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# Oceanographic gradients and seabird prey community dynamics in glacial fjords

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## ABSTRACT

Glacial fjord habitats are undergoing rapid change as a result of contemporary global warming, yet little is known about how glaciers influence marine ecosystems. These ecosystems provide important feeding, breeding and rearing grounds for a wide variety of marine organisms, including seabirds of management concern. To characterize ocean conditions and marine food webs near tidewater glaciers, we conducted monthly surveys of oceanographic variables, plankton, fish and seabirds in Kenai Fjords, Alaska, from June to August of 2007 and 2008. We also measured tidal current velocities near glacial features. We found high sediment load from glacial river runoff played a major role in structuring the fjord marine ecosystem. Submerged moraines (sills) isolated cool, fresh, stratified and silt-laden inner fjord habitats from oceanic influence. Near tidewater glaciers, surface layers of turbid glacial runoff limited availability of light to phytoplankton, but macrozooplankton were abundant in surface waters, perhaps due to the absence of a photic cue for diel migration. Fish and zooplankton community structure varied along an increasing temperature gradient throughout the summer. Acoustic measurements indicated that low density patches of fish and zooplankton were available in the surface waters near glacial river outflows. This is the foraging habitat occupied most by Kittlitz's murrelet (*Brachyramphus brevirostris*), a rare seabird that appears to be specialized for life in glacially influenced environments. Kittlitz's murrelets were associated with floating glacial ice, and they were more likely to occur near glaciers, in deeper water, and in areas with high acoustic backscatter. Kittlitz's murrelet at-sea distribution was limited to areas influenced by turbid glacial outflows, and where prey was concentrated near the surface in waters with low light penetration. Tidewater glaciers impart unique hydrographic characteristics that influence marine plankton and fish communities, and this has cascading effects on marine food webs in these ecosystems.

**Key words**: Alaska, *Brachyramphus brevirostris*, capelin, chlorophyll, ecosystem, euphausiid, Kenai Fjords, Kittlitz's Murrelet, marine food web, marine sill, nutrients, tidal currents, tidewater glacier, turbidity

## INTRODUCTION

Spatial and temporal variability in environmental gradients structure prey community assemblages and habitat use by predators in marine and estuarine systems (Rakocinski et al., 1992; Speckman et al., 2005). In tidewater glacier fjord systems, high sediment load and freshwater run-off from melting ice create strong gradients in light penetration, temperature, and salinity (Etherington et al., 2007). While linkages between oceanography and faunal community dynamics have been demonstrated for many marine and estuarine systems (e.g. Becker et al., 2007; Ehrich et al., 2009), few studies have focused on glacial fjord ecosystems. These systems are important for many Arctic and subarctic species (Kuletz et al., 2003; Mathews and Pendleton, 2006; Arimitsu et al., 2008) and likely will experience dramatic changes as glacially influenced landscapes respond to climate change.

At-sea distribution of seabirds is generally regulated by the availability of prey resources, such as zooplankton and small, schooling fish (Birkhead and Furness, 1985; Becker and Beissinger, 2003; Jahncke et al., 2005). In fjord systems, zooplankton communities are influenced by advective processes in dynamic shallow

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waters above marine sills, and by diurnal migration patterns within more stable deep-water masses adjacent to sills (Gorsky et al., 2000; Basedow et al., 2004). Similarly, forage fish communities are sensitive to environmental factors such as turbidity, temperature and salinity gradients (Utne-Palm, 2002; Abookire and Piatt, 2005; Speckman et al., 2005).

Some marine predators are associated with glacial marine habitats where they forage and breed. For example, Kittlitz's murrelet (*Brachyramphus brevirostris*) is a small diving seabird that usually nests inland within glacially influenced alpine areas and often forages at sea in proximity to tidewater glaciers (Day et al., 2003; Kuletz et al., 2003). They feed on small schooling fishes and macrozooplankton (Hobson et al., 1994; Day and Nigro, 2000). Kittlitz's murrelets are uniquely adapted to foraging in turbid waters. Compared to the congeneric marbled murrelet (*Brachyramphus marmoratus*), which occupies a higher trophic position (Hobson et al., 1994), Kittlitz's murrelets also have proportionately larger eyes that may aid in light gathering, and a smaller bill size (Day et al., 1999), which allows them to capture smaller prey (such as euphausiids) in silty water.

At-sea surveys in Alaska indicate that Kittlitz's murrelet populations have declined by as much as 85% since the late 1980s (Kuletz et al., 2011a,b; Piatt et al., 2011), and the species is currently a candidate for listing under the Endangered Species Act (69 FR 24875-24904). Kittlitz's murrelet in the Gulf of Alaska often nest on or near glaciers, and their dependence on glaciated habitats increases the species' vulnerability to negative effects of global warming by reducing suitable nesting habitat in glacial areas and changing their prey availability and composition (Anderson and Piatt, 1999; Kuletz et al., 2003). Other threats include oil spills, vessel disturbance, and interactions with commercial fisheries (Piatt et al., 2007; Agness et al., 2008).

Owing to its strong association with glacial marine systems, and its role as a marine predator, in this paper we focus on the Kittlitz's murrelet and its use of foraging habitat in Kenai Fjords within southcentral Alaska. We measured physical (conductivity, temperature, currents) and biological (plankton, fish, and seabird abundance) variables in two glacial fjords during summer 2007 and 2008. We identified spatial and temporal changes in oceanographic gradients, chlorophyll *a*, nutrients, seabird prey community structure, and prey distribution relative to proximity to glacial features. To elucidate the importance of glacial features on marine food webs in fjord ecosystems, we also examined foraging habitat selection of Kittlitz's murrelet relative to prey availability and oceanography.

## MATERIALS AND METHODS

### *Study area*

Kenai Fjords is a glaciated fjord system located in southcentral Alaska (Fig. 1). Separated by shallow marine sills, the outer fjords are exposed to more direct oceanic influence from the Gulf of Alaska, whereas the recently deglaciated (<250 yr) inner fjords are influenced by tidewater glaciers that extend from the largest contiguous ice field in the region. Both fjords are about 25 km in length and contain at least three tidewater glaciers in addition to several hanging glaciers, all of which have undergone recession and thinning in the recent decades (Molnia, 2008). In this study, we selected Northwestern Lagoon and Aialik Bay because they were known to support a variety of marine bird predators, and particularly, Kittlitz's murrelets. Both fjords contain a neoglacial terminal moraine shoal (i.e. a shallow marine sill) demarcating the glacier terminus during the Little Ice Age (1200–1900 A.D.; Wiles et al., 1995).

### *Sampling overview*

Physical and biological characteristics of the marine ecosystem were sampled monthly during June–August in 2007 and 2008 (Table 1). The primary research platform was the 15.2-m R/V *Alaskan Gyre*. Currents and nearshore fish sampling was conducted from a 4.8-m rigid-hulled inflatable skiff. Oceanography surveys were conducted in both years at the same set of stations (Fig. 1) using a conductivity-temperature-depth profiler (CTD), and additional sensors were available to sample oxygen, light and water clarity in June and July 2008. We measured current velocities near glacial features in August 2007 with an acoustical Doppler current profiler. Biological attributes of the marine habitat were sampled in July 2007 when we conducted a pilot study using a random stratified sampling design. We sampled macrozooplankton and small nekton with a 3-m Isaacs-Kidd midwater trawl (IKMT) that was designed to catch larger, faster-swimming fish compared to the 1.8-m IKMT (Friedl, 1971). However, during trawl sampling in 2007, we found the 3-m IKMT was inefficient and did not improve fishing performance compared to the 1.8-m IKMT. We also determined that greater spatial and temporal effort was required to assess ecosystem processes. We therefore adopted a monthly systematic sampling approach the following year. In 2008, at even-numbered oceanography stations we sampled zooplankton and small fish with the 1.8-m IKMT. We also collected nearshore fish with a beach seine at suitable beaches during both years of the study. To estimate prey availability relative to seabird


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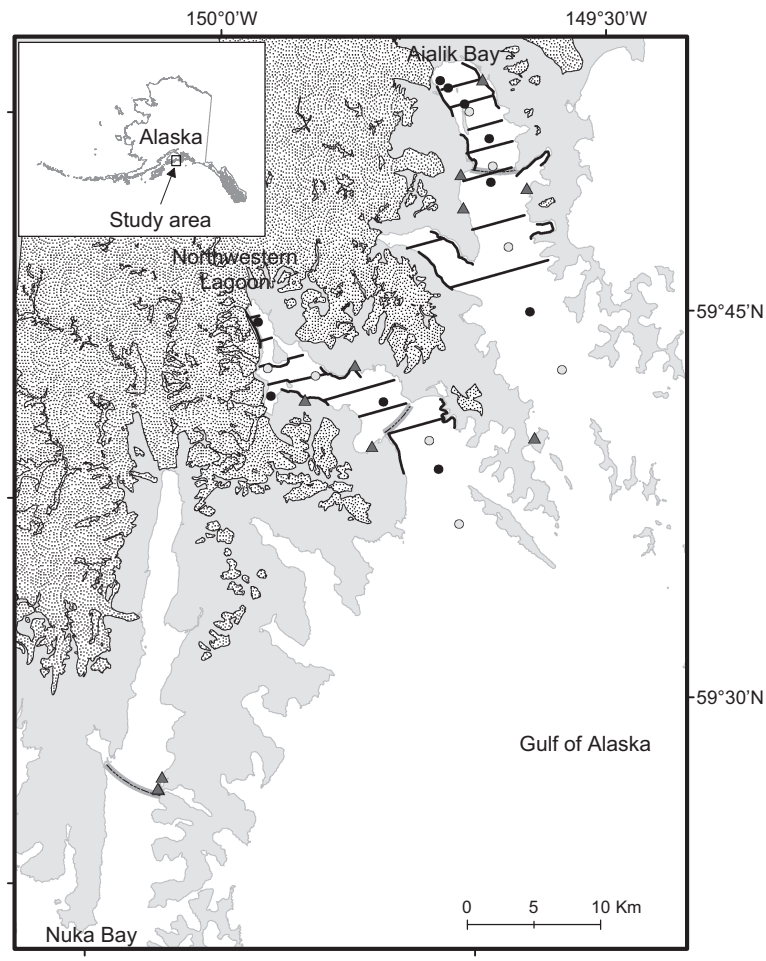


**Figure 1.** Map of study area, hydroacoustic and bird survey lines (black lines), oceanography stations (black and gray circles), water sample and trawl stations (gray circles), and beach seine locations (triangles) in Kenai Fjords, Alaska in 2007–2008. Ice extent is represented by black stipple, and marine sills are represented by dashed gray lines.

distribution, we conducted hydroacoustic surveys simultaneously with seabird surveys along systematic transect lines in 2008.

*Data collection*

Mesoscale (~25 km) gradients in marine habitat were measured from the face of the glaciers to the outer fjords (Fig. 1). Oceanic variables were measured monthly between June and August in 2007 and 2008 at stations previously established by Gay and Armato (1999). At each station, we deployed a CTD (SeaBird Electronics® SBE-19, Bellevue, WA, USA) equipped with a fluorometer (WetLabs® WetStar, Philomath, OR, USA) to measure chlorophyll *a* concentrations. In June and July 2008, we deployed additional sensors, including a dissolved oxygen sensor (SeaBird Electronics® SEB-43), photosynthetically active radiation (PAR) sensor (Biospherical® Quantum Scalar 2300L, San Diego, CA, USA) to measure light availability, and a beam transmissometer (WetLabs® C-STAR) to measure water clarity.

Nutrients and biological parameters were sampled in 2008 at a subset of oceanographic stations including two inner-fjord and two outer-fjord stations (hereafter 'glacial' and 'distal' stations, respectively; Fig. 1). A water sampler (Seabird Electronics® SBE 55) was deployed in conjunction with the CTD and water samples were collected at 2-m and 10-m depths. During a pilot study in July 2007, nutrient samples also were collected from 10 m depth using a Niskin bottle at 21 randomly selected stations stratified by distance to glacial features in both fjords (Fig. 2). Water samples were frozen in the field and later analyzed for ammonium, phosphate, silicic acid, nitrate, and nitrite concentrations.

We mapped tidal current velocities in Aialik and Northwestern Lagoons on 14–17 August 2007 using a 600-kHz acoustic Doppler current profiler (ADCP) interfaced with a differentially corrected GPS. Typically, lower frequency units are used in marine applications but the higher frequency unit was better suited for shallow and high velocity conditions found near


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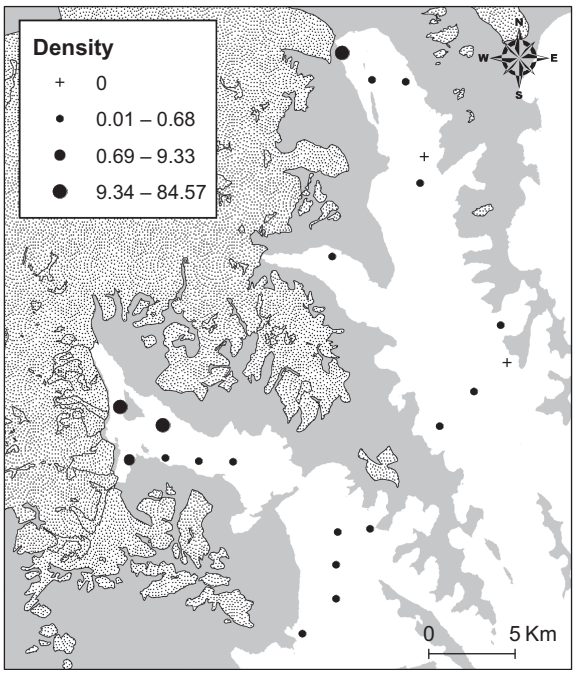
**Table 1.** Sampling effort by year, month and survey component during fjord ecosystem study in Kenai Fjords, Alaska.

| Year | Month | Currents (no. transects) | Oceanography (no. casts) | Nutrients (no. stations) | Chlorophyll (no. casts) | Zooplankton (no. stations) | Midwater Trawl (no. tows) | Beach Seine (no. sets) | Hydroacoustics (no. transects/ total length in km) | Seabird (no. transects/ total length in km) |
|---|---|---|---|---|---|---|---|---|---|---|
| 2007 | June | – | 14 | – | 14 | – | – | 5 | – | – |
| | July | – | – | – | – | – | 21* | 1 | – | – |
| | August | 10 | 18 | – | 18 | – | – | 5 | – | – |
| 2008 | June | – | 16† | 8 | 16 | 8 | 7 | – | 24/84.8 | 25/87.7 |
| | July | – | 18† | 8 | 18 | 8 | 8 | 2 | 26/92.7 | 26/91.4 |
| | August | – | 16 | 8 | – | 8 | 8 | – | 26/95.9 | 27/96.9 |

*Sampling was conducted at randomly selected locations using an Isaacs–Kidd midwater trawl with net dimensions that differed from the net used in 2008 (see Methods for further details).
†Water column profiles of oxygen, photosynthetically active radiation and beam transmission were collected in addition to oceanographic variables sampled in other months.

**Figure 2.** Density of near-surface euphausiids ($m^{-3} \times 1000$) in Isaacs–Kidd midwater trawl stations sampled in Kenai Fjords, Alaska, during July 2007. Ice extent is represented by black stipple.




submerged moraines. We measured tidal discharge at the submerged glacial moraines in both fjords. The ADCP was deployed using a small trimaran towed by an inflatable boat. Data were collected during peak ebb and flood tides and at slack tide. The path of data collection was normal to the primary direction of tidal flow. This cross-section pattern allowed quantification of tidal flux in and out of the fjords during tidal shifts. A CTD profile was made at a station near the center of each cross section.

We sampled zooplankton and small nekton taxa with midwater trawls. In 2007, an IKMT with a 3-m depressor bar, 3-mm mesh and 1-mm mesh screen in the cod end was deployed at 21 randomly selected stations (Fig. 2). In 2008, we used an IKMT outfitted with a 1.8-m depressor bar, 3-mm stretched knotless mesh near the mouth, and a 333-$\mu$m mesh ring net in the aft section and cod end (Friedl, 1971). Because the net dimensions, mesh size and sample design differed, we did not attempt to make direct comparisons of catches between years. Both nets were deployed in an oblique manner and deployed with a depth sensor (VEMCO® minilog T data logger, Halifax, Nova Scotia, Canada, or Star Oddi® DST CTD, Reykjavik, Iceland) to record the maximum depth of collection and a flowmeter (General Oceanics®, Miami, FL,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USA) to estimate volume filtered. Maximum depth towed was 35 m, average ± SD distance towed was 1.2 ± 0.1 km, and speed during the tow was approximately 5.5 km $h^{-1}$.

For each IKMT haul, total catch volume was estimated to the nearest 10 mL after water was drained through a sieve. All fishes collected in IKMT hauls were identified to species, when possible, and fork lengths of up to 25 individuals from each species were measured to the nearest 1.0 mm. Zooplankton sample contents were preserved in a 3–5% buffered formaldehyde seawater solution. In the lab, zooplankton 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 1.0 mg. Large zooplankton samples were subsampled with a Folsom plankton splitter after rare organisms were counted and removed.

To document nearshore fish species occurrence, we deployed a beach seine opportunistically at suitable beaches with no surf, boulder-free substrate, and a shallow incline for skiff access (Fig. 1). 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 two or three people. Upon recovery of the net, the fish catch was sorted by species, enumerated, and fork length was measured to the nearest 1.0 mm for a maximum of 25 individuals for each species.

Relative abundance of seabird prey was estimated in 2008 during hydroacoustic surveys conducted along systematic transects established to estimate marine bird density in the fjords (Fig. 1; see also Arimitsu et al., 2011). Coastal and offshore transects were oriented parallel to the shoreline in nearshore shallow habitats (<10 m depth), and perpendicular to the shoreline across the deep fjord basin (>300 m depth), respectively. This transect layout enabled sampling of glacial and distal areas (0.25–16.33 km from tidewater glacier influence) with strong gradients in sea surface temperature (6.2–15.1 °C), and sea surface salinity (21.94–28.84). We used a single beam, 120 kHz transducer (Biosonics DT-X®, Seattle, WA, USA) with a beam angle of 6.5° and collected data at 2 pings $s^{-1}$ with a pulse length of 0.5 ms. The transducer was deployed from a hydrodynamic fin and towed along side of the boat at an approximate depth of 2 m below the surface. The maximum depth of data collection was 120 m. The vessel generally travelled at speeds of 9–11 km $h^{-1}$. Field calibration was conducted according to Foote et al. (1987) on 2 June and 11 July 2008 using a 33-mm standard calibration sphere of known target strength. During hydroacoustic transects, we also deployed a thermosalinograph (Seabird Electronics® SBE 45 MicroTSG) to identify surface temperature and salinity conditions.

To relate seabird distribution to prey availability, we conducted marine bird surveys concurrently with hydroacoustic sampling following standard strip survey guidelines (Gould and Forsell, 1989). Two observers identified and enumerated all marine birds sighted within 150 m forward or to either side of the vessel (see Arimitsu et al., 2011 for further details). We also recorded the presence of floating glacial ice within the survey window. Data were recorded along with their GPS locations using DLOG-CE v.1.5.0 (Glenn Ford Consulting, Portland, OR, USA). Seabird and hydroacoustic surveys usually overlapped in space and time (Fig. 1, Table 1), and surveys were not conducted if wave height exceeded 0.5 m. Seabirds were counted on two transects with too much ice cover to safely tow the hydroacoustic transducer; however, only transects with both hydroacoustic and seabird data measurements were used for analysis.

### *Data analysis*

Raw CTD data were processed using SBE DATA PROCESSING MODULES v. 7.16 (Sea-Bird Electronics Inc., 2007). Photic depth was calculated as the depth at which PAR was 1% of the surface value. Water column profile data were contoured in MATLAB v. 7.5 (MathWorks Inc., Natick, MA, USA) relative to depth and the distance from tidewater glaciers at the head of the fjord.

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, Cary, NC, USA). Treatments included glacial influence (glacial versus distal), fjord (Northwestern versus Aialik), and month factors. Response variables were tested for normality with Shapiro–Wilks' tests, and homogeneity of variance was assessed with residual plots and Levene's tests at $\alpha < 0.05$. For multifactorial tests, additive models were applied when interaction terms were not significant. Nutrient data were fourth-root transformed to induce normality and homoscedasticity, or a Spearman rank correlation was used when assumptions of normality were not valid. A Tukey HSD multiple comparison test was employed to examine differences among months when the null hypothesis for the month factor was rejected.

Multivariate statistical analyses of seabird prey community structure were conducted in PRIMER® v6 (PRIMER-E Ltd, Lutton, Ivybridge, United Kingdom). Before analysis, we reduced the trawl catch dataset to


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include only species that were previously identified as important in murrelet diets (Day et al., 1999; Piatt et al., 2007). Euphausiids, shrimp, amphipod and gadid species' catch per unit effort (CPUE; abundance divided by distance towed) were aggregated at the group level due to low abundance by individual species; copepod species and capelin (*Mallotus villosus*) were analyzed at the species level (a complete list of zooplankton is given in the Appendix). The Bray–Curtis dissimilarity statistic, ranging from 0 to 100%, with greater values indicating greater dissimilarity, was computed on abundance data that were log(x + 1)-transformed and standardized.

We used a three-way permutation-based MANOVA (hereafter PERMANOVA) analysis to test for differences in seabird prey species composition relative to glacial influence (glacial versus distal), month and fjord (Aialik versus Northwestern) factors. We validated the assumption of homogeneity of multivariate dispersions in seabird prey species composition between levels of factors using the PERMDISP routine (Clarke and Warwick, 2001). Homogeneity of multivariate dispersions was met for glacial influence (PERMDISP: $F_{1,21} = 3.97$, $P = 0.07$) and fjord (PERMDISP: $F_{1,21} = 0.63$, $P = 0.47$) factors. The null hypothesis 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 ($P = 0.27$). Therefore, the month factor included only July and August samples in the PERMANOVA analysis. 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 of seabird prey in trawl catches were examined using the SIMPER routine, which calculates the average and standard deviation (SD) dissimilarity between groups for each species. The ratio of average dissimilarity to SD indicates how consistently a species contributes to the dissimilarity between groups (Clarke and Warwick, 2001). Non-metric multidimensional scaling (MDS) was used to obtain an ordination of Bray–Curtis dissimilarities 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, Hobart, Tasmania, Australia). We set 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. The bottom signal was excluded from the analysis. Additionally, the upper 1 m of data was removed to eliminate the effects of noise in the near field of the transducer. 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 and MacLennan, 2005). We summed NASC over 40 m of water depth ($NASC_{40}$) to estimate the acoustic backscatter within the foraging depth of 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 two-way ANOVA was applied to acoustic data summed by transect to test for differences between fjords and months. We used least-squares linear regression to examine the relationship between the log-transformed and normalized sum of $NASC_{40}$ $km^{-1}$ and the transect distance to nearest tidewater glacier by month and fjord.

To assess changes in schooling fish distribution over the course of the 2008 breeding season, we separated dense fish aggregations, hereafter 'schools', from more dispersed prey and weaker scattering targets with the hydroacoustic data, as in Mehlum *et al.* (1996). We integrated dense forage fish schools encountered on hydroacoustic transects by month using the school detection module in SONARDATA ECHOVIEW (Coetzee, 2000). Discrete schools were identified with the following minimum criteria: school length >2 m, school height >1 m, connected length >5 m, connected height >2 m, vertical linking distance <1 m.

To relate Kittlitz's murrelet distribution to environmental variables, we employed a combination of general linear models (GLM) and generalized linear mixed effects models (GLMM) using seabird survey data, bathymetry, and concurrent hydroacoustic and thermosalinograph data from July 2008. Kittlitz's murrelets were rare and clumped in their distribution in the fjords (Arimitsu et al., 2011), we used categorical data (presence/absence) instead of continuous data because the density data were highly skewed and normality could not be approximated through transformation. We explored the use of transect data for modeling habitat fine-scale habitat preferences at several segment lengths because transect length varied from 0.5 to 7.6 km, and a single transect crossed multiple habitat gradients (i.e. shallow to deep, glacial to distal, cool to warm, etc.). Raw data corresponding to


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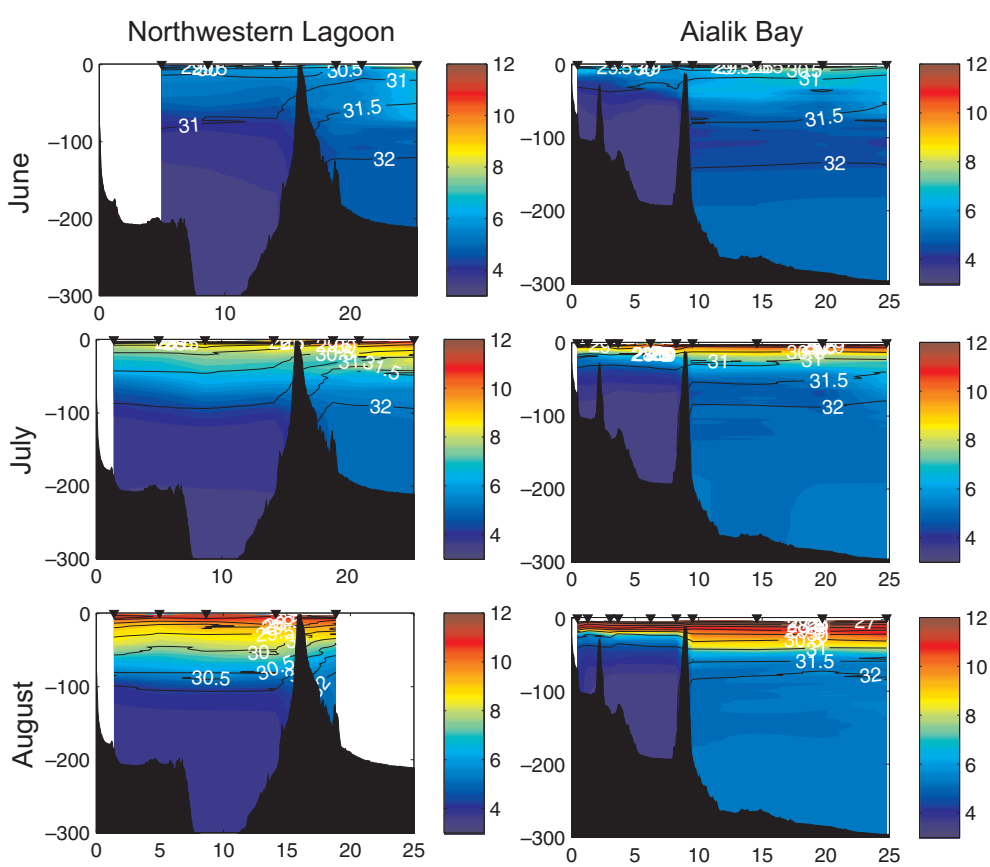
the marine bird and acoustic transects (Fig. 1) were divided into 200-, 400-, 800- and 1600-m segments. Data were then binned by segment and analyzed in R statistical software v. 2.7.2 (R development Core Team, Vienna, Austria). For each distance class, the response variable was presence/absence of Kittlitz's murrelets within each segment, and independent variables were calculated as the mean acoustic backscatter (NASC), sea surface salinity, and bottom depth (m) within each segment. Distance from the midpoint of each transect segment to the nearest tidewater glacier also was included as an explanatory variable. Sea surface temperature was not included as an independent variable because it was highly correlated with distance to tidewater glacier. The presence/absence of drifting ice (calved from tide-water glaciers), transect type (coastal or offshore), and fjord were coded as categorical variables. We log-transformed mean NASC (x + 0.0001) and then normalized continuous predictor variables prior to analysis. The presence/absence of Kittlitz's 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 never were present where drifting ice was absent; therefore, modeling of habitat predictor variables was restricted to the set of observations where ice was present. To account for spatial autocorrelation between segments on a single transect, we 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 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, whereby a

**Figure 3.** Temperature (°C, color) and salinity (lines, range: 24.34–33.00) vertical contours relative to depth (m; *y*-axis) and distance to tidewater glaciers (km; *x*-axis) in Kenai Fjords, Alaska during 2008. Sample locations are represented by black arrows. Bathymetric features are indicated in black, with minimum sill depth of 4 and 10 m, in Northwestern Lagoon and Aialik Bay, respectively.





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predicted probability of ≥0.5 was considered to indicate presence. This approach indicated the 400-m segment scale afforded the best resolution of the survey data relative to murrelet occurrence.

## RESULTS

### *Oceanography*

Temperature and salinity profiles demonstrated the importance of marine sills for modifying the exchange of inner and outer-fjord waters. Cool, fresh waters pooled behind the sills in the inner fjord and warmer, more saline waters were held outside (Fig. 3). The sill in Northwestern Lagoon was shallower (sill depth <4 m) and the passage was more constricted than in Aialik Bay (sill depth <10 m). 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 mixing with outer fjord waters in Northwestern Lagoon.

Relative chlorophyll *a* concentrations were the lowest during June 2007, and shallow photic depth near the glaciers corresponded with smaller chlorophyll *a* concentrations at depth (Fig. 4). Chlorophyll *a* concentrations were consistently greater in Northwestern Lagoon compared with Aialik Bay, particularly in August 2007. Northwestern Lagoon had more consistent and sustained chlorophyll *a* patterns throughout the 2008 summer, with relatively high chlorophyll *a* concentrations in glacial areas during June and July. In contrast, chlorophyll *a* concentrations were greater in distal areas compared with glacial areas of Aialik Bay (Fig. 4).

The surface water was least clear near tidewater glaciers, and clarity decreased from June to July 2008

**Figure 4.** Chlorophyll *a* vertical contours (mg $m^{-3}$, color) relative to depth (m; *y*-axis) and distance to tidewater glaciers (km; *x*-axis) in Kenai Fjords, Alaska. Sample locations are represented by black arrows. Photic depth is indicated as black diamonds for 2008, and locations of the prominent marine sills are indicated in solid black, with minimum sill depth of 4 and 10 m, in Northwestern Lagoon and Aialik Bay, respectively. Fluorometer data were not collected at core oceanography stations in July 2007 or August 2008.

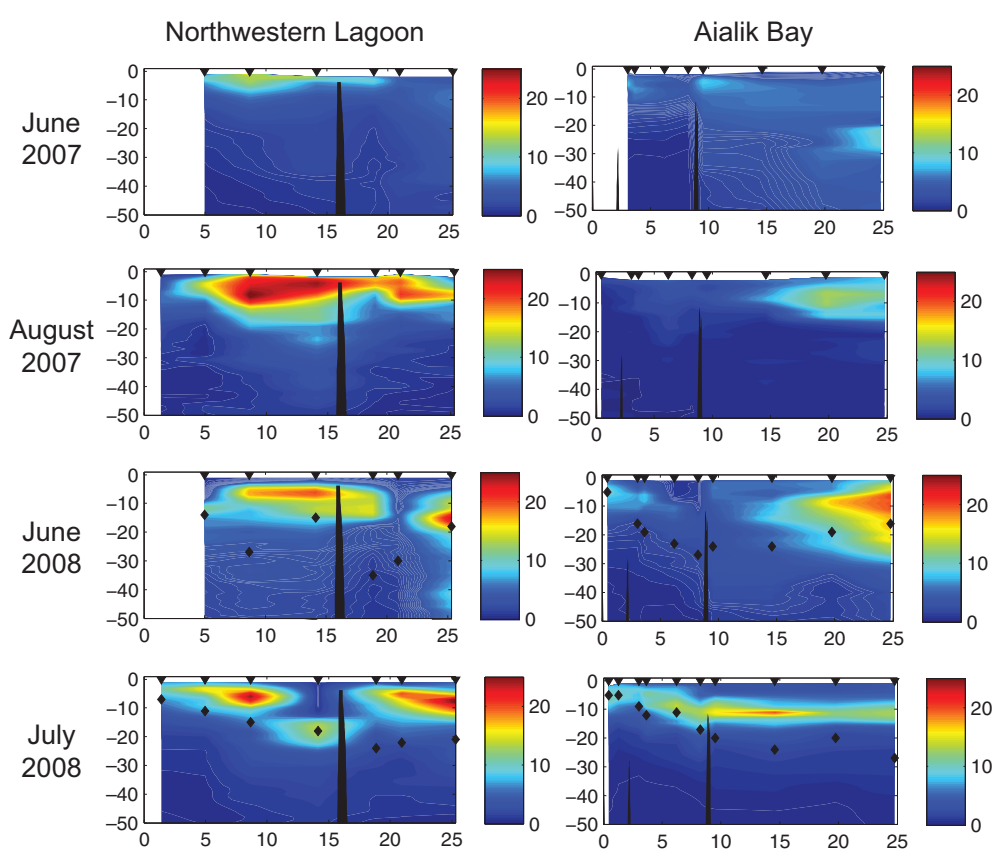



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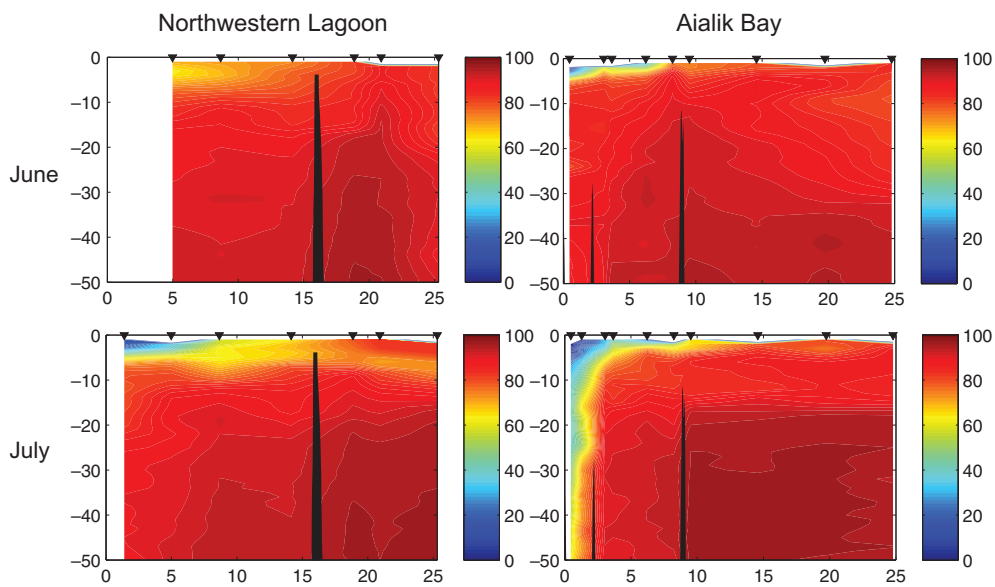
**Figure 5.** Water clarity vertical contours (% beam transmittance, color) relative to depth (m; *y*-axis) and distance to tidewater glaciers (km; *x*-axis) in Kenai Fjords, Alaska, during 2008. Sample locations are represented by black arrows, and the locations of the prominent marine sills are indicated in solid black.




(Fig. 5). Greater turbidity, indicated by lower values of % beam transmittance, in the upper 50 m of the water column within 3 km of the tidewater glacier in Aialik Bay indicated increased sedimentation from glacial runoff in July compared with June. Beam transmittance in the upper 3 m of the water column at stations within 3 km of tidewater glaciers was 54.6 ± 9.6% (average ± SE) in June and 28.4 ± 6.8% in July. In contrast, average transmittance below 3 m depth at stations within 3 km of a tidewater glacier was 87.5 ± 0.9% in June and 79.5 ± 5.2% in July. The median depth of 80% transmittance 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 <1 km from Aialik Glacier in July had low water clarity throughout the water column, with maximum transmittance of 73.5% at 99 m, and 66.7% at 88 m (Fig. 5).

In 2008, average dissolved inorganic nitrogen (DIN; sum of nitrite, nitrate and ammonium concentrations) generally decreased throughout the summer, and was greater in glacial areas than distal areas (Table 2). DIN was greater at glacial compared with distal areas, and differed among months, but did not differ significantly between fjords (three-way ANOVA: $F_{4,21}$= 4.15, $R^2$ = 0.45, $P$ < 0.05). DIN was significantly greater in June than July and August, but July and August were not significantly different from one another (Tukey HSD, $\alpha$ = 0.05). Phosphate concentrations decreased through the summer months and were higher in Northwestern Lagoon compared to Aialik Bay, but did not differ significantly between glacial and distal areas (three-way ANOVA: $F_{4,21}$= 21.41, $R^2$ = 0.83, $P$ < 0.0001). June, July and August phosphate concentrations differed from one another (Tukey HSD, $\alpha$ = 0.05). Silicic

**Table 2.** Average (SE) nutrient concentrations ($\mu$M) 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) |

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**Table 3.** Location and tidal flow information during acoustic Doppler current profiles in Kenai Fjords, Alaska.

| Location | Date | Time | Tide | Discharge ($m^3$ $s^{-1}$) | Width (m) | Area ($m^2$) | Average velocity (m $s^{-1}$) |
|---|---|---|---|---|---|---|---|
| Aialik Glacier | 8/14/2007 | 17 : 05 | Ebb | −13.1 | 1460 | 56 300 | 0.00 |
| Aialik Glacier | 8/14/2007 | 18 : 17 | Ebb | 655 | 1370 | 47 400 | 0.01 |
| Aialik Glacier | 8/14/2007 | 18 : 37 | Ebb | 17.3 | 1420 | 55 400 | 0.00 |
| Aialik Moraine | 8/15/2007 | 6 : 33 | Ebb | 6170 | 2390 | 25 500 | 0.24 |
| Aialik Moraine | 8/15/2007 | 9 : 42 | Slack | −1810 | 3020 | 29 800 | 0.05 |
| Aialik Moraine | 8/15/2007 | 12 : 18 | Flood | −12 200 | 3110 | 31 305 | 0.36 |
| Northwestern moraine | 8/15/2007 | 16 : 16 | Slack | 2460 | 2350 | 21 800 | 0.11 |
| Northwestern moraine | 8/15/2007 | 19 : 10 | Ebb | 10 290 | 1900 | 17 900 | 0.57 |
| Northwestern moraine | 8/17/2007 | 7 : 26 | Ebb | 7880 | 1740 | 22 000 | 0.36 |
| Northwestern moraine | 8/17/2007 | 10 : 23 | Slack | −284 | 1620 | 21 600 | 0.01 |

acid concentrations were not significantly different among factors.

Currents at marine sills in Aialik and Northwestern Lagoons were characterized by high velocities and complex flow during tidal exchanges (Table 3). The horizontal and vertical constriction of the fjord geometry accelerated the tidal velocities over the sill and induced three-dimensional currents. Sediment transport was detected at both the Aialik and Northwestern sills at peak flow. The maximum tidal discharge volume (12 200 $m^3$ $s^{-1}$) at the marine sill in Aialik Bay occurred during the peak flood tide on 15 August 2007. Similarly, the maximum tidal discharge volume (10 290 $m^3$ $s^{-1}$) at the marine sill in Northwestern Lagoon occurred during the peak ebb tide on 15 August 2007. The maximum measured velocity of 1.8 m $s^{-1}$ was recorded on that date. These large discharges and high velocities measured at the marine sills act to mix fresh water from the upper Fjords with waters from the Gulf of Alaska. In contrast, current measurements made near Aialik Glacier were characterized by low velocity and greater haline stratification. Average velocities near Aialik Glacier were <0.01 m $s^{-1}$ (Table 3). Thick ice pack, depths in excess of the instrument's range, and poor GPS position information hindered similar measurements near Northwestern Glacier. Inflow from the glaciers was not distinguishable in the velocity data, but a distinct freshwater lens was evident in both the salinity and ADCP measurements of acoustical backscatter data, a proxy for turbidity at the ADCP frequency (data not shown). Subsurface freshwater inflow was indicated by deeper extent of acoustical backscatter near the north end of the Aialik Glacier face.

*Fish community*

A minimum of 28 fish species were captured by IKMT in 2007 and 2008 (Table 4), including forage fish such as capelin, Pacific herring (*Clupea pallasii*) and Pacific sand lance (*Ammodytes hexapterus*). Saffron cod (*Eleginus gracilis*) was the most abundant gadoid; 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 21 fish species were collected in beach seines (Table 4). Pacific sand lance (61% of the catch), pink salmon (*Oncorhynchus gorbuscha*, 22% of the total catch), and Pacific herring (5% of the total catch) were the most abundant and all three species occurred in 31% of all beach seine sets. Chum salmon (*Oncorhynchus keta*, 3% of the total catch) and Surf smelt (*Hypomesus pretiosus*; 2% of the total catch) also were among the more common species.

Five species of euphausiids were collected in Kenai Fjords – (in descending order of abundance) *Thysanoessa inermis*, *Thysanoessa raschii*, *Euphausia pacifica*, *Thysanoessa spinifera*, and *Thysanoessa longipes*. In 2007, euphausiid CPUE was negatively associated with distance to tidewater glaciers (Spearman $\rho = -0.63$, $P < 0.01$), (Fig. 2). However, in 2008, euphausiid density and glacial distance were not significantly correlated.

There was a significant difference in seabird prey community structure between fjords (Pseudo $F_{1,12} = 2.40$, $P = 0.03$), and also between months (Pseudo $F_{1,12} = 7.25$, $P = 0.003$), but glacial and distal stations were not significantly different from one another. Spatial and temporal differences in the abundance of seabird prey taxa were evident with SIMPER analysis (Table 5). The oceanic copepod *Eucalanus bungii* consistently was more abundant in Aialik Bay, and the neritic copepod *Centropages abdominalis* was more abundant in Northwestern Lagoon. These two species contributed most to the dissimilarity between fjords (Table 5). Average abundance of capelin larvae


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**Table 4.** Species, size (fork length, mm), and sample size (*N*) of fishes captured in Isaacs–Kidd midwater trawls (IKMT) and beach seines in Kenai Fjords, Alaska, 2007–2008. Species are arranged in taxonomic order.

| | | IKMT | | Beach seine | |
|---|---|---|---|---|---|
| Common name | Scientific name | Size range (*N*) | Average (SD) | Size range (*N*) | Average (SD) |
| Pacific herring | *Clupea pallasii* | 14–22 (5) | 17 (3.1) | 30–143 (155) | 98 (20.9) |
| Northern smoothtongue | *Leuroglossus schmidti* | 27 (1) | 27 | – | – |
| Capelin | *Mallotus villosus* | 5–30 (845) | 14 (5.3) | 105 (1) | 105 |
| Eulachon | *Thaleichthys pacificus* | 26 (1) | 26 | – | – |
| Surf smelt | *Hypomesus pretiosus* | – | – | 37–145 (62) | 87 (32.8) |
| Larval smelt | Osmeridae (Family) | 14–26 (2) | 20 (8.5) | – | – |
| 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 | *Salvelinus malma* | – | – | 150–202 (3) | 184 (29.5) |
| Coho | *Oncorhynchus kisutch* | – | – | 149 (1) | 149 |
| Lanternfish | Myctophidae (Family) | 15 (1) | 15 | – | – |
| Saffron cod | *Eleginus gracilis* | 7–69 (152) | 28 (14.3) | – | – |
| Walleye pollock | *Theragra chalcogramma* | 7–41 (108) | 23 (6.7) | – | – |
| Pacific cod | *Gadus macrocephalus* | 12–36 (3) | 27 (13.1) | 50–95 (86) | 64 (8.3) |
| Gadid | Gadidae (Family) | 12–32 (32) | 22 (5.2) | – | – |
| Threespine stickleback | *Gasterosteus aculeatus* | – | – | 29 (1) | 29 |
| Rockfish | *Sebastes* spp. | 11–19 (6) | 14 (3.2) | – | – |
| Rock greenling | *Hexagrammos lagocephalus* | – | – | 140 (1) | 140 |
| White-spotted greenling | *Hexagrammos stelleri* | – | – | 64–82 (15) | 71 (4.5) |
| Greenling | *Hexagrammos* sp. | – | – | 28 (1) | 28 |
| Spinyhead sculpin | *Dasycottus setiger* | 12–30 (114) | 22 (4.4) | – | – |
| Padded sculpin | *Artedius fenestralis* | 14 (1) | 14 | 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 sculpin | *Myoxocephalus* sp. | – | – | 12–20 (21) | 17 (2.3) |
| Sculpin | Cottidae (family) | 7–12 (4) | 10 (2.2) | 12–15 (2) | 14 (2.1) |
| Soft sculpin | *Psychrolutes sigalutes* | 12–54 (6) | 37 (15.8) | – | – |
| Crested sculpin | *Blepsias bilobus* | 21–27 (5) | 24 (2.4) | – | – |
| Silverspotted sculpin | *Blepsias cirrhosus* | 13 (1) | 13 | – | – |
| Northern ronquil | *Ronquilus jordani* | 12–43 (4) | 26 (13.5) | – | – |
| Snailfish | Liparidae (family) | 12–18 (4) | 16 (3.2) | – | – |
| Sturgeon poacher | *Podothecus accipenserinus* | 20 (1) | 20 | – | – |
| Poacher | Agonidae (family) | 8–20 (23) | 15 (3.6) | – | – |
| Eelpout | *Lycodapus* sp. | – | – | 37 (1) | 37 |
| Daubed shanny | *Leptoclinus maculatus* | 28–45 (4) | 37 (6.9) | 61 (1) | 61 |
| Snake prickleback | *Lumpenus sagitta* | 22–67 (37) | 40 (13.5) | – | – |
| Longsnout prickleback | *Lumpenella longirostris* | 50 (1) | 50 | – | – |
| Lumpenus sp. | *Lumpenus* sp. | 23 (2) | 23 (0) | – | – |
| Larval prickleback | Sticheaidae (Family) | 26 (1) | 26 | – | – |
| Crescent gunnel | *Pholis laeta* | – | – | 39 (1) | 39 |
| Quillfish | *Ptilichthys goodei* | 173 (1) | 173 | – | – |
| Prowfish | *Zaprora silenus* | 13–36 (10) | 23 (8.4) | – | – |
| Pacific sandfish | *Trichodon trichodon* | 57 (1) | 57 | 32–156 (1757) | 97 (33.9) |
| Pacific sand lance | *Ammodytes hexapterus* | 16–43 (7) | 28 (8.3) | – | – |
| Flathead sole | *Hippoglossoides elassodon* | 9–38 (241) | 21 (5.2) | – | – |
| Butter sole | *Isopsetta isolepis* | 18–25 (8) | 21 (2.4) | – | – |
| Sand sole | *Psettichthys melanosticus* | 10–21 (5) | 14.6 (4.0) | – | – |

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**Table 4.** (*Continued*)

| Common name | Scientific name | IKMT | | Beach seine | |
|---|---|---|---|---|---|
| | | Size range (*N*) | Average (SD) | Size range (*N*) | Average (SD) |
| Yellowfin sole | *Pleuronectes asper* | – | – | 45 (1) | 45 |
| Northern rock sole | *Lepidopsetta polyxystra* | 12–21 (9) | 17 (2.9) | – | – |
| Rock Sole (unidentified) | *Lepidopsetta* sp. | 13–22 (3) | 16 (4.9) | – | – |
| Larval flatfish | Pleuronectidae (Family) | 12–24 (23) | 19 (3.5) | – | – |

was greater in Northwestern Lagoon than in Aialik Bay, and capelin larvae were one order of magnitude greater in July than in June or August (Table 5). Age-0 gadoids were most abundant in June and decreased through the remainder of the summer. Maximum euphausiid abundance occurred in July but decreased abruptly by August. Shrimp were nearly one order of magnitude greater in abundance in Northwestern Lagoon compared with Aialik Bay, and abundance was greatest in June and decreased in July and August (Table 5).

Differences in seabird prey community structure between fjords and over the course of the summer were evident in the MDS plot (Fig. 6). The first axis was negatively correlated with distance from marine sills ($r = -0.49$, $P < 0.05$), while the second axis was negatively correlated with temperature ($r = -0.83$, $P < 0.0001$), and positively correlated with salinity ($r = 0.69$, $P < 0.001$), phosphate ($r = 0.52$, $P < 0.05$), and nitrite ($r = 0.50$, $P < 0.05$). Community assemblages varied most significantly along an increasing temperature gradient throughout summer. In June, community composition was associated with distance from glacial features, particularly distance to the sill. Two outer-Aialik samples in June were distinct from the other samples and contributed to the large dispersion in June (Fig. 6). These two samples had the least biomass among all stations, lesser abundance of all taxa combined, and a greater proportion of gelatinous zooplankton in the catch compared with other June stations. August samples were the least dispersed (most homogeneous) of all months, with generally lower abundance across most seabird prey taxa compared with other months (Table 5, Fig. 6).

Acoustic backscatter among transects differed significantly by month and fjord (two-way ANOVA: $F_{3,72} = 6.28$, $R^2 = 0.21$, $P < 0.001$). The interaction between factors was not significant. June biomass was less than July and August but July and August were not significantly different (Tukey HSD, $\alpha = 0.05$). Acoustic biomass in Aialik Bay was significantly greater than in Northwestern Lagoon ($P < 0.01$).

The density of forage fish schools ($N$ km$^{-2}$) differed among months but was not significantly different between fjords (two-way ANOVA: $F_{3,75} = 3.06$, $R^2 = 0.11$, $P < 0.05$). School density in June was lower than July and August, but there was no significant difference between July and August (Tukey HSD, $\alpha = 0.05$; Fig. 7). Mean ± SE depth of schools sampled during daylight hours (6 : 00–20 : 00 h) was 48.2 ± 5.6 m in June, 37.4 ± 3.3 m in July and 38.6 ± 3.2 m in August. Likewise, acoustic backscatter due to individual forage fish schools differed by month but not by fjord (two-way ANOVA: $F_{3,177} = 3.66$, $R^2 = 0.06$, $P < 0.05$). Backscatter was higher in August than June and July, but June and July values were not significantly different (Tukey HSD, $\alpha = 0.05$).

Weaker acoustic scattering by nekton, including ichthyoplankton, macrozooplankton and gelatinous zooplankton, also showed seasonal variability. Stronger intensity scattering generally was associated with nearshore areas, marine sills, and tidewater glaciers (Fig. 7). Net sampling indicated that weak acoustic backscatter in glacial areas primarily was by macrozooplankton, such as euphausiids and copepods, whereas gelatinous zooplankton were most abundant in distal areas.

The relationship between acoustic backscatter and distance to glaciers also differed by fjord and month (Fig. 8). In Northwestern Lagoon, acoustic backscatter decreased with distance in June ($R^2 = 0.43$, $P < 0.05$) and July ($R^2 = 0.35$, $P < 0.05$). In Aialik Bay, however, acoustic biomass increased with distance in June ($R^2 = 0.55$, $P < 0.01$). This relationship was driven by the occurrence of dense schooling fish in distal areas (Fig. 7).

### *Kittlitz's murrelet distribution and at-sea habitat*

Kittlitz's murrelets generally were restricted to areas closest to tidewater glaciers, and were usually found north of the terminal moraines in Northwestern Lagoon and Aialik Bay (Arimitsu et al., 2011). Where ice was present, the best model indicated that Kittlitz's murrelets had greater probability of occurrence in


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**Table 5.** SIMPER analysis of dissimilarity of seabird prey composition in trawls between fjords [Aialik Bay (AB), and Northwestern Lagoon (NW)] and months. An index of average abundance, ratio of dissimilarity to standard deviation (Diss/SD), % contribution (contrib.) to overall dissimilarity, and % cummulative (cum.) dissimilarity are given for each comparison.

| Average dissimilarity: 54.88<br>Species | AB index | NW index | Diss/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|
| *Eucalanus bungii* | 5.27 | 3.34 | 1.54 | 9.93 | 9.93 |
| *Centropages abdominalis* | 3.22 | 5.58 | 1.03 | 9.19 | 19.12 |
| Amphipod | 2.35 | 6.53 | 0.93 | 8.49 | 27.61 |
| *Metridia* spp. | 5.95 | 2.60 | 0.88 | 8.43 | 36.04 |
| Shrimp zoea | 1.96 | 6.96 | 0.85 | 8.41 | 44.45 |
| Capelin | 0.60 | 8.44 | 0.64 | 7.95 | 52.40 |
| Shrimp | 0.97 | 8.03 | 0.66 | 7.49 | 59.89 |
| Euphausiid | 4.01 | 4.72 | 1.07 | 7.34 | 67.24 |
| *Neocalanus* spp. II-IV | 5.36 | 3.24 | 0.87 | 7.30 | 74.54 |
| Gadid | 3.31 | 5.48 | 0.65 | 6.44 | 80.98 |
| *Acartia* spp. | 2.75 | 6.09 | 0.74 | 6.34 | 87.32 |
| *Calanus marshallae* | 4.34 | 4.36 | 1.51 | 4.76 | 92.08 |
| Average dissimilarity: 69.95<br>Species | June index | July index | Diss/SD | Contrib% | Cum.% |
| *Metridia* spp. | 0.66 | 9.63 | 0.97 | 11.12 | 11.12 |
| *Eucalanus bungii* | 4.71 | 7.14 | 1.55 | 10.60 | 21.72 |
| *Neocalanus* spp. II-IV | 9.63 | 3.72 | 1.80 | 8.75 | 30.47 |
| Gadid | 11.99 | 1.90 | 1.13 | 8.56 | 39.03 |
| Capelin | 0.17 | 11.99 | 0.75 | 8.44 | 47.46 |
| *Acartia* spp. | 0.63 | 8.37 | 1.80 | 7.68 | 55.14 |
| *Pseudocalanus* spp. V | 2.73 | 8.72 | 1.51 | 6.95 | 62.09 |
| Euphausiid | 4.62 | 6.63 | 1.34 | 6.42 | 68.51 |
| *Calanus marshallae* | 2.30 | 6.33 | 1.42 | 6.26 | 74.77 |
| Amphipod | 0.74 | 7.58 | 1.09 | 6.03 | 80.81 |
| Shrimp | 8.26 | 5.09 | 0.76 | 6.01 | 86.81 |
| *Centropages abdominalis* | 4.00 | 5.05 | 0.87 | 5.75 | 92.56 |
| Average dissimilarity: 69.92<br>Species | June index | August index | Diss/SD | Contrib% | Cum.% |
| Gadid | 11.99 | 0.11 | 1.37 | 16.52 | 16.52 |
| *Neocalanus* spp. II-IV | 9.63 | 0.35 | 1.08 | 13.32 | 29.84 |
| *Centropages abdominalis* | 4.00 | 3.95 | 1.17 | 9.55 | 39.38 |
| Shrimp zoea | 7.22 | 1.03 | 1.17 | 8.68 | 48.07 |
| *Eucalanus bungii* | 4.71 | 1.24 | 1.63 | 7.91 | 55.97 |
| *Calanus marshallae* | 2.30 | 4.16 | 1.21 | 7.50 | 63.48 |
| Shrimp | 8.26 | 0.18 | 0.70 | 6.96 | 70.44 |
| Amphipod | 0.74 | 4.27 | 1.12 | 6.56 | 77.00 |
| Euphausiid | 4.62 | 1.82 | 1.30 | 5.75 | 82.75 |
| *Acartia* spp. | 0.63 | 3.57 | 0.94 | 5.11 | 87.86 |
| *Pseudocalanus* spp. V | 2.73 | 1.39 | 1.31 | 4.17 | 92.03 |
| Average dissimilarity: 63.81<br>Species | July index | August index | Diss/SD | Contrib% | Cum.% |
| Capelin | 11.99 | 0.36 | 0.88 | 13.69 | 13.69 |
| *Metridia* spp. | 9.63 | 2.30 | 1.09 | 12.95 | 26.64 |
| *Pseudocalanus* spp. V | 8.72 | 1.39 | 2.20 | 9.67 | 36.31 |
| *Acartia* spp. | 8.37 | 3.57 | 1.70 | 8.12 | 44.43 |

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**Table 5.** (*Continued*)

| Average dissimilarity: 63.81<br>Species | July index | August index | Diss/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|
| Euphausiid | 6.63 | 1.82 | 1.57 | 8.07 | 52.50 |
| *Eucalanus bungii* | 7.14 | 1.24 | 1.00 | 7.92 | 60.42 |
| Amphipod | 7.58 | 4.27 | 1.08 | 7.41 | 67.83 |
| *Centropages abdominalis* | 5.05 | 3.95 | 1.18 | 7.17 | 75.00 |
| Shrimp zoea | 5.15 | 1.03 | 2.06 | 5.15 | 80.15 |
| Shrimp | 5.09 | 0.18 | 0.67 | 4.93 | 85.08 |
| *Neocalanus* spp. II-IV | 3.72 | 0.35 | 0.98 | 4.75 | 89.83 |
| *Calanus marshallae* | 6.33 | 4.16 | 1.55 | 4.25 | 94.08 |

Aialik Bay, over deeper water, in proximity to the glaciers, and where acoustic biomass was high (Tables 6 and 7). Coefficients for all predictor variables were significantly different from zero.

## DISCUSSION

We found cool, sediment-laden glacial meltwater is a primary feature structuring glacial fjord ecosystems during summer (see also Pickard and Stanton, 1980; Etherington et al., 2007). Glaciers contribute significant amounts of silty meltwater runoff, which creates a turbid stratified surface layer that prevents light penetration and provides nutrients for primary production. These features have important implications for food webs. Although the potential for primary production is enhanced by nutrients in glacial runoff (Hood and Scott, 2008; Hood et al., 2009), production appears restricted to the shallow surface layers because low light penetration hinders phytoplankton growth at depth (Piwosz et al., 2009). Similarly, low light conditions may affect the vertical migration habits of fishes and zooplankton (Abookire et al., 2002; Frank and 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 in glacial-marine ecosystems.

### *Glacial influence on fjord oceanographic conditions*

Low water clarity as a result of glacial runoff generally was constrained to the surface layer (5–9 m) near tidewater glaciers, and this is a common physical feature in glacial fjords elsewhere (Barron and Barron, 2005; Etherington et al., 2007; Kuletz et al., 2008).

**Figure 6.** Non-metric multidimensional scaling (MDS) of Bray–Curtis dissimilarities in community structure at trawl stations in Kenai Fjords, Alaska, summer 2008. Triangles represent Aialik Bay (black) and Northwestern Lagoon (gray) trawl samples, and numbers above symbols represent the month in which they were sampled (6 = June, 7 = July, 8 = August). Axis labels and arrows indicate the magnitude and direction (up = positive, down or left = negative) of significant Pearson correlation (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$) of environmental variables with MDS axis scores.

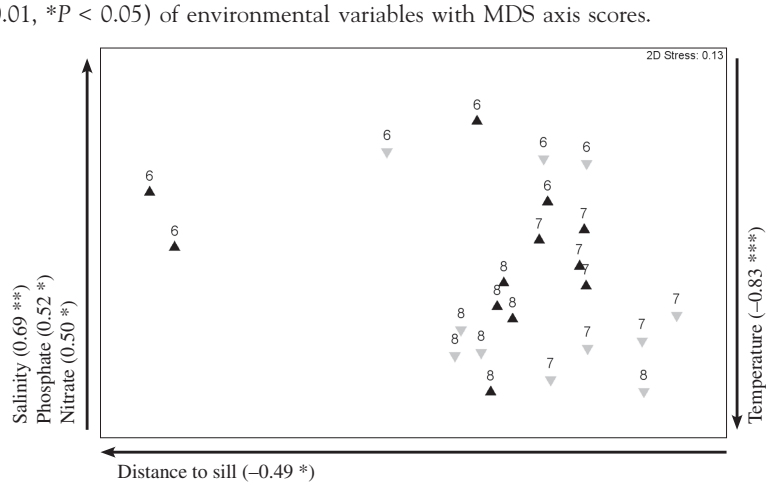



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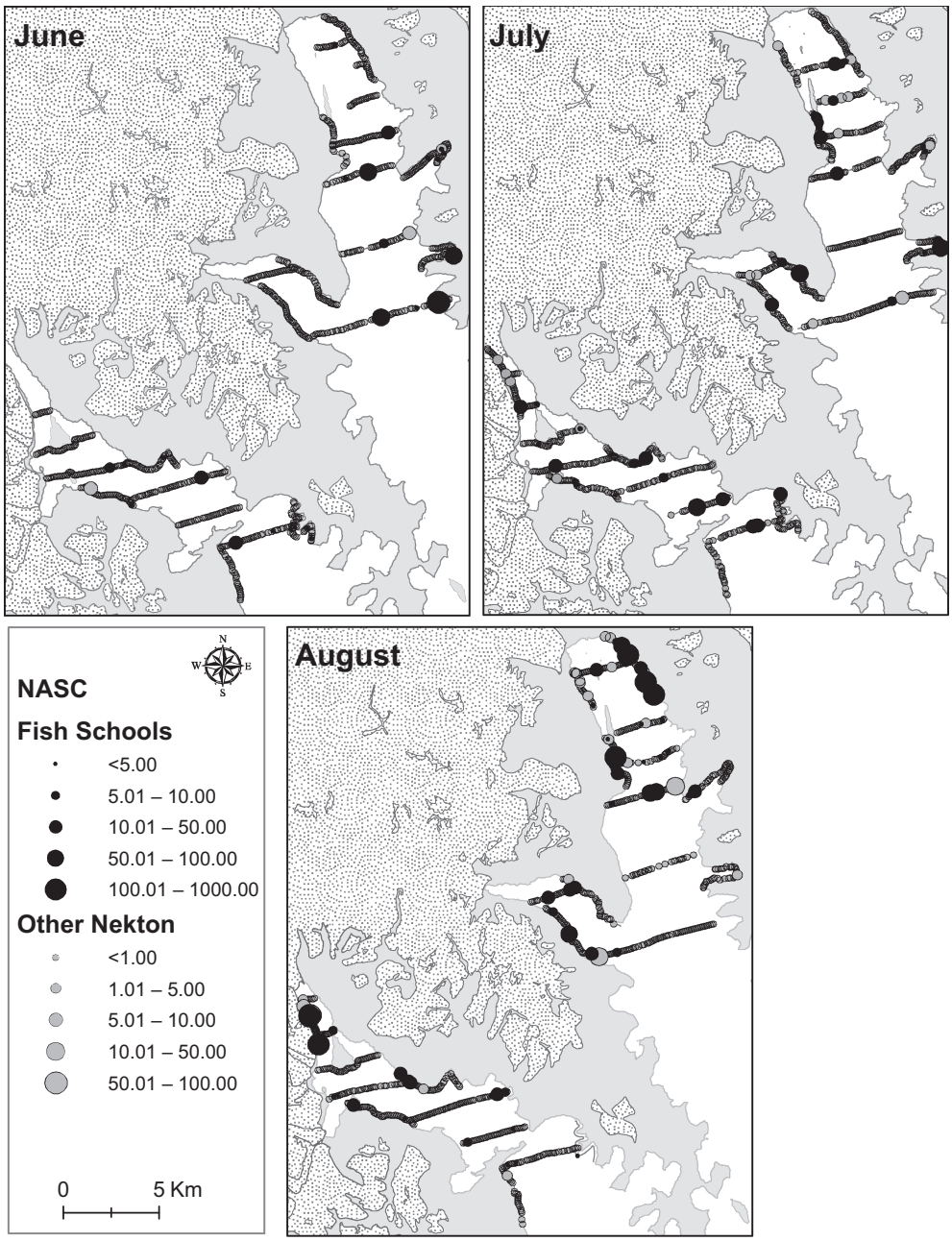
**Figure 7.** Monthly acoustic backscatter (nautical area scattering coefficient, NASC) during 2008 hydroacoustic surveys in Kenai Fjords, Alaska. Glacial extent is indicated as gray stipple.




However, immediately adjacent to Aialik Glacier, low water clarity was detected throughout the water column in July (Fig. 5), indicating greater subsurface sediment outflow as glacial melt increased throughout the summer warming period. This glacial plume effect was localized (<1 km from glacier) as near-surface water clarity was greater at stations further away from the glacier.

Vertical velocities indicative of upwelling and bathymetrically steered currents were detected in ADCP cross sections at marine sills (data not shown). It has been shown previously that variability in current speed (Etherington et al., 2007; Hill et al., 2009), and carbon transport from shelf waters into fjords and bays was dependent on bathymetric and topographic features such as marine sills (Gay and Vaughan, 2001),


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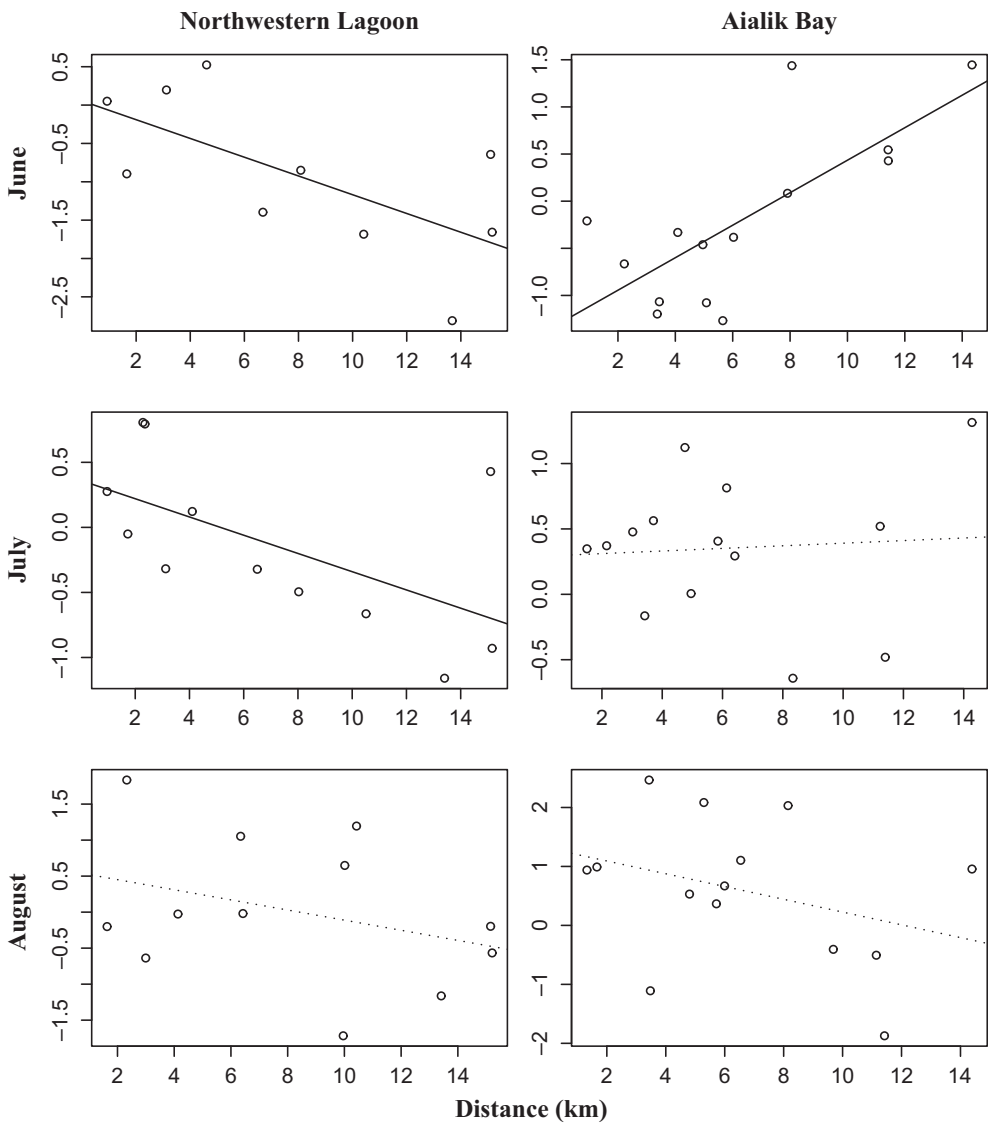
**Figure 8.** Acoustic backscatter (log-transformed nautical area scattering coefficient per killimeter) monthly response to distance from tidewater glaciers. Significant relationships ($P < 0.05$) are drawn as solid lines.




and our work further highlights the importance of these bathymetric features in regulating fjord oceanographic processes.

Spatial and temporal characteristics of phytoplankton abundance were influenced by local hydrographic regimes, such as sill depth and fjord orientation relative to the Alaska Coastal Current. For example, in Northwestern Lagoon, sill characteristics induced greater isolation from outer shelf waters and resulted in a more stable environment that promoted sustained chlorophyll *a* concentrations through the summer in glacial areas. In contrast, in Aialik Bay, lower chlorophyll *a* concentrations in glacial areas compared with distal areas during all sampling periods (Fig. 4) indicate that the chlorophyll *a* production there was most influenced by shelf waters. Similarly, local hydrographic regimes are responsible for dramatic differences between the bifurcated arms of Glacier Bay in southeast Alaska (Etherington et al., 2007; Arimitsu et al., 2008) and also between bays within Prince William Sound in southcentral Alaska (Gay and Vaughan, 2001).

*Near-surface euphausiids*

The near-surface occurrence of euphausiids during daylight hours was negatively related to the distance to


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**Table 6.** Delta Akaike's Information Criterion (Δ AIC), degrees of freedom (d.f.), and predictor variables included in the top candidate generalized linear models for Kittlitz's murrelet binomial response to habitat variables at the 400-m scale. Acoustic backscatter (Acoustic) data were log-transformed prior to analysis.

| Δ AIC | d.f. | Habitat variables |
|---|---|---|
| 0.00 | 5 | Depth + Acoustic + Glacier Distance + Fjord |
| 1.88 | 6 | Depth + Acoustic + Glacier Distance + Fjord + Transect Type |
| 3.11 | 5 | Acoustic + Glacier Distance + Fjord+ Transect Type |
| 3.52 | 7 | Salinity + Depth + Acoustic + Glacier Distance + Fjord + Transect Type |

**Table 7.** Parameter estimates for best fit model using generalized linear mixed models (GLMM) to relate Kittlitz's murrelet binomial response to marine habitat variables. Acoustic backscatter was log-transformed, and all continuous variables, were normalized prior to analysis to allow comparison of coefficients.

| | Coefficient | SE | *t* | *P* |
|---|---|---|---|---|
| Intercept | −8.7408 | 1.8674 | −4.68 | <0.001 |
| Depth | 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 | 6.9365 | 1.9259 | 3.60 | <0.01 |

turbid glacial outflows. Weslawski *et al.* (2000), who also found euphausiids were most abundant in surface waters near glaciers, suggest that macrozooplankton may become entrapped in inner fjord basins by physical processes such as estuarine circulation. Typically, euphausiid distribution in the water column is maintained by diel migration in response to light, coupled with their relatively strong swimming abilities (Zhou et al., 2005).

It is likely that once entrained in glacial areas, the distribution of euphausiids in the surface waters was influenced by turbid glacial outflows that inhibited a photic cue for diel vertical migration. However, there are several alternative explanations for the near-surface occurrence of euphausiids that are independent of a photic cue, such as reproductive behavior, net avoidance in clear water, or subsurface upwelling near submerged tidewater glaciers. Euphausiids may swarm to reproduce in surface waters during daylight hours (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). The most abundant species collected within Kenai Fjords was *T. inermis*, which usually reproduces between April and May (Pinchuk et al., 2008), earlier than the commencement of our sampling. Euphausiids collected in Northwestern Lagoon in July 2007 had spawned previously but were not actively reproducing at the time of capture (samples verified by A. Pinchuk, University of Alaska Fairbanks). Thus we rule out reproductive behavior as a cause of this phenomenon. Moreover, subsurface glacial outflow can cause local upwelling, or 'brown zones' near the face of tidewater glaciers that bring biomass to the surface and can be an important physical structuring mechanism for zooplankton (Hartley and Dunbar, 1938). We found that many tidewater glaciers in Kenai Fjords are currently grounded at low tide and subsurface outflow is too localized to account for the observed distribution of near-surface euphausiids (Figs 2 and 5). Finally, net avoidance in clear water could explain higher CPUE of euphausiids in turbid water; however, a trawl net large enough (mouth opening of 50 $m^2$) to rule out net avoidance was used in another study where high abundance of euphausiids near tidewater glaciers occurred in surface waters (Robards et al., 2003, J. Piatt, unpublished data).

Furthermore, our hypothesis that the near-surface occurrence of marine organisms that typically undergo diel vertical migrations may be due to the lack of a photic cue beneath turbid glacial outflows is supported by other work. For example, Carpenter (1983) also found shrimp and other zooplankton were abundant throughout the water column near the face of Aialik Glacier, whereas these crustaceans were collected only in deeper water during the day at the marine sill just 10 km away. Abookire *et al.* (2002) also speculated that low light conditions explained the daytime presence of mesopelagic fishes in the turbid surface waters in Glacier Bay.

### *Spatial and temporal patterns of seabird prey*

Lower acoustic backscatter in June compared with July and August suggests there was a lagged response by forage fish to marine production at lower trophic levels. The pattern of higher prey abundance later in the summer may result from migratory patterns consistent with inshore spawning (Robards et al., 1999), and greater copepod availability following the spring bloom


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in April–May (Eslinger et al., 2001; Coyle and Pinchuk, 2003).

Patterns of acoustic backscatter varied spatially as well. Greater abundance of weak scattering organisms (e.g. zooplankton and loose aggregations of forage fish) in the upper 40 m of the water-column in glacial waters was a driver of the negative relationship between biomass and distance to glaciers in Northwestern Lagoon. The relationship between acoustic backscatter and distance to glaciers 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. However, in the middle and late summer, dense forage fish schools moved into glacial areas of Aialik Bay (Fig. 7), a seasonal pattern that is consistent with studies of forage fishes in nearshore areas of Alaska (Robards et al., 1999).

We found that capelin, an important forage species for marine predators and indicator of marine climate (Brown, 2002; Rose, 2005; Arimitsu et al., 2008), spawned on beaches and also used the fjords as a nursery area. The capelin spawning period was synchronous in Kenai Fjords during 2008 sampling; larval capelin were an order of magnitude more abundant in trawl catches during July than they were in other months (Table 5), and there was little variation in length frequency (Table 4). In contrast, the spawn timing for capelin was protracted in Glacier Bay (about 450 km to the southeast), with spatial and temporal variation in maturation of ripe females and wide variation in larval length frequencies during the summer months (Arimitsu et al., 2008). Spawning capelin may therefore be available to marine predators for a shorter duration in Kenai Fjords compared with Glacier Bay.

### *Kittlitz's murrelet foraging habitat*

Concurrent hydroacoustic and bird survey data indicated Kittlitz's murrelets were associated with greater availability of forage fish and euphausiids that occurred in the turbid glacial plume near tidewater glaciers. The near-surface availability of euphausiids near glacial stream outflows likely influenced the at-sea distribution of Kittlitz's murrelets, as euphausiids are known to be a significant component of adult murrelet diets in the Northern Gulf of Alaska (Sanger, 1987; Hobson et al., 1994; Day et al., 1999). Furthermore, the availability of euphausiids in the surface waters may have offered a prey resource at an efficient foraging depth as the mean depth of dense forage fish schools approached the maximum diving depth of murrelets.

Dense schools of forage fish moved into the inner fjords by August, and this temporal pattern would increase prey availability for murrelet chicks with high energetic demands prior to fledging in mid- to late summer. The timing of the influx of dense forage fish into glacial areas is important because although adult murrelets may forage substantially on plankton, chicks feed exclusively on fish brought to the nest by the parents (Day et al., 1999). Higher turbidity near the glaciers may increase the availability of loosely aggregated fish prey because visual cues that aid in dense schooling behavior or predator avoidance may be suppressed in very turbid water (Partridge and Pitcher, 1980).

In Kenai Fjords and elsewhere, Kittlitz's murrelets are associated with areas where floating ice occurs (Day et al., 2000, 2003; this study). The presence of tidewater glaciers and the floating ice they shed 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 outflow of sediment-laden freshwater from glacial streams and a downstream increase in availability of certain near-surface prey. Indeed, in some areas Kittlitz's murrelets are associated with glacier river outflows from wholly land-locked glaciers where floating ice does not occur at sea. They also breed in locations where glaciers are only small remnants of their former size (e.g. Kodiak Island, Unalaska Island), found on high volcanic slopes (e.g. Alaska Peninsula), or no longer exist (e.g. Agattu Island, Seward Peninsula) (Kaler et al., 2009; Day et al., 2011; Madison et al., 2011).

## CONCLUSION

Tidewater glaciers create unique and productive marine habitats. In these ecosystems, cold, sediment-laden glacier meltwater is a shaping feature that influences food webs in these fjord ecosystems. Glacier runoff provides nutrients and contributes to stratification necessary for phytoplankton production. However, low light availability limits phytoplankton in proximity to turbid glacial plumes and the lack of a photic cue may enhance near-surface zooplankton abundance by suppressing diel vertical migration. Marine sills created by historical locations of tidewater glacier termini are key structural features that promote mixing of inner fjord waters with oceanic waters, and thus facilitate transport of nutrients, plankton, and forage species from shelf waters into glacial areas. Glacial fjords in Alaska provide important spawning habitat and nursery areas for forage fish such as capelin


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and this in turn creates prime foraging habitat for marine predators.

In the coming decades, we expect glacial-marine habitats to experience dramatic changes in sedimentation rate (Hood and Scott, 2008), freshwater input (Neal et al., 2002; Di Lorenzo et al., 2009), stratification (Bernal, 1991; Weingartner et al., 2009) and temperature (Harley et al., 2006), which will undoubtedly impact food webs in these systems. In this paper we examined glacial influence on ocean conditions and foraging habitat of the Kittlitz's murrelet, an example of a species with a strong association to glacial-marine ecosystems. Along with continued monitoring of indicator species populations, a better understanding of ecosystem functioning within glacial fjords will enhance our ability to discern natural and anthropogenic causes for changes in marine food webs.

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**APPENDIX.** Zooplankton species, frequency of occurrence at stations (FO), mean biomass (mg $m^{-3}$), and standard error (SE) at stations sampled with a 1.8-m Isaacs–Kidd midwater trawl in Kenai Fjords during summer 2008. Species are arranged in taxonomic order.

| Taxon | Species | FO | Mean biomass | SE |
|---|---|---|---|---|
| Cnidarian | *Corymorpha* sp. | 0.09 | 0.006 | 0.004 |
| | *Coryne pinceps* | 0.57 | 0.667 | 0.210 |
| | *Bougainvillia* sp. | 0.48 | 0.848 | 0.374 |
| | *Perigonimus* sp. | 0.30 | 0.104 | 0.046 |
| | *Proboscidactyla flavicirrata* | 0.57 | 0.188 | 0.059 |
| | *Rathkea* sp. | 0.17 | 0.001 | 0.001 |
| | *Aequorea* sp. | 0.09 | 0.075 | 0.055 |
| | *Eirene indicans* | 0.78 | 2.639 | 0.991 |
| | Siphonophore | 0.09 | 0.200 | 0.138 |
| | *Aglantha digitale* | 0.65 | 0.730 | 0.453 |
| Gastropod | *Corolla* sp. | 0.09 | 0.009 | 0.006 |
| | *Limiacina helicina* | 0.91 | 0.102 | 0.031 |
| Cladoceran | *Evadne* sp. | 0.09 | 0.000 | 0.000 |
| | *Podon* sp. | 0.35 | 0.008 | 0.003 |
| Decapod | Lithodidae | 0.04 | 0.000 | 0.000 |
| | Paguridae | 0.87 | 0.068 | 0.019 |
| | Brachyura | 0.22 | 0.007 | 0.004 |
| | Oregoniidae | 0.26 | 0.002 | 0.001 |
| | *Hyas* sp. | 0.17 | 0.057 | 0.031 |
| | Pisidae | 0.43 | 0.002 | 0.001 |
| | Pinnotheridae | 0.17 | 0.005 | 0.003 |
| | Hippolytidae | 0.83 | 0.476 | 0.182 |
| | Crangonidae | 0.17 | 0.014 | 0.011 |
| | Pandalidae | 0.26 | 0.072 | 0.057 |
| | *Pandalopsis dispar* | 0.52 | 1.504 | 0.880 |
| | *Pandalus* sp. | 0.17 | 0.354 | 0.348 |
| | *Pandalus platyceros* | 0.17 | 0.032 | 0.024 |
| | *Pasiphaea pacifica* | 0.04 | 0.001 | 0.001 |

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**APPENDIX.** (*Continued*)

| Taxon | Species | FO | Mean biomass | SE |
|---|---|---|---|---|
| Euphausiid | Euphausiid (unidentified) | 0.96 | 0.645 | 0.205 |
| | *Euphausia pacifica* | 0.13 | 0.369 | 0.363 |
| | *Thysanoessa* sp. | 0.04 | 0.024 | 0.024 |
| | *Thysanoessa inermis* | 0.39 | 0.875 | 0.552 |
| | *Thysanoessa longipes* | 0.04 | 0.002 | 0.002 |
| | *Thysanoessa raschii* | 0.04 | 0.376 | 0.376 |
| | *Thysanoessa spinifera* | 0.22 | 0.129 | 0.117 |
| Amphipod | *Cyphocaris challengeri* | 0.22 | 0.079 | 0.069 |
| | *Gammarus* sp. | 0.09 | 0.016 | 0.013 |
| | *Hyperia meduserum* | 0.09 | 0.002 | 0.001 |
| | *Hyperoche meduserum* | 0.04 | 0.002 | 0.002 |
| | *Themisto* sp. | 0.74 | 0.048 | 0.018 |
| | *Themisto libellula* | 0.48 | 0.287 | 0.209 |
| | *Themisto pacifica* | 0.04 | 0.003 | 0.003 |
| | *Primno macropa* | 0.22 | 0.006 | 0.004 |
| Cumacean | Cumacea | 0.04 | 0.000 | 0.000 |
| Copepod | *Acartia longirmis* | 0.96 | 0.177 | 0.078 |
| | *Acartia tumida* | 0.09 | 0.001 | 0.001 |
| | *Calanus marshallae* | 0.91 | 4.212 | 1.073 |
| | *Calanus pacificus* | 0.13 | 0.003 | 0.002 |
| | *Neocalanus* sp. | 0.04 | 0.001 | 0.001 |
| | *Neocalanus cristatus* | 0.39 | 0.106 | 0.047 |
| | *Neocalanus flemingeri* | 0.26 | 0.461 | 0.248 |
| | *Neocalanus plumchrus* | 0.65 | 0.589 | 0.206 |
| | *Centropages abdominalis* | 0.61 | 0.018 | 0.006 |
| | *Pseudocalanus* spp. | 0.96 | 0.178 | 0.053 |
| | *Eucalanus bungii* | 0.87 | 0.588 | 0.193 |
| | *Metridia okhotensis* | 0.13 | 0.039 | 0.037 |
| | *Metridia pacifica* | 0.65 | 0.121 | 0.052 |
| | *Epilabidocera amphitrites* | 0.13 | 0.002 | 0.001 |
| | *Oithona similis* | 0.04 | 0.000 | 0.000 |
| | *Oithona spinirastra* | 0.04 | 0.000 | 0.000 |
| Arthropod | Cirripedia | 0.13 | 0.001 | 0.000 |
| | Diptera | 0.04 | 0.001 | 0.001 |
| | Tipulidae | 0.09 | 0.005 | 0.004 |
| | *Ctenophora* | 0.04 | 0.007 | 0.007 |
| Chaetognath | *Parasagitta elegans* | 0.87 | 8.378 | 4.951 |
| | *Eukrohnia hamata* | 0.04 | 0.001 | 0.001 |
| Larvacean | *Oikopleura* sp. | 0.65 | 0.079 | 0.030 |
| Tunicate | *Salpa* sp. | 0.04 | 0.000 | 0.000 |

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