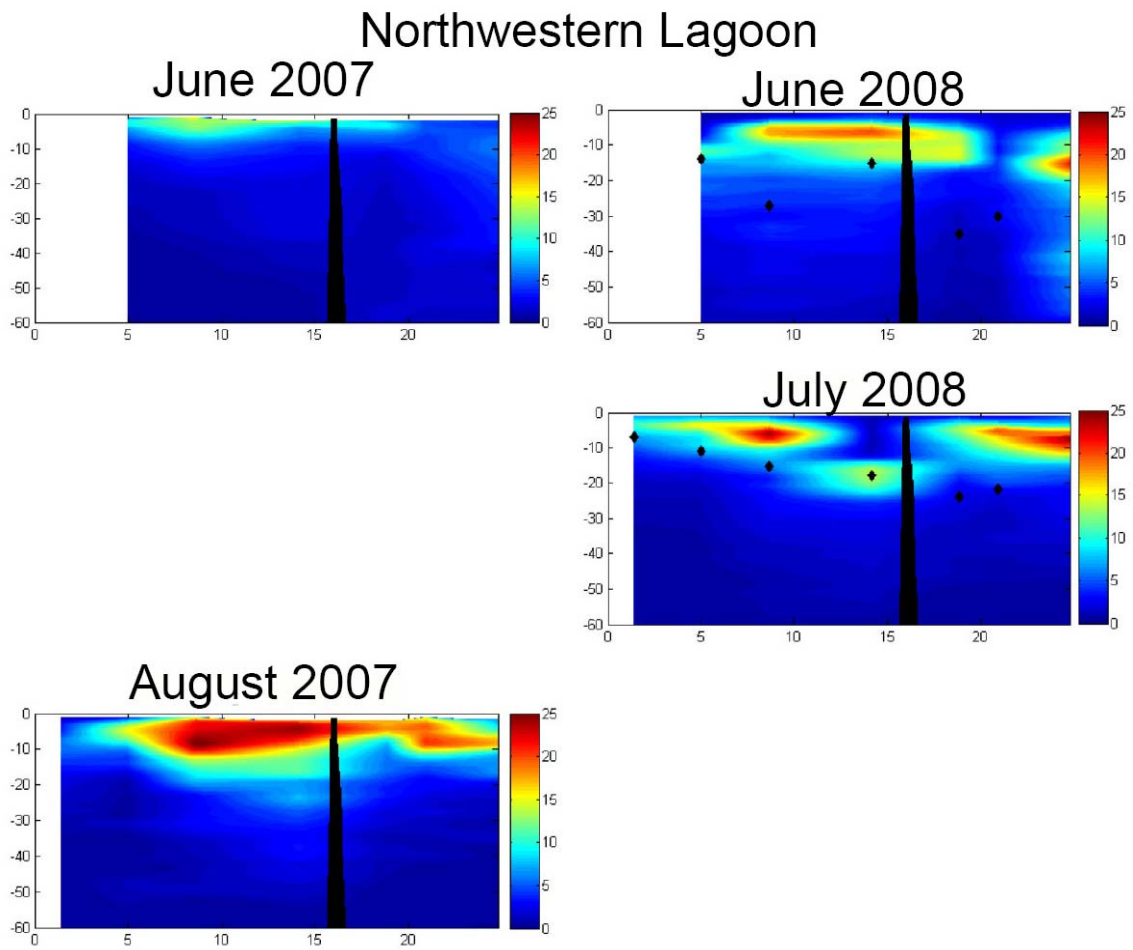

Figure 6. Chlorophyll *a* vertical contours (color) relative to depth (m, x-axis) and distance to tidewater glaciers (km, y-axis) in Northwestern Lagoon, Kenai Fjords National Park, Alaska. Photic depth is indicated as black diamonds, and position and depth of the moraine is indicated in solid black.

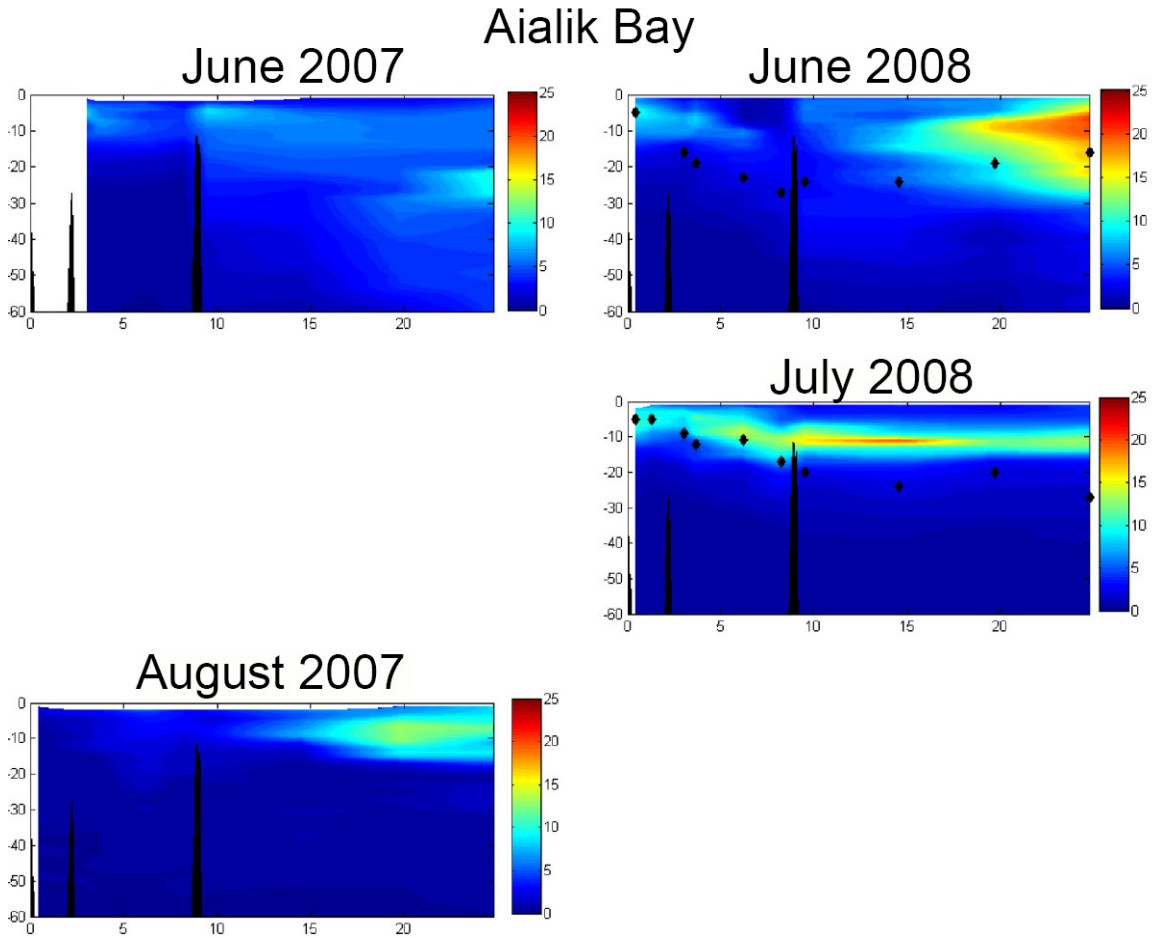

Figure 7. Chlorophyll *a* vertical contours relative to depth (m, y-axis), and distance to tidewater glacier (km, x-axis) in Aialik Bay, Kenai Fjords National Park, Alaska. Photic depth is indicated as black diamonds, and position and depth of the moraine is indicated in solid black.

Surface water clarity was lowest near tidewater glaciers, and decreased from June to July, 2008 (Fig. 8). In July, low water clarity over the upper 50 m of the water column less than 3 km from Aialik Glacier indicated increased glacial runoff. Beam transmission, expressed as a percentage of light transmitted through a parcel of water, in the upper 3 m of the water column at stations within 3 km of tidewater glaciers was on average ± SE 54.6 ± 9.58 % in June, and 28.4 ± 6.76 % in July. In contrast, average ± SE beam

transmission below 3 m depth at stations within 3 km of a tidewater glacier was 87.52 ± 0.94 % in June and 79.54 ± 5.16% in July. The median depth of 80% water clarity occurred at 5 and 6.5 m in June and July, respectively for Aialik Bay stations, and at 9 m in both June and July in Northwestern Lagoon. Two stations sampled within 1 km from Aialik Glacier in July had low water clarity throughout the water column, with maximum water clarity of 73.46 % at 99 m, and 66.65 % at 88 m (Fig. 8).

In 2008, average DIN levels generally decreased throughout the summer, and were higher in glacial areas than distal areas (Table 2). Fourth root-transformed DIN differed between glacial and distal areas, and among months, but did not differ significantly between fjords (3-way ANOVA: $F_{[3, 21]} = 4.15$, $R^2 = 0.45$, $p < 0.05$). Glacial areas were higher in DIN than distal areas ($p < 0.05$) and DIN was significantly higher in June than July and August, but July and August were not significantly different from one another (Tukey HSD, $\alpha = 0.05$). Average ± SE DIN to phosphate ratios were 2.70 ± 0.58 at the surface, and 4.30 ± 0.57 µm at 10 m depth and were well below the Redfield ratio of 16:1(Redfield, 1958) during all sample periods.

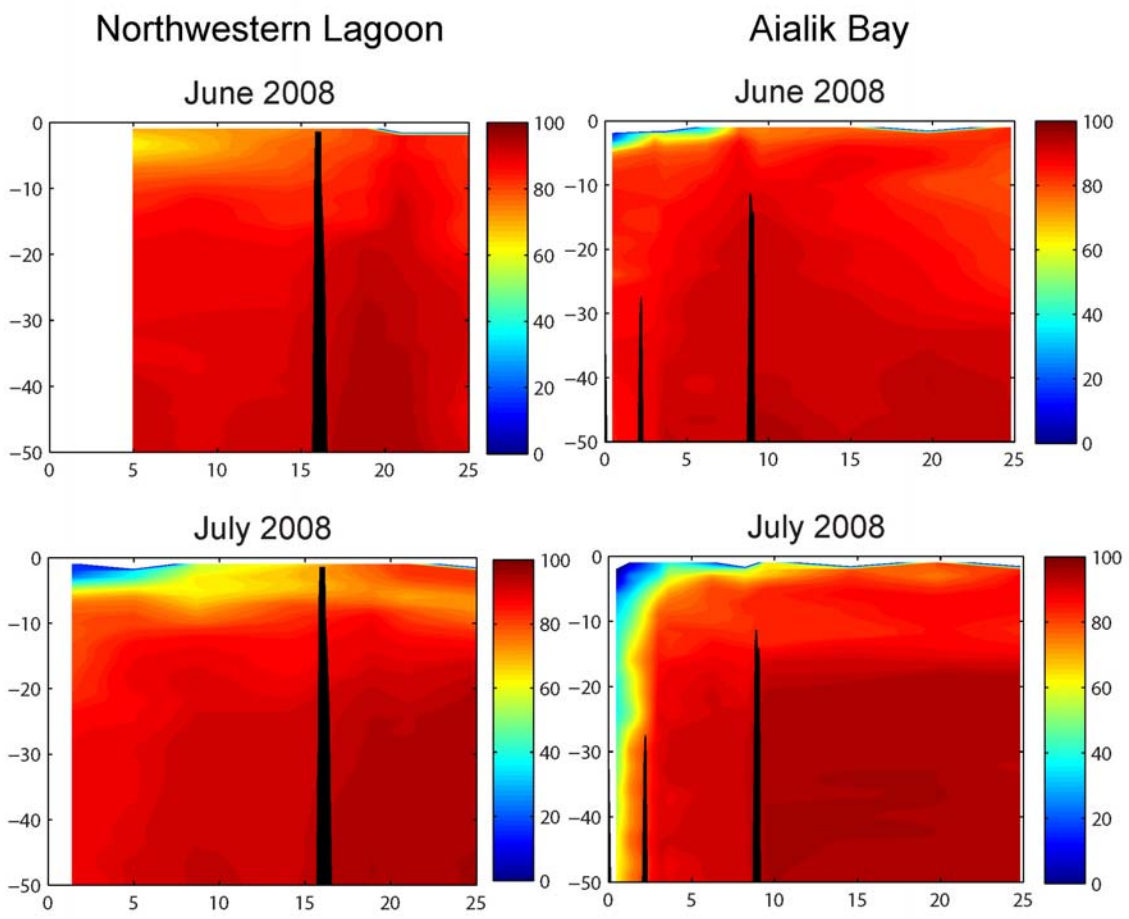

Figure 8. Water clarity vertical contours (beam transmission, %) relative to depth (m, y-axis) and distance to tidewater glaciers (km, x-axis) in Kenai Fjords National Park, Alaska. Bathymetric features are indicated in black.

Table 2. Average (SE) nutrient concentrations (μM) from 2 and 10 m depths collected in Kenai Fjords during 2008.

	Northwestern Lagoon			Aialik Bay		
	June	July	August	June	July	August
Phosphate	0.583 (0.092)	0.563 (0.046)	0.286 (0.037)	0.590 (0.061)	0.346 (0.030)	0.247 (0.035)
Silicic Acid	3.857 (0.571)	6.100 (0.372)	5.539 (0.657)	5.386 (0.889)	5.538 (0.274)	3.146 (0.268)
Nitrate	1.857 (0.677)	1.162 (0.379)	0.089 (0.008)	2.128 (0.684)	0.310 (0.120)	0.130 (0.051)
Nitrite	0.079 (0.018)	0.071 (0.015)	0.009 (0.003)	0.068 (0.013)	0.009 (0.006)	0.009 (0.004)
Ammonium	1.137 (0.374)	1.416 (0.339)	0.449 (0.278)	1.333 (0.284)	0.135 (0.071)	1.089 (0.582)

Ammonium values in the surface waters differed within and between fjords, despite the difference in sampling techniques between years (see methods). In July 2007, fourth root-transformed ammonium concentrations were significantly higher in glacial areas compared to distal areas, but not between Northwestern Fjord and Aialik Bay (2-way ANOVA: $F_{[2,19]} = 5.45$, $R^2 = 0.36$, $p < 0.05$). In 2008, fourth root-transformed ammonium values were higher at glacial stations compared to distal stations, and also in Northwestern Fjord compared to Aialik Bay (3-way ANOVA: $F_{[4,17]} = 3.48$, $R^2 = 0.45$, $p < 0.05$). June ammonium concentrations were higher than those in July and August, while July and August ammonium concentrations were not significantly different from one another (Tukey HSD, $\alpha = 0.05$).

Prey Availability

At least 28 species of fish were captured with an IKMT in 2007 and 2008 (Table 3), including species important in murrelet diets such as capelin, Pacific herring, and Pacific sandlance. Saffron cod (*Eleginus gracilis*) was the most abundant species of

gadid; however, Pacific cod (*Gadus macrocephalus*) and walleye pollock (*Theragra chalcogramma*) were also present. Mesopelagic fishes included lanternfish (Myctophidae) and the northern smoothtongue (*Leuroglossus schmidti*).

At least five species of euphausiids were collected in Kenai Fjords, including (in order of abundance) *Thysanoessa inermis*, *T. raschii*, *Euphausia pacifica*, *T. spinifera*, and *T. longipes* (Appendix 1). In 2007, trawl-caught euphausiid density was negatively associated with distance to tidewater glaciers (Spearman $\rho = -0.63$, $p < 0.01$). This was especially true when considering only samples from glacial areas (Spearman $\rho = -0.86$, $p < 0.001$), (Fig. 3). In 2008, euphausiid density and glacial distance were not significantly correlated (Spearman $\rho_{June} = -0.64$, $p = 0.12$, $p_{July} = 0.74$, $p_{August} = 0.49$).

Table 3. Species, size range (forklength, mm), sample size (n), mean size with standard deviation (SD) of fishes captured in small and large Isaacs-Kidd Midwater Trawls (IKMT) in Kenai Fjords during 2007-2008. Species are sorted taxonomically.

		Small IKMT		Large IKMT	
Common Name	Scientific Name	Size Range (n)	Average (SD)	Size Range (n)	Average (SD)
Pacific herring	*Clupea pallasii*	-	-	14-22 (5)	17 (3.1)
Northern smoothtongue	*Leuroglossus schmidti*	27 (1)	27	-	-
Capelin	*Mallotus villosus*	-	-	5-30 (845)	14 (5.3)
Eulachon	*Thaleichthys pacificus*	26 (1)	26	-	-
Larval smelt	Osmeridae (Family)	26 (1)	26	14 (1)	14
Lanternfish	Myctophidae (Family)	-	-	15 (1)	15
Saffron cod	*Eleginus gracilis*	12-51 (97)	31 (9.8)	7-69 (55)	24 (19.1)
Walleye pollock	*Theragra chalcogramma*	17-41 (86)	25 (4.5)	7-16 (24)	10 (2.7)
Pacific cod	*Gadus macrocephalus*	33-36 (2)	35 (2.1)	12 (1)	12
Gadid	Gadidae (Family)	12-32 (32)	22 (5.2)	-	-
Rockfish	*Sebastes* spp.	11-19 (6)	14 (3.2)	-	-
Spinyhead sculpin	*Dasycottus setiger*	12-25 (142)	14 (3.2)	25-30 (31)	28 (1.4)
Padded sculpin	*Artedius fenestralis*	-	-	14 (1)	14
Sculpin	Cottidae (Family)	-	-	7-12 (4)	10 (2.2)
Soft sculpin	*Psychrolutes sigalutes*	12-54 (4)	34 (19.0)	35-48 (2)	42 (9.2)
Crested sculpin	*Blepsias bilobus*	21-27 (5)	24 (2.2)	-	-
Silverspotted sculpin	*Blepsias cirrhosus*	-	-	13 (1)	13
Northern ronquil	*Ronquilus jordani*	30 (1)	30	12-43 (3)	25 (16.3)
Snailfish	Liparidae (Family)	13-19 (9)	15 (2.2)	12-18 (4)	16 (3.2)
Poacher	Agonidae (Family)	8-20 (19)	16 (3.5)	10-18 (4)	14 (4.3)
Sturgeon poacher	*Podothecus acipenserinus*	20 (1)	20	-	-
Daubed shanny	*Leptoclinus maculatus*	28-45 (4)	37 (6.9)	-	-
Snake prickleback	*Lumpenus sagitta*	22-67 (15)	45 (17.1)	23-47 (22)	37 (9.5)
Longsnout prickleback	*Lumpenella longirostris*	-	-	50 (1)	50
Lumpenus spp.	*Lumpenus* spp.	23 (2)	23 (0)	-	-
Larval prickleback	Stichaeidae (Family)	21-63 (19)	41 (15.5)	26 (1)	26
Quillfish	*Ptilichthys goodei*	-	-	173 (1)	173
Prowfish	*Zaprora silenus*	26-36 (4)	31 (4.8)	25 (1)	25
Pacific sandfish	*Trichodon trichodon*	57 (1)	57	-	-
Pacific sandlance	*Ammodytes hexapterus*	23-43 (5)	30 (7.9)	16-28 (2)	22 (8.5)
Flathead sole	*Hippoglossoides elassodon*	12-25 17)	20 (3.1)	9-38 (224)	21 (5.5)
Butter sole	*Isopsetta isolepis*	18-25 (8)	21 (2.4)	-	-
Northern rock sole	*Lepidopsetta polyxystra*	15-21 (6)	18 (2.4)	12-17 (3)	15 (2.5)
Sand sole	*Psettichthys melanosticus*	13-21 (4)	16 (3.6)	10 (1)	10
Rock Sole (unidentified)	*Lepidopsetta* spp.	13-22 (3)	16 (4.9)	-	-
Larval flatfish	Pleuronectidae (Family)	12-24 (23)	19 (3.5)	-	-

For community analysis of trawl catch data, homogeneity of multivariate dispersions was met for glacial influence (PERMDISP: $F_{[1,21]} = 3.97$, $p = 0.07$) and location (PERMDISP: $F_{[1,21]} = 0.63$, $p = 0.47$) factors. The null hypothesis of homogeneity of multivariate dispersions was rejected for the month factor (PERMDISP: $F_{[1,21]} = 4.00$, $p = 0.05$); however, pairwise tests indicate July and August samples were not significantly different from one another ($p = 0.27$). Therefore, only July and August samples from both fjords were used in the PERMANOVA analysis.

Trawl catch community structure at glacial and distal stations were not significantly different from one another (Pseudo $F_{[1,12]} = 1.35$, $p = 0.22$). There was a significant difference between fjords (Pseudo $F_{[1, 12]} = 2.40$, $p = 0.03$), and also between months (Pseudo $F_{[1, 12]} = 7.25$, $p = 0.003$). The copepod *Eucalanus bungii* was consistently more abundant in Aialik Bay and contributed most to dissimilarities between fjords. Average abundance of the copepod *Centropages abdominalis* and amphipods were higher in Northwestern Lagoon, contributing 9.19 and 8.5% of the dissimilarity between fjords, respectively. Average abundance of capelin larvae was also higher in Northwestern Lagoon than Aialik Bay and contributed 8.0% of the dissimilarity between fjords. Capelin larvae were most abundant in July and contributed 13.7% of the dissimilarity between July and August. Age-0 gadids were most abundant in June and contributed 8.6% of the dissimilarity between June and July, and 16.5% of dissimilarity between June and August. Euphausiids were most abundant in July, and accounted for 6.4% of dissimilarities between June and July, and 8.1% of dissimilarities between July and August. Gelatinous zooplankton comprised the lowest proportion of the catch in

close proximity to tidewater glaciers, and a higher proportion of the catch at distal stations (Fig. 9).

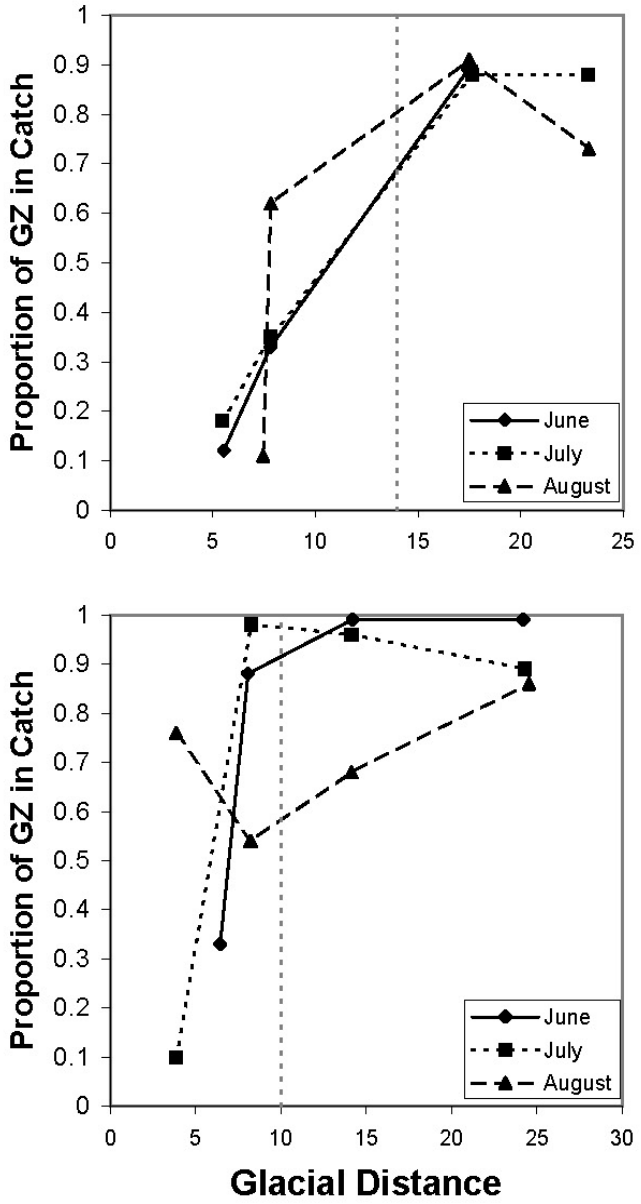

Figure 9. Proportion of Isaacs-Kidd Midwater Trawl catches that were comprised of gelatinous zooplankton (GZ) relative to distance to nearest tidewater glacier (km) in Northwestern Lagoon (top) and Aialik Bay (bottom) during 2008. The location of the terminal moraine is indicated as a dotted vertical line.

Differences in trawl catch community structure between fjords and over the course of the summer are evident in the MDS plot (Fig. 10). MDS 2 (y-axis) was negatively correlated with temperature ($r = -0.83$, $p < 0.0001$), and positively correlated with salinity ($r = 0.69$, $p < 0.001$), phosphate ($r = 0.52$, $p < 0.05$), nitrite ($r = 0.50$, $p < 0.05$), and nitrate ($r = 0.43$, $p < 0.05$), while MDS1 (x-axis) was negatively correlated with distance from submerged moraines ($r = -0.49$, $p < 0.05$). Community composition varied along an increasing temperature gradient throughout the summer. In June, community composition was associated with distance from glacial features, particularly distance to the moraine. Two outer-Aialik samples in June were distinct from the other samples and contributed to the large dispersion in June. These two samples had the lowest biomass of all stations. They had lower abundance of all taxa and a greater proportion of gelatinous zooplankton in the catch relative to other June stations. August samples were the least dispersed of all months.

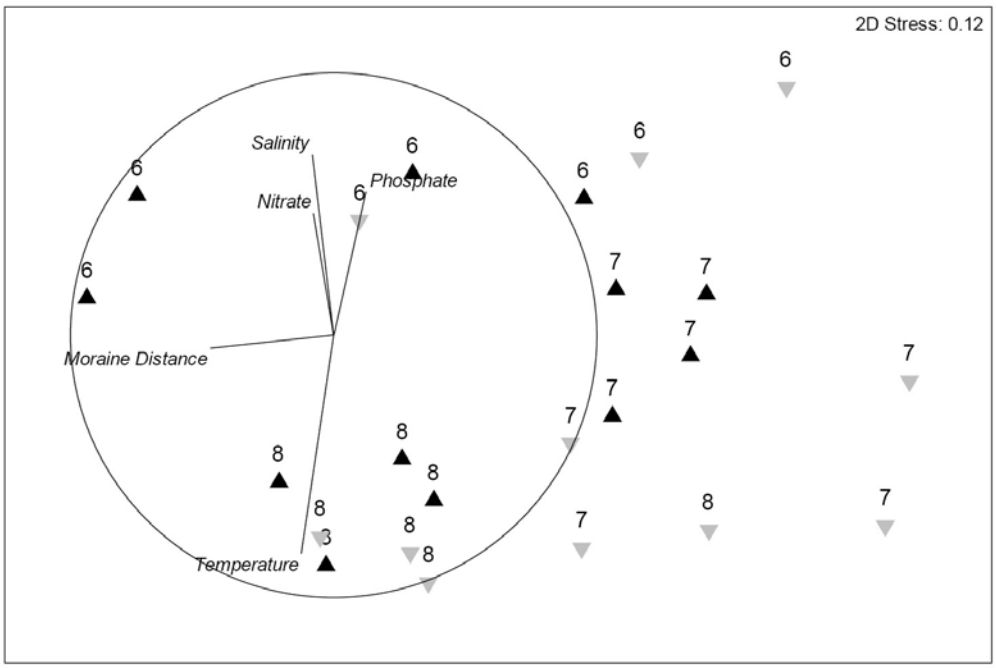

Figure 10. Non-metric multidimensional scaling (MDS) of Bray-Curtis dissimilarities in community structure at trawl stations in Kenai Fjords during summer 2008. Triangles represent Aialik Bay (black) and Northwestern Lagoon (grey) samples, and numbers above symbols represent the month in which they were sampled (6 = June, 7 = July, 8 = August). Correlation of environmental variables with MDS axes is represented by the vectors originating at an arbitrary point. Vectors are drawn such that the x- and y-components of each vector are proportional to the correlation of the respective variable with the x- and y- axis. Vectors extending to the circle have the maximum possible correlations.

Log-transformed acoustic backscatter ($NASC_{40}$ km^{-1}) on transects differed significantly by month and fjord (2-way ANOVA: $F_{[3,72]} = 6.28$, $R^2 = 0.21$, $p < 0.001$). June backscatter was lower than July and August but July and August were not significantly different from each other (Tukey HSD, $\alpha = 0.05$). Acoustic backscatter in Aialik Bay was significantly higher than in Northwestern Lagoon ($p < 0.01$).

Hydroacoustic measurements of schooling fish showed between-fjord and among month differences in 2008 (Figs. 11-12). Dense forage fish aggregations were scarce in

Northwestern Lagoon during June while the highest abundance occurred in July, and an intermediate abundance was observed in August (Fig. 11). Fish aggregations in Aialik Bay were most abundant in distal areas in June and by August they were most abundant in glacial areas (Figs. 11-12). Aialik Bay's northeastern shore in August had more numerous schools of greater magnitude than any other area during the summer. Mean ± SE depth of schools was 39.0 ± 6.7 m in June, 46.7 ± 7.4 m in July and 32.2 ± 3.4 m in August.

Weaker scattering nekton, including ichthyoplankton, zooplankton and gelatinous zooplankton also showed seasonal variability (Fig. 11). Based on visual examination of plots, higher intensity scattering was generally associated with nearshore areas, submerged moraines, and tidewater glaciers. Net sampling suggested that acoustic backscatter in glacial areas was due primarily to zooplankton, while gelatinous zooplankton were more abundant in distal areas. In August, a transect near the head of Northwestern Lagoon had the highest acoustic backscatter due to weak scattering organisms. In Aialik Bay, weak scattering organisms were also abundant in glacial areas in August.

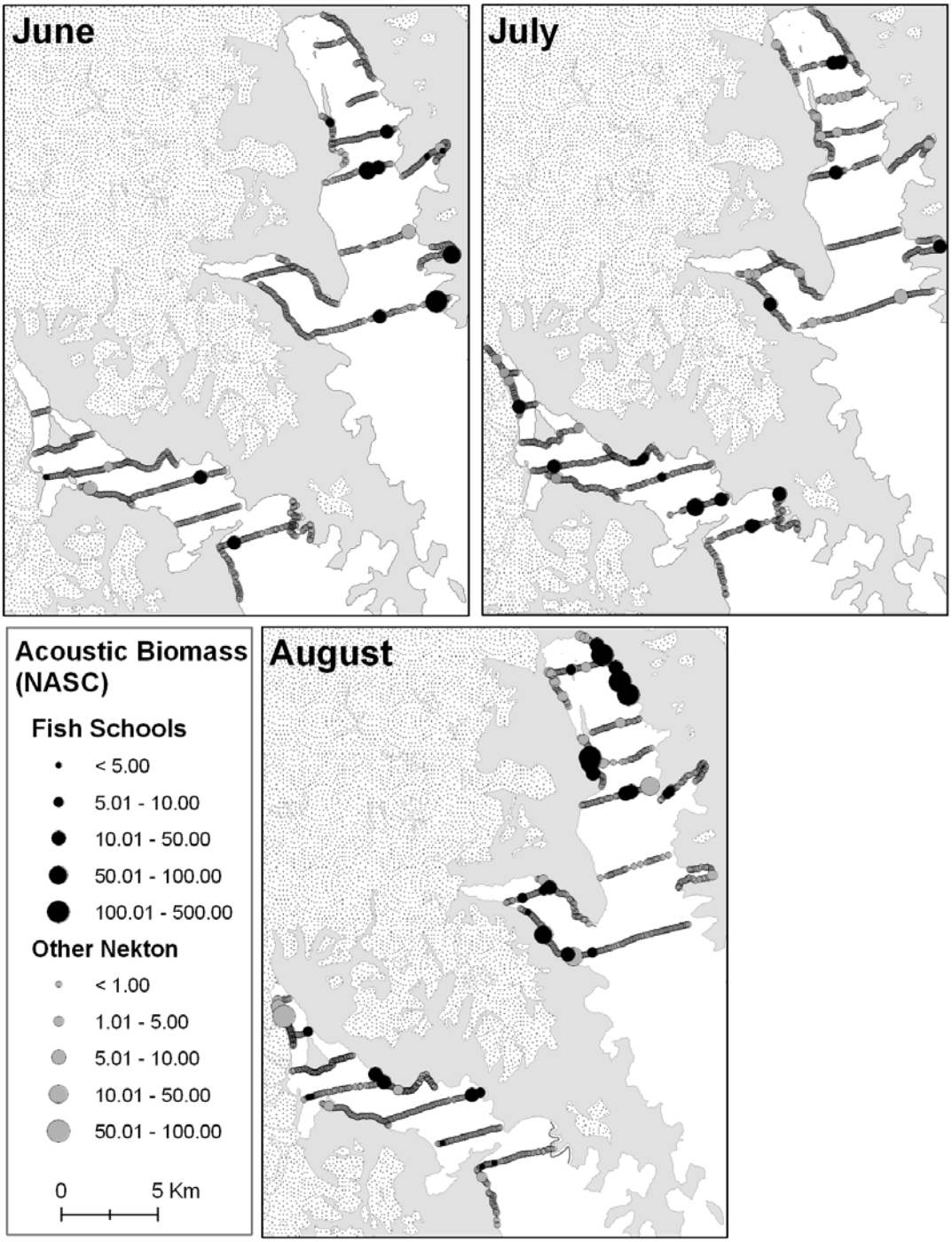

Figure 11. Monthly acoustic biomass (nautical area scattering coefficient, NASC) due to dense forage fish schools and weaker scattering nekton measured during hydroacoustic surveys in Kenai Fjords, 2008. Glacial extent is indicated as grey stipple.

The relationship between acoustic biomass and glacial distance also differed by fjord and month (Fig. 12). In Northwestern Lagoon, log-transformed acoustic backscatter decreased with glacial distance in June ($R^2 = 0.43$, $p < 0.05$) and July ($R^2 = 0.35$, $p < 0.05$). In Aialik Bay, log-transformed acoustic backscatter increased with distance to the glacier in June ($R^2 = 0.55$, $p < 0.01$), while the relationship apparently shifted over the course of the summer, although it was not significant (Fig. 12).

At least 21 species of fish were collected in beach seines (Table 4). Pacific sandlance (n = 1757), pink salmon (*Oncorhynchus gorbuscha*, n = 636), and Pacific herring (n = 155) were most abundant and all three species occurred in 31 % of beach seine sets. Pacific sandlance were collected at the McCarty moraine and in Northwestern Lagoon. Pacific herring were collected on the northeast shore of Aialik Bay, in Northwestern Lagoon, in Pederson Lagoon, and Verdant Cove. Surf smelt (n = 62) also were among the more common species, and were caught at the McCarty moraine, Pederson Lagoon, and Northwestern Lagoon. We also collected spawning capelin in Pederson Lagoon.

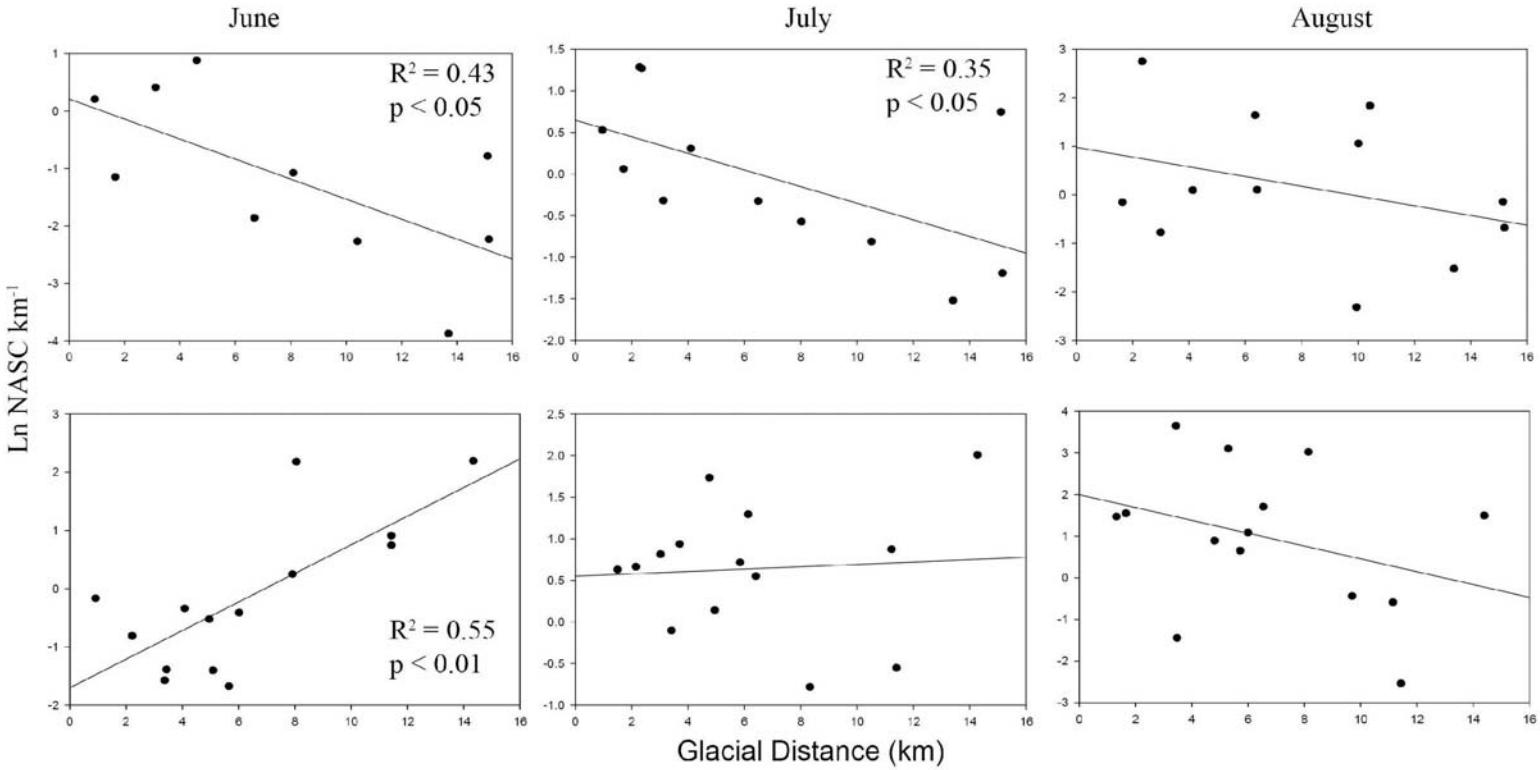

Figure 12. Monthly relationship between log-transformed acoustic backscatter and transect distance to tidewater glaciers in Northwestern Lagoon (top) and Aialik Bay (bottom) in 2008.

Table 4. Species, size range (fork length, mm), sample size (n), and mean size with standard deviation (SD) of fishes captured in beach seines in Kenai Fjords, 2007-2008.

Common Name	Scientific Name	Size Range (n)	Average (SD)
Pacific herring	*Clupea pallasii*	30-143 (155)	98 (20.9)
Capelin	*Mallotus villosus*	105 (1)	105
Surf smelt	*Hypomesus pretiosus*	37-145 (62)	87 (32.8)
Chum salmon	*Oncorhynchus keta*	39-69 (96)	59 (7.6)
Pink salmon	*Oncorhynchus gorbuscha*	32-134 (636)	87 (21.1)
Sockeye	*Oncorhynchus nerka*	59-104 (46)	84 (12.7)
Dolly Varden char	*Salvelinus malma*	150-202 (3)	184 (29.5)
Silver Salmon	*Oncorhynchus kisutch*	149 (1)	149
Pacific cod	*Gadus macrocephalus*	50-95 (86)	64 (8.3)
Threespine stickleback	*Gasterosteus aculeatus*	29 (1)	29
Greenling	*Hexagrammos* sp.	28 (1)	28
Rock greenling	*Hexagrammos lagocephalus*	140 (1)	140
White-spotted greenling	*Hexagrammos stelleri*	64-82 (15)	71 (4.5)
Sculpin	Cottidae (Family)	12-15 (2)	14 (2.1)
Padded sculpin	*Artedius fenestralis*	34 (1)	34
Buffalo sculpin	*Enophrys bison*	45-119 (7)	78 (23.0)
Great sculpin	*Myoxocephalus polyacanthocephalus*	32-159 (5)	68 (51.3)
Sharpnose sculpin	*Clinocottus acuticeps*	17-27 (2)	22 (7.1)
Myox sp.	*Myoxocephalus* sp.	12-20 (21)	17 (2.3)
Eelpout	*Lycodapus* sp.	37 (1)	37
Daubed shanny	*Lumpenus maculatus*	61 (1)	61
Crescent gunnel	*Pholis laeta*	39 (1)	39
Pacific sandlance	*Ammodytes hexapterus*	32-156 (1757)	97 (33.9)
Yellowfin sole	*Pleuronectes asper*	45 (1)	45

Murrelet Distribution and Habitat Preferences

Kittlitz's murrelets were largely restricted to the areas closest to tidewater glaciers, and were nearly always found above the terminal moraines in Northwestern Lagoon and Aialik Bay, while marbled murrelets were more widely distributed (Figure 13). Density estimates for Kittlitz's murrelets sighted within 100 m of either side of the vessel on transects repeated in Aialik Bay and Northwestern Fjord were on average ± SE 2.63 ± 0.12 birds km^{-2} in the early season, 3.18 ± 0.69 birds km^{-2} for mid-season, and 1.46 ± 0.65 birds km^{-2} for late season surveys. In 2008 there was an increase in Kittlitz's

murrelet density from early to mid-season, followed by a decrease late in the season. In 2007, the early and mid-season densities were lower than in 2008, while late season density was higher than 2008. During mid-season coastwide surveys, the average density for Kittlitz's murrelets was highest in offshore (> 200 m from shore) glacial areas within fjords, with average ± SE density of 5.82 ± 1.81 birds km^{-2} across years, and lowest in the offshore areas outside of fjords with an average density of 0.02 ± 0.02 birds km^{-2} across years.

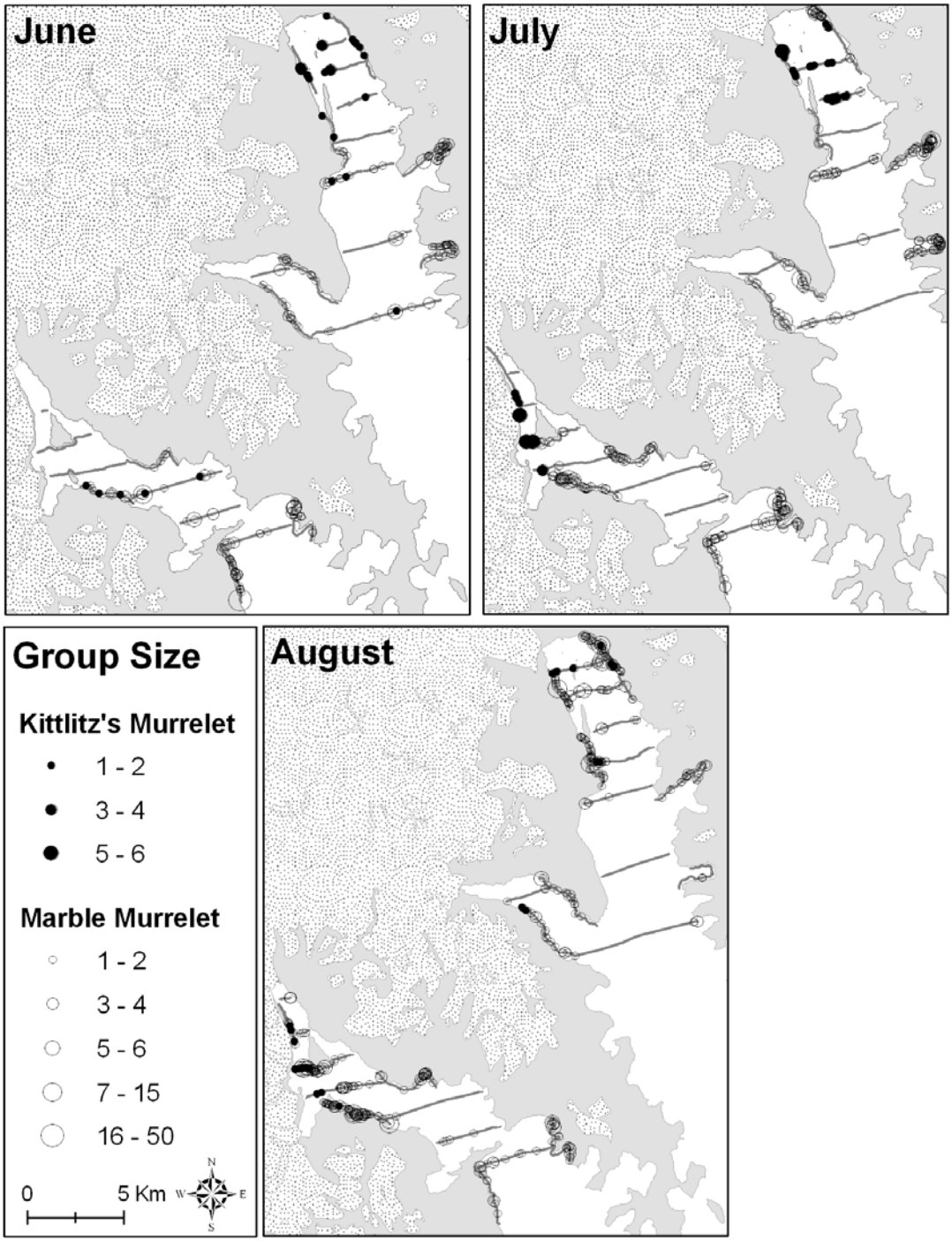

Figure 13. Distribution of Kittlitz's and marbled murrelets in Kenai Fjords National Park during 2008. Grey lines indicate effort, and glaciers are indicated as grey stipple.

Although I examined models at multiple spatial scales, only the most parsimonious model with the highest correct prediction rate for each species is presented. In general, the glmm, which incorporated spatial autocorrelation among observations within transects, performed better than glm. This suggests that spatial autocorrelation was present in the residuals after accounting for the effects of covariates. For Kittlitz's murrelets at the 400 m scale, a glmm correctly predicted presence or absence in 89 % (75/84) of observations compared to 81 % (68/84) for the glm model. The glmm correctly predicted the presence of Kittlitz's murrelets in 61 % (11/18) of the 400 m segments where Kittlitz's murrelets were observed. In contrast, the glm correctly predicted the presence of Kittlitz's murrelets only 33 % (6/18) of segments where they were observed. An exponential correlation structure indicated spatial autocorrelation was relatively weak, with a range of 155 m. A smaller segment size resulted in the best model for Kittlitz's murrelets because modeling was restricted to observations where ice was present, and greater segment sizes resulted in sample sizes that were too low for drawing meaningful inferences.

Similarly, the glmm outperformed the glm for marbled murrelet response to habitat variables at all scales. At the 800 m segment scale, a glmm correctly predicted presence or absence in 81 % (100/124) of observations compared to 71 % (88/124) for the glm. The glmm correctly predicted the presence of marbled murrelets in 86 % (55/64) of segments where they were present compared to 75 % (48/64) for the glm. Again, the correlation structure suggests weak spatial autocorrelation (range = 37 m). Although I tried to account for between-transect variability by including variables for glacial

distance, fjord and transect type, these variables had little influence on the response and were not included in the final model.

Habitat preferences differed between Kittlitz's and marbled murrelets, despite their apparent distributional overlap in Kenai Fjords. Where ice was present, the best model showed that Kittlitz's murrelets had higher probability of occurrence in Aialik Bay, over deeper water, closer to the glacier, and over waters where log-transformed acoustic biomass was higher (Table 5). Coefficients for all variables were significantly different from zero. In contrast, the probability of marbled murrelet occurrence was negatively related to bottom depth and ice cover; however, only the negative response to ice had a coefficient that was significantly different from zero. Bathymetry was included in the final model because at all scales, marbled murrelets had a higher probability of occurrence in shallow waters, and glm models including bottom depth as a variable outperformed models without (based on lower AIC values). At small scales (200 m and 400 m), marbled murrelets were more likely to occur along coastal transects than offshore transects; however, the inclusion of the transect type as a factor did not improve the models' ability to correctly predict the presence or absence of murrelets at any scale.

Table 5. Parameter estimates for best fit models using generalized linear mixed models to relate Kittlitz's and marbled murrelet presence/absence (binomial response) to marine habitat variables measured in Kenai Fjords National Park during July 2008. Acoustic backscatter was log-transformed, and all continuous variables were normalized prior to analysis to allow comparison of coefficients. The coefficient for fjord reflects the difference in mean probability of occurrence between fjords on the logit scale.

Kittlitz's murrelet (400 m segment lengths)

	Coefficient	SE	t	p
Intercept	-8.7408	1.8674	-4.68	< 0.001
Bathymetry	1.7453	0.5563	3.14	< 0.01
Acoustic	1.8992	0.5461	3.48	< 0.001
Glacial Distance	-6.0131	1.3055	-4.61	< 0.001
Fjord (Aialik = 1)	6.9365	1.9259	3.60	< 0.01

Marbled murrelet (800 m segment lengths)

	Coefficient	SE	t	p
Intercept	0.6718	0.3770	1.78	0.0779
Bathymetry	-0.3268	0.2414	-1.35	0.179
Ice	-1.4687	0.5425	-2.71	< 0.01

Discussion

Cool, sediment laden glacial melt water is a primary structuring feature in glacial fjord ecosystems during summer (Pickard & Stanton, 1980; Etherington *et al.*, 2007). Tidewater glacial river runoff is an important source of freshwater that imparts stratification in the surface waters (Kipphut, 1990) and also provides some nutrients required by the marine primary production (Hood & Scott, 2008). Low light availability in glacial river plumes, however, hinders phytoplankton growth and influences interactions between visual predators and their prey (Aksnes *et al.*, 2004). Low light conditions may also affect the vertical migration habits of fishes and zooplankton (Abookire *et al.*, 2002; Frank & Widder, 2002), making near-surface prey more available to predators that are adapted to foraging in low-light conditions. For this reason, high

surface turbidity in marine waters near glacial river outflows appears to be important to foraging Kittlitz's murrelets.

Our data support the hypothesis that a water clarity profile characterized by high turbidity near the surface and clearer water below is important to Kittlitz's murrelets feeding in glacial-marine environments (Kuletz *et al.*, 2008). Low water clarity as a result of glacial runoff in Kenai Fjords was generally constrained to the surface layer (5-9 m) near tidewater glaciers (Fig. 8). The water column below the turbid freshwater lens was clearer, and this physical feature is common in Kittlitz's murrelet foraging habitat elsewhere (Barron & Barron, 2005; Kuletz *et al.*, 2008). Low water clarity was detected throughout the water column near Aialik Glacier in July, however, indicating higher subsurface sediment outflow as glacial melt increased throughout the summer warming period. This effect was very localized as subsurface beam transmission reached 80 % at 12 m depth at a station sampled 2.3 km from the glacier.

Seasonal fluctuations in chlorophyll *a* and nutrient dynamics during summer 2008 suggest that the mechanisms governing these ecosystem components differ between fjords. The relatively low chlorophyll *a* concentrations in glacial areas compared to distal areas of Aialik Bay during all sampling periods indicate that chlorophyll *a* production there is more influenced by shelf waters. This is likely due to the orientation of the mouth of the Aialik Bay relative to the Alaska Coastal Current, the dominant density-driven surface-oriented current on the Gulf of Alaska shelf. This was also supported by the structure of the trawl catch community, which differed between fjords, and was dominated by oceanic zooplankton species in Aialik Bay. Northwestern Lagoon had more

consistent chlorophyll *a* patterns throughout the 2008 summer, with relatively high chlorophyll *a* concentrations in glacial areas in June and July. In contrast to Aialik Bay, Northwestern Lagoon is more enclosed with a narrower passage and shallower sill, which inhibits exchange with more oceanic waters in distal areas. For these reasons, Northwestern Lagoon may have provided a more stable environment for phytoplankton production than Aialik Bay.

Meso-scale patterns of phytoplankton production may influence interannual variability in numbers of murrelets at sea. Kittlitz's murrelet counts within the survey area were down in 2007, coincident with anomalous oceanographic conditions relative to the long-term average in the Gulf of Alaska. Specifically, spring/summer temperature and salinity profiles fell outside the long term average standard deviations in May, with cooler temperatures throughout the water column, fresher water at depth and more saline water near the surface (Janout *et al.,* in press). Kittlitz's murrelet at-sea abundance estimate for Kenai Fjords in 2007 was 62% lower than 2006 and 42% lower than 2008 (J. Piatt, U.S. Geological Survey, pers. comm.). Furthermore, Kittlitz's murrelet density estimates over the course of the 2007 breeding season did not follow the pattern of seasonally increasing density through July followed by a sharp decline in August observed in 2006 and 2008. Instead, the highest density of Kittlitz's murrelets occurred late in 2007, which suggested a delay in the onset of breeding during that year. Oceanographic sampling along the Gulf of Alaska shelf adjacent to Kenai Fjords confirmed that 2007 was an anomalous year.

Macrozooplankton such as euphausiids are an important prey type in Kittlitz's murrelet diets (Sanger, 1987; Hobson *et al.*, 1994; Day *et al.*, 1999), comprising as much as 44 % of Kittlitz's murrelet and 31 % of marbled murrelet diets in Alaska (Hobson *et al.*, 1994). The near surface availability of euphausiids in the turbid waters near glacial stream outflows provides a prey resource for Kittlitz's murrelets, and may be an important factor in their at-sea distribution patterns. The increased availability of euphausiids near the surface in glacial plumes, which was also documented in other glacial fjords, may be due to lower light from the turbid freshwater outflow causing an absence of a photic cue for vertical migration. Abookire *et al.* (2002) speculated that this may explain the daytime presence of mesopelagic fishes in the turbid glacial surface waters in Glacier Bay. Also, euphausiids swarm in surface waters during daylight hours to reproduce (Hanamura *et al.*, 1989) and timing of surveys in Kenai Fjords overlapped with the reproductive period of euphausiids in nearby Prince William Sound and along the Gulf of Alaska shelf (Pinchuk *et al.*, 2008). However, the most abundant species collected within Kenai Fjords was *T. inermis*, which usually reproduces between April and May (Pinchuk *et al.*, 2008) and which is earlier than my sampling commenced. It is also possible that net avoidance in clear water may explain the higher euphausiid catches in turbid water. I believe this was not the case, however, because trawl catches in Glacier Bay, using a net large enough to rule out net avoidance by organisms as small as euphausiids, showed a similar pattern of high daytime euphausiid abundance in surface waters nearest the glaciers (Robards *et al.*, 2003, J. Piatt, U.S. Geological Survey, pers. comm.).

Higher secondary productivity in the surface waters near glaciers may also contribute to the high ammonium levels observed there in 2007 and 2008. Ammonium is the primary inorganic nitrogenous product of excretion by zooplankton (Steinberg *et al.*, 2002). Ammonia excreted by zooplankton can provide a large proportion of the nitrogen required by phytoplankton production and may be found in higher concentrations at locations influenced by river-induced entrainment (Jawed, 1973).

Monthly acoustic backscatter measurements in Kenai Fjords during 2008 revealed lower prey availability in June compared to later in the summer. Patterns of acoustic biomass differed between fjords, with biomass in Northwestern Lagoon generally decreasing with distance from tidewater glaciers throughout the summer. Higher abundance of weak-scattering organisms such as zooplankton in the upper 40 m of the water-column near the head of Northwestern Lagoon was a driver of this relationship. The relationship between acoustic biomass and glacial distance in Aialik Bay was more variable over the summer, with a significant positive response in the early season, and no significant relationship later in the season. In the middle and late summer, however, dense forage fish schools had clearly moved into glacial areas of Aialik Bay (Fig. 9), a seasonal pattern that is consistent with studies of forage fishes elsewhere (Robards *et al.*, 1999).

Concurrent hydroacoustic and bird survey data suggest that Kittlitz's murrelets utilize lower density forage fish aggregations and zooplankton that occur in the turbid glacial plume near tidewater glaciers. Although monthly acoustic measurements indicate that dense forage fish schools moved into the inner fjords by August 2008, earlier in the

season the area closest to tidewater glaciers contained only weak scattering organisms such as zooplankton and low-density fish schools. Higher turbidity near the glaciers may increase the availability of this type of prey because 1) the lack of a photic cue may inhibit vertical migration for zooplankton and fish, and 2) visual cues that aid in dense schooling behavior may be suppressed in very turbid water (Partridge & Pitcher, 1980).

Kittlitz's murrelets are uniquely adapted to foraging in turbid waters. Compared to the congeneric marbled murrelet, they have larger eyes, which probably aid in light gathering, and a smaller bill size (Day *et al.*, 1999), which allows them to capture smaller prey in silty water. In Kenai Fjords and elsewhere, Kittlitz's murrelets prefer turbid waters associated with tidewater glaciers (Day *et al.*, 2000; Day *et al.*, 2003; Kuletz *et al.*, 2003), but they do also breed in locations where glaciers are small remnants of their former size (e.g., Kodiak Island, Unalaska Island) or no longer exist (e.g., Aggatu Island, Seward Peninsula) (Piatt *et al.*, 2007; USFWS, 2008). In these areas, little work has been done to document at-sea preferences; however, recent surveys in Kodiak suggest Kittlitz's murrelets there are concentrated in the heads of fjords in remnant glacial areas with some glacial river runoff (J. Piatt, pers. comm.).

I used a scaled approach to assess habitat associations for murrelets in Kenai Fjords. Although this multi-scale approach necessarily makes assumptions about the theoretical significance of aggregations within a given scale (Haney & Schauer, 1994), it does compensate for the inability to resolve resource use patterns below or above an arbitrary sample unit (Piatt, 1990). Spatial autocorrelation among observations and between-transect variability was handled with a glmm approach after main effects were

assessed by glm. This approach improved correct prediction rates and reduced bias. The most appropriate scale for Kittlitz's and marbled murrelets was 400 m and 800 m, respectively. The use of a smaller scale for Kittlitz's murrelets was largely due to their patchy distribution. In contrast, marbled murrelets were more abundant and occurred in a wider variety of habitats. Future study designs should incorporate a sampling design that better accounts for the clumped distribution of Kittlitz's murrelets, particularly in areas like Kenai Fjords where the breeding population size is low.

Analysis of murrelet distribution relative to marine habitat characteristics suggests that Kittlitz's murrelets in Kenai Fjords are probably more sensitive to climate change than marbled murrelets. While Kittlitz's murrelets were more influenced by prey availability, and distance to glaciers (a proxy for cool, fresh, and turbid surface conditions), marbled murrelets were most influenced by bathymetry and ice (or lack thereof). In Kenai Fjords, Kittlitz's murrelets did not occur where ice was absent, and when ice was present they were more likely to occur in deeper water, in areas with higher acoustic backscatter, and in proximity to tidewater glaciers. In contrast, marbled murrelets were more likely to occur in shallow, ice-free areas. Although this suggests a preference for nearshore areas and an avoidance of areas with ice, it is clear that marbled murrelets have a wider tolerance to changes in marine habitat. With global warming, changes in prey availability (Anderson & Piatt, 1999; Hare & Mantua, 2000) and glacial extent (VanLooy *et al.*, 2006) are expected. In contrast, habitat preferences of marbled murrelets including shallower water and ice free conditions will be less affected by global warming.

In Kenai Fjords (this study) and elsewhere, Kittlitz's murrelets prefer areas where ice occurs (Day *et al.*, 2000; Day *et al.*, 2003). Indeed, during this study Kittlitz's murrelets were limited in their distribution to areas where ice was present. However, the presence of ice is less likely to be of biological importance to foraging murrelets than other factors for which ice occurrence could be considered a proxy, such as increased turbidity from glacial outflow and increased availability of certain near-surface prey. Similarly, the apparent avoidance of ice by marbled murrelets may actually be an avoidance of areas with high turbidity where they are unable to adequately capture prey.

Pinpointing the cause for declines of threatened and endangered species has proven to be a difficult task, despite concerted effort and debates within the scientific community (e.g., Fritz & Hinckley, 2005; Trites *et al.*, 2007). Adequate prey resources are a necessary condition for growth and reproduction of marine predators, and an understanding of changes in the marine ecosystem is required to make causal linkages with declining marine species. There is increasing evidence that climate change has already played a role in the decline of Kittlitz's murrelets through the reduction of nesting habitat in glacial areas and changes in the forage base (Anderson & Piatt, 1999; Kuletz *et al.*, 2003; USFWS, 2008). In this study, I described prey availability relative to oceanography and glacial features in Kenai Fjords National Park and found that Kittlitz's murrelets responded to marine habitat features that will likely change in the face of a warming climate. My study was limited to a single region where only a small fraction of the Kittlitz's murrelet population breeds. Therefore, to better understand region-wide

marine habitat requirements for murrelets and other marine predators, a multi-year ecosystem approach in core breeding areas should be undertaken.

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Appendix. Zooplankton species, frequency of occurrence (FO), and mean biomass (mg m^{-1}) at stations sampled with an Isaacs Kidd midwater trawl in Kenai Fjords during summer 2008. Species are arranged in order of frequency of occurrence.

Taxon	Species	FO	Mean Biomass	SE
Copepod	*Acartia longirmis*	0.96	0.486	0.091
Copepod	*Pseudocalanus* spp.	0.96	0.527	0.075
Euphausiid	Euphausiid (unidentified)	0.96	0.929	0.247
Gastropod	*Limiacina helicina*	0.91	0.341	0.049
Copepod	*Calanus marchelli*	0.91	4.544	1.166
Decapod	Paguridae	0.87	0.307	0.051
Copepod	*Eucalanus bungii*	0.87	0.877	0.230
Chaetognath	*Sagitta elegans*	0.87	10.282	6.247
Decapod	Hippolytidae	0.83	0.706	0.224
Hydrozoan	*Eirene indicans*	0.78	3.409	1.244
Amphipod	*Parathemistosp.*	0.74	0.302	0.065
Larvacean	*Oikopleura* sp.	0.65	0.307	0.061
Copepod	*Metridia pacifica*	0.65	0.349	0.076
Copepod	*Neocalanus plumchrus*	0.65	0.896	0.248
Cnidarian	*Aglantha digitale*	0.65	1.060	0.598
Copepod	*Centropages abdominalis*	0.61	0.226	0.048
Hydrozoan	*Lars flavicirratus*	0.57	0.279	0.091
Cnidarian	*Coryne pinceps*	0.57	0.844	0.265
Decapod	*Pandalopsis dispar*	0.52	1.897	1.109
Amphipod	*Parathemisto libellula*	0.48	0.499	0.262
Hydrozoan	*Bougainvillia* sp.	0.48	1.069	0.471
Decapod	Pisinae	0.43	0.146	0.050
Copepod	*Neocalanus cristatus*	0.39	0.205	0.069
Euphausiid	*Thysanoessa inermis*	0.39	1.140	0.696
Cladocrean	Podon	0.35	0.175	0.057
Hydrozoan	*Perigonimus* sp.	0.30	0.152	0.060
Decapod	Oregoninae	0.26	0.096	0.042
Decapod	Pandalidae	0.26	0.147	0.077
Copepod	*Neocalanus flemigeri*	0.26	0.621	0.321
Amphipod	*Primno macropa*	0.22	0.064	0.036
Decapod	Brachyrhancha	0.22	0.107	0.050
Amphipod	*Cyphocaris challengeri*	0.22	0.175	0.108
Euphausiid	*Thysanoessa spinifera*	0.22	0.189	0.147
Decapod	*Pandalus platyceros*	0.17	0.048	0.031
Decapod	Crangonidae	0.17	0.050	0.024
Decapod	Pinnotheridae	0.17	0.071	0.037
Decapod	*Hyas* sp.	0.17	0.093	0.044
Cnidarian	Rathkea	0.17	0.101	0.059
Decapod	*Pandalus* sp.	0.17	0.114	0.060
Copepod	*Calanus pacifica*	0.13	0.040	0.026
Copepod	*Epilabidocera amphitrites*	0.13	0.043	0.024

Appendix. Continued.

Taxon	Species	FO	Mean Biomass	SE
Decapod	Paguridae	0.13	0.049	0.037
Crustacean	Barnacle	0.13	0.087	0.051
Euphausiid	*Euphausia pacifica*	0.13	0.094	0.069
Copepod	*Metridia ochatensis*	0.13	0.133	0.087
Copepod	*Acartia tumida*	0.09	0.014	0.010
Cladocrean	Evadnae	0.09	0.019	0.015
Hydrozoan	*Corymorpha* sp.	0.09	0.025	0.020
Amphipod	*Hyperia meduserum*	0.09	0.026	0.018
Gastropod	*Corolla* sp.	0.09	0.046	0.039
Arthropod	Tipulidae	0.09	0.057	0.045
Amphipod	*Gammarus* sp.	0.09	0.058	0.044
Cnidarian	*Aequeria* sp.	0.09	0.097	0.070
Siphonophore	Siphonophore bract	0.09	0.252	0.174
Nemata	Nematoda	0.04	0.005	0.005
Copepod	*Neocalanus* sp.	0.04	0.007	0.007
Crustacean	Cumacea	0.04	0.009	0.009
Ctenophore	Ctenophore	0.04	0.009	0.009
Copepod	*Oithona spinirastra*	0.04	0.011	0.011
Chaetognath	*Eukrohnia hamata*	0.04	0.013	0.013
Decapod	*Pasiphaea pacifica*	0.04	0.013	0.013
Arthropod	Diptera	0.04	0.018	0.018
Decapod	Lithodidae	0.04	0.020	0.020
Euphausiid	*Thysanoessa longipes*	0.04	0.024	0.024
Amphipod	*Hyperoche meduserum*	0.04	0.025	0.025
Copepod	*Oithona similis*	0.04	0.032	0.032
Euphausiid	*Thysanoessa* sp.	0.04	0.034	0.034
Tunicate	Salpa	0.04	0.035	0.035
Amphipod	*Parathemisto pacifica*	0.04	0.037	0.037
Euphausiid	*Thysanoessa raschii*	0.04	0.084	0.084