*Exxon Valdez* Oil Spill
Restoration Project Final Report


At-sea Ecological Segregation and Overlap of *Brachyramphus* murrelets
in Prince William Sound, Alaska


Restoration Project 00516
Final Report


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**Study History:**  This project, which was initiated in 2000, investigated at-sea habitat use and ecological segregation and overlap in two closely related species of *Brachyramphus* murrelets (Kittlitz's *B. brevirostris* and Marbled B. *marmoratus*) in Prince William Sound.  This study used an extant data set (from Restoration Projects 96142–98142) collected in four bays in the glaciated fjords of the northwestern Sound to describe and compare habitat use between the two species in 1996–1998.

**Abstract:**  We compared at-sea habitat use, niche overlap, and morphological differentiation in Kittlitz's (*Brachyramphus brevirostris*) and Marbled (*B. marmoratus*) murrelets in Prince William Sound in 1996-1998.  Within bays, Kittlitz's Murrelets' distribution diverged the most from randomness for habitat type and Secchi depth; they occurred with greater probability as ice cover increased, water became more turbid, water depth increased, and distance to shore decreased. Marbled Murrelets diverged the most from randomness for habitat type, ice cover, and sea-surface temperatures and occurred with greater probability as ice cover decreased, water became less turbid, salinity increased, water depth decreased, and distance to shore increased.  The probability of birds being Kittlitz's Murrelets was determined most strongly by Secchi depth.  Marbled Murrelets had the least niche overlap with Kittlitz's Murrelets in Secchi depth and sea-surface temperature, whereas Kittlitz's Murrelets had the least overlap with Marbled Murrelets in habitat type and Secchi depth.  Kittlitz's Murrelets occurred in more turbid water than Marbled Murrelets did and had eyes that were significantly proportionately larger than those of Marbled Murrelets. We propose that the primary ecological isolating mechanism between these congeners is water clarity, with Kittlitz's Murrelets being adapted for turbid water and Marbled Murrelets being adapted for clear water.

**Key Words:**  Alaska, *Brachyramphus*, ecological overlap, ecological segregation, *Exxon Valdez* oil spill, habitat use, Kittlitz's Murrelet, Marbled Murrelet, Prince William Sound.

**Project Data:** *Description of data*—Data files consist of (1) a file for all nearshore bay-visits in 1996–1998; (2) a file of morphological measurements; and (3) digital maps of each bay with locations of groups of birds.  *Format*—Numerical and descriptive data were keypunched in *Microsoft Excel*, and maps and locations of birds were digitized in the GIS software *ArcView*. *Availability*—Data from this study are archived at ABR, Inc. (P.O. Box 80410, Fairbanks, AK 99708-0410) under Project 00-311.  Robert H. Day (bday@abrinc.com; PH 907-455-67777) is the custodian of these data, and all questions and requests should be made to him.

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ECOLOGICAL SPECIALIZATION AND OVERLAP OF *BRACHYRAMPHUS*

MURRELETS IN PRINCE WILLIAM SOUND, ALASKA

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ABSTRACT.—We compared habitat use, niche overlap, and morphological differentiation in the closely related seabirds Kittlitz's (*Brachyramphus brevirostris*) and Marbled (*B. marmoratus*) murrelets in nearshore waters of Prince William Sound, Alaska, in 1996–1998. Within bays, the distribution of Kittlitz's Murrelets diverged the most from randomness for the variables habitat type (preferring [i.e., using significantly more than what is available] glacial-affected and glacial-stream-affected habitats) and water clarity (preferring highly turbid water), whereas the distribution of Marbled Murrelets diverged the most from randomness for the variables habitat type (preferring glacial-unaffected habitats), ice cover (preferring area of no ice), and sea-surface temperature (preferring SST's ≥6°C). The probability of a group of birds being Kittlitz's Murrelets was determined most strongly by water clarity. Kittlitz's Murrelets were more common in College and Harriman fjords than in the other bays and more common in early and mid-summer than in late summer; the reverse was true for Marbled Murrelets. Marbled Murrelets had the least niche overlap with Kittlitz's Murrelets in water clarity and SST, whereas Kittlitz's Murrelets had the least overlap with Marbled Murrelets in water clarity and habitat type. Similarly, Kittlitz's Murrelets occurred in water significantly more turbid than did Marbled Murrelets in three of four habitat types. Morphologically, Kittlitz's Murrelets had eyes that were significantly larger in proportional size than did those of Marbled Murrelets. We propose that these two species are specialized for foraging in different water types, with Kittlitz's Murrelets specialized for more turbid water of glacial origin that has led to optical specialization.

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**INTRODUCTION**

The closely related seabirds Kittlitz's (*Brachyramphus brevirostris*) and Marbled (*B. marmoratus*) murrelets overlap in range across southern Alaska (Gaston and Jones 1998). The Kittlitz's Murrelet is a boreal–low-arctic species, whereas the Marbled Murrelet is a northeastern Pacific temperate–boreal species (Gaston and Jones 1998). Both are mottled brown in summer, and both are small-bodied, nearshore feeders with bills and tongues that are adapted for feeding primarily on fishes (Bédard 1969, 1985).

Although much has finally been learned about their specializations in nesting-habitat use of these two species (Day et al. 1983, 1999; Ralph et al. 1995, Nelson 1997), data on feeding ecology and feeding habitat use are limited. The few comparative data on the feeding biology of these piscivorous species suggest that they overlap extensively in diet; however, Kittlitz's Murrelets eat proportionately more invertebrates than Marbled Murrelets do (Sanger 1987, Day et al. 1999, Day and Nigro 2000). Examination of habitat use for foraging suggests that these two species exhibit extensive overlap in many aspects (e.g., similar preferences for shallow foraging depths, decreased foraging effort as ice cover increases), with the primary differences related to preferences for specific habitat types (e.g., preference of Kittlitz's Murrelets for feeding in waters of glacial origin, preference of Marbled Murrelets for feeding in marine-sill habitats) that suggest that Kittlitz's Murrelets are more closely associated with glacial-derived water than Marbled Murrelets are (Day and Nigro 2000). The two species also exhibit extensive overlap in dive times and time of day of foraging and some overlap in tendency to participate in mixed-species feeding flocks (Day and Nigro 2000).

Data on macroscale at-sea habitat use in these two congeners are limited but suggest little overlap. At a regional scale, most of the Kittlitz's Murrelet population summers primarily near glaciated fjords in the Gulf of Alaska, with the remainder occurring in the Bering and Chukchi seas in areas that formerly were glaciated during the Pleistocene (Day et al. 1999, Piatt et al. 1999). As such, their at-sea habitat use has been described as involving primarily icebergs and protected bays (Day et al. 1999); however, the only quantitative analysis of any aspects of at-sea habitat use has considered just a few habitat variables (Day et al. 2000). Marbled Murrelets are associated primarily with protected bays and fjords, especially those in the vicinity of suitable nesting trees, and exhibit no association with glaciation (Nelson 1997). Recent sampling in the glaciated fjords of Prince William Sound, Alaska, however, has found large numbers of Marbled Murrelets (Day and Nigro, unpublished data), suggesting that this species' avoidance of glaciers is not as pronounced as has been believed. No quantitative data have been presented on nearshore habitat use by Marbled Murrelets, and nearshore habitat use of these two congeners has not been compared quantitatively.

While studying the ecology of Kittlitz's Murrelets in glaciated fjords in Prince William Sound, field observations suggested to us that Kittlitz's and Marbled murrelets generally occurred and foraged in waters that differed in origin and characteristics. In addition, it appeared to us that the eyes of the two species were noticeably different in size, suggesting a possible relationship between aspects of foraging ecology or habitat use and optical characteristics. This study describes nearshore habitat use and niche overlap and examines the relationship between nearshore habitat use and morphology of these two species within glaciated fjords.

**METHODS**
**Study area**
Prince William Sound is a large, estuarine embayment of the northern Gulf of Alaska (Fig. 1). The central and northern Sound is either glaciated or recently deglaciated and consists of numerous fjords and complex, mostly rocky shorelines (Isleib and Kessel 1973). The region has cool temperatures and frequent precipitation, fog, heavy cloud cover, and strong winds (Wilson and Overland 1986). Most deglaciated areas are ice-free all year, although glaciated fjords are at least partially covered with glacial ice most of the year. Fresh water enters the Sound from glaciers, rivers, and precipitation and mixes with the Alaska Coastal Current, especially in the southern and central Sound (Niebauer et al. 1994). The glaciated fjords and the northern Sound are characterized by marine waters with an overlying low-salinity layer resulting from extensive freshwater input in the summer and fall.

The four study bays, which were located in the northwestern quarter of the Sound (Fig. 1), are believed to contain a significant percentage of the Kittlitz's Murrelets in the Sound (Isleib and Kessel 1973, Kendall and Agler 1998, Day et al. 1999) and contain large numbers of Marbled Murrelets at times (Day and Nigro, unpublished data). These four glaciated fjords generally are deep and have 1–5 tidewater and several hanging glaciers (i.e., glaciers that have retreated from tidewater) each. The terrestrial vegetation consists of conifers and shrubs at low elevations and toward the mouths of the bays, forbs at moderate elevations, and bare rock and permanent snowfields above ~750 m elevation and near recent deglaciation. Shorelines consist of bedrock, various sizes of alluvium, or ice.

Those parts of the nearshore zone in the four bays that we sampled varied in area between 11.3 km$^2$ (Unakwik Inlet) and 15.6 km$^2$ (Harriman Fjord). One bay had one tidewater glacier (Unakwik Inlet), one had two (Blackstone Bay), and two had five each (College and Harriman fjords). All four bays had glacial-fed streams from both tidewater and hanging glaciers, and two bays (Unakwik Inlet and Blackstone Bay) had shallow marine sills created as terminal moraines of tidewater glaciers that since have retreated. Glacial-unaffected habitat represented 64% of the combined area of the nearshore zone, followed by glacial-stream-affected habitat (23%), glacial-affected habitat (9%), and marine-sill-affected habitat (4%).

**Data collection**
In 1996–1998, we studied Kittlitz's and Marbled murrelets during two 20-day research cruises/ year conducted from ~25 May to ~20 June (early summer) and from ~15 July to ~15 August (late summer). In 1998, we also had a mid-summer cruise, running from 28 June to 5 July. We sampled each bay 2–4 times during each early- and late-summer cruise and once during the mid-summer cruise.

We sampled the inner two-thirds of the bay in two of the four study bays (Unakwik Inlet, College Fjord) and nearly the entire bay in the others. During each sampling visit, we conducted nearshore surveys that measured densities in each bay, sampling 100% of the nearshore zone (waters ≤200 m from shore). Although we also used offshore surveys to sample murrelets >200 m from shore (following Day et al. 1995, 1997), the nearshore zone is where the most feeding in both species occurs (Day and Nigro 2000) and where the most habitat variation occurs; hence, we consider here only the results of analyses for the nearshore zone.

Following Day et al. (1997) and Kendall and Agler (1998), we boated ~100 m from shore and counted and mapped locations of all murrelets seen ≤200 m from shore or flying over this zone, including those flushing ≤300 m ahead of the boat. Each survey resulted in a count of the number of murrelets for each nearshore segment-visit. Segments were along-shore sections of the nearshore zone into which we had stratified the bays' waters for habitat analyses; we measured the length and area of each segment from digitized maps with GIS software. Each bay was divided into 20–30 nearshore segments of different sizes, ranging from 0.75 to 9.45 km in length (mean 2.84 km; n = 99) and from 0.11 to 1.72 km$^2$ (mean 0.54 km$^2$; n = 99) in area.

*Habitat characterization.*—We classified each nearshore segment into one of four habitat types that had been determined *a priori* and that reflected a generally decreasing influence of glaciers on the nearby marine habitat: glacial-affected (≤200 m from a tidewater glacier); glacial-stream-affected (>200 m from a tidewater glacier but with ≥1 glacial meltwater stream entering the segment); marine-sill-affected (>200 m from a tidewater glacier but ≤200 m from a marine sill); and glacial-unaffected (having none of these characteristics). If a segment had two characteristics of different glacial influence (e.g., both a tidewater glacier and glacial streams), we classified it as that of the stronger characteristic (i.e., glacial-affected).

For each nearshore segment-visit, we recorded several variables that varied both geographically and temporally: ice cover, water clarity (Secchi depth), sea-surface temperature (SST), and sea-surface salinity (SSS). Following Day and Nigro (2000), we estimated percent ice cover for each segment as a whole (0%, <1%, 1%, 3%, or 5–100% in 5% increments) and assigned the Secchi depth (measured to the nearest 0.5 m), SST (measured at 0.5 m depth to the nearest 0.1°C), and SSS (measured at 0.5 m depth to the nearest 0.1‰) measured at the beginning of each segment as the Secchi depth, SST, and SSS for all of the birds on that segment-visit. We also assigned the mean water depth (m) for a segment as the depth in which all of the birds on that segment were found; measurements were made with either a ship's fathometer or a hand-held fathometer (Day and Nigro 2000).

For each mapped nearshore observation, we used GIS software (ArcView v.3.1) to calculate the distance from shore (to the nearest 1 m) and the distance to nearest fresh water (same) and to classify the nearest shoreline substrate (following Day and Nigro 2000). We calculated the distance from the nearest fresh water from digitized maps of "significant" inputs (i.e., streams or larger) of fresh water in each bay (Day and Nigro 2000); because fresh water flowed through and under glaciers, entire faces of tidewater glaciers were considered to have "significant" inputs of fresh water. We mapped and digitized shoreline substrate as four main categories—bedrock, large alluvium (cobble, boulder), fine alluvium (mud, sand, gravel), and ice (along the faces of tidewater glaciers)—in ArcView and classified each bird as being nearest one substrate type (Day and Nigro 2000).

*Optical differentiation.*—We measured museum skeletons of Kittlitz's and Marbled murrelets to determine skull and orbit characteristics, with the latter being used as an indicator of eye size. To minimize possible effects of geographic variation on analyses, we used specimens collected only from the northern Gulf of Alaska (Prince William Sound to Kodiak Island). We measured (to the nearest 0.1 mm) the diameter of the orbit from the lower end of the *Prominentia cerebellaris* to the notch of the *Os lacrimale* ("orbit diameter"), the total length of the skull including the bill

("total head length"), and the length of the skull excluding the bill ("post-bill head length") from the back of the skull to the notch of the *Os lacrimale*. Other attributes, such as the inner diameter of the sclerotic rings, would have been useful, but the amount of skeletal material of these two species was too limited for adequate sample sizes of these other attributes.

**Data analysis**
Values reported below in the "Results" section are mean ± 1 SE. All statistical tests were two-tailed, with $\alpha = 0.05$.

In most analyses, we used a suite of nine nearshore habitat variables that included habitat type, ice cover, water clarity (Secchi depth), SST, SSS, water depth, distance to shoreline, distance to fresh water, and shoreline substrate. Water clarity and SSS were not measured in 1996, so that year's data were dropped from the logistic regression analyses; they were, however, included in all other analyses. In the logistic regressions, we also excluded SST because of collinearity with ice cover and excluded shoreline substrate because of collinearity with habitat type. Logistic regression was the only analysis that included >1 variable at a time, so it was the only one for which we needed to be concerned about collinearity of variables.

Although habitat type was, to some extent, associated with particular values (e.g., glacial habitats tended to have cooler, more turbid, and icier water), the relationship was far from perfect because winds and currents sometimes moved waters among segments on hourly, tidal, and daily scales. For example, a glacial-unaffected segment may have had cold, turbid, and/or icy water flow into it from a nearby glacial-affected segment, and winds and tidal currents easily moved ice throughout the bays. Not surprisingly, none of the other variables exhibited collinearity with habitat type. Hence, we retained habitat type in the analyses.

*Within-species habitat use versus availability.*—We compared habitat use and availability for each species in 1996–1998. For this analysis, we first generated random points ≤200 m from shore for each species, then compared those with the actual set of data points; numbers of random points were equal to the number of observations of each species in each site (bay) on each visit. This random data set represents a hypothetical population in which murrelets were distributed similarly with respect to bay, season, year, and visit but were randomly distributed with respect to specific areas within a bay. Any difference between random and actual locations therefore should represent nonrandom use of specific locations within a bay.

We generated random points with ArcView GIS software and calculated distance to shore, distance to nearest fresh water, and nearest shoreline substrate for each point. We also assigned the appropriate segment-level habitat type to each point. During some visits, several segments had 100% ice cover, a habitat characteristic in which we never recorded murrelets of either species (Day and Nigro, unpublished data). Hence, if a point fell in a segment with 100% ice cover, we discarded that point and selected a new random point for that visit.

After we partitioned all continuous variables into four categories, we conducted Likelihood-ratio Chi-square tests separately for each habitat variable to test for differences between random and actual locations for each species and habitat variable; we used Bonferroni multiple comparisons to test differences (Marcum and Loftsgaarden 1980). The null hypothesis was that birds were

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occupying locations within a bay randomly with respect to each habitat variable. In the context of this paper, "preference" indicates that a species uses a particular resource category significantly more than randomly, and "avoidance" refers to using a particular habitat variable significantly less than randomly. These terms do not imply behavioral preferences.

We also used a logistic regression for each species to compare the relative influence of all habitat variables together in predicting actual locations in 1997–1998. The dependent variable was coded as a random (0) or actual (1) data point before testing whether we could use the independent variables to distinguish between random and actual points. Independent variables included habitat type, ln ice cover, ln Secchi depth, SSS, water depth, distance to shore, and distance to fresh water. For each species, the null hypothesis was that habitat variables had no effect on our ability to predict actual locations within a bay.

*Comparative habitat use.*—We conducted a logistic regression on all murrelet groups observed during nearshore surveys in 1997–1998 to use habitat and other variables to predict the probability that a given murrelet group would be of a particular species. The dependent variable was species. Independent variables included the habitat variables (habitat type, ice cover, water clarity, SSS, depth, distance to shore, and distance to fresh water), site (Blackstone Bay, College Fjord, Harriman Fjord, and Unakwik Inlet), year (1997 and 1998), and season (early, mid-, and late summer). In the earlier logistic regressions, site, year, and season were accounted for during the original random-point-generation procedure. The null hypothesis was that habitat and other variables could not be used to predict the identity of a murrelet group. We also calculated mean ± 1 SE habitat characteristics for each species for those variables that were continuous.

*Niche width and niche overlap.*—We calculated niche width and niche overlap for each of the nine habitat variables based on the proportional use of each category. Following Hespenheide (1975), we calculated niche width (B) as $1/(\Sigma p_i^2)$, and niche overlap($\alpha$) as $(\Sigma p_i p_j)/(\Sigma p_i^2)$.

Because the results of the niche-overlap calculations indicated that the two species exhibited little overlap in water clarity (see Results), we investigated further the clarity relationships of these two species. We calculated mean available Secchi depths by habitat type and tested for differences in mean water clarity among habitat types with a one-factor ANOVA. The null hypothesis was that water clarity did not differ by habitat type. We also calculated mean Secchi depths used by each species in each habitat type and tested for differences in ln water clarity between species with a separate *t*-test for each habitat type; for these tests, we made a Bonferroni adjustment to $\alpha$ by dividing our standard $\alpha$ level by the number of tests (4) to determine our new significance level (following Neter et al. 1990). We then back-transformed the mean values as geometric means for each species and habitat type.

*Optical differentiation.*—For each skeletal specimen, we calculated proportions of the total head length and of the total post-bill head length occupied by the orbit diameter. The latter attribute also was used because of the difference between the two species in bill length. We used *t*-tests to test for differences between species in the two proportional measurements; prior to conducting the tests, we arcsine-transformed the data. In both tests, the null hypothesis was that mean proportions did not differ between species.

**RESULTS**
**Within-species habitat use versus availability**
Kittlitz's Murrelets exhibited non-random distribution with respect to all nine habitat variables. Although all variables were significant (P < 0.001 for all), Kittlitz's Murrelets exhibited the greatest divergence from randomness for habitat type and water clarity, as indicated by the largest Chi-square values. They preferred glacial-affected and glacial-stream-affected habitats and avoided marine sills and glacial-unaffected habitats (Fig. 2). They preferred areas with 0.5–45% ice, water clarity <1 m (i.e., highly turbid water), SST's of 3–6°C, and SSS's 10–17‰ and avoided areas with 0% ice, water clarity ≥1 m, SST's >9°C, and SSS's 17–24‰ (Figs. 3–6). Kittlitz's Murrelets also preferred water depths 41–60 m, areas 51–100 m from shore and ≤250 m from fresh water, and icy shoreline substrates; they avoided water depths 0–40 m, areas >150 m from shore and >250 m from fresh water, and both large- and fine-alluvium shoreline substrates (Figs. 7–10).

With the use of all habitat variables together, we correctly classified Kittlitz's Murrelet locations versus random points 66.2% of the time. Habitat type was the most important variable determining the distribution of Kittlitz's Murrelets within bays, as indicated by the large likelihood ratio (Tables 1 and 2). They occurred with higher probability than expected in glacial-affected and glacial-stream-affected habitats and with lower probability in marine-sill-affected and glacial-unaffected habitats. They occurred with higher probability than expected as ice cover increased, water became more turbid, water depth increased, and distance to shore decreased. (The latter two seemingly contradictory patterns actually are not: Kittlitz's Murrelets preferred deep segments [glacial-affected segments in particular tended to be deep] but, within segments, tended to occur close to shore.) In contrast, their distribution with respect to SSS and distance to fresh water did not differ significantly from random points.

Marbled Murrelets also exhibited non-random distribution with respect to all nine habitat variables. Although all variables were significant (*P* < 0.001), Marbled Murrelets exhibited the greatest divergence from randomness for habitat type, ice cover, and SST. They preferred glacial-unaffected habitats and avoided glacial-affected and marine-sill-affected habitats (Fig. 2). They preferred areas with ≤15% ice cover, water clarity 2–4 m, and SST's >6°C and avoided areas with >15% ice cover, water clarity <2 m, SST's ≤6°C, and SSS's 10–17‰ (Figs. 3–6). They preferred water depths ≤40 m, areas 51–150 m from shore, areas 101–250 m and >1,000 m from fresh water, and fine-alluvium substrates and avoided water depths >40 m, areas ≤50 m and >150 m from shore, areas 251–1,000 m from fresh water, and icy substrates (Figs. 7–10).

With all habitat variables together, we correctly classified Marbled Murrelet locations 59.0% of the time. As was seen for Kittlitz's Murrelets, habitat type was the most important variable determining the distribution of Marbled Murrelets within bays, as indicated by the large likelihood ratio (Tables 1 and 2). Marbled Murrelets occurred with greater probability in glacial-stream-affected and glacial-unaffected habitats and with lower probability in glacial-affected and marine-sill-affected habitats. They occurred with greater probability than expected as ice cover decreased, water became less turbid, salinity increased, water depth decreased, and the distance to shore increased. (Again, the latter two seemingly contradictory patterns are not: Marbled Murrelets preferred segments that were shallower but, within segments, tended to occur farther from shore.) Their distribution with respect to distance to fresh water did not differ significantly from randomness.

**Comparative habitat use**
We used logistic regression with habitat variables to model the probability that a murrelet group contained Kittlitz's or Marbled murrelets (Table 3).  This model accurately classified which groups were Kittlitz's Murrelets 46.6% of the time, in spite of the fact that Kittlitz's Murrelet groups represented only 13.1% of the total 10,677 groups examined.  Although 6 of 7 habitat variables, plus site, were significant in determining the identity of murrelet groups, water clarity was the most significant (i.e., had the largest likelihood ratio), with ice cover second in importance; all other variables had much lower likelihood ratios.  Distance to fresh water was the one variable that was not significant.  When including all environmental variables simultaneously, the probability that a murrelet group contained Kittlitz's, rather than Marbled Murrelets, was highest in glacial-affected habitats, moderate in glacial-stream-affected and glacial-unaffected habitats, and lowest in marine-sill-affected habitats.  As indicated by the signs of the β values, it also was higher in high ice cover, low water clarity, high salinities, low distances to shore, and deep water (Figs. 2–10).  It also was higher in College and Harriman fjords than in Unakwik Inlet and lowest in Blackstone Bay and was higher in early and mid-summer than in late summer.  The probability that a group of birds was Kittlitz's Murrelets was not affected by year and distance to fresh water.

**Niche width and niche overlap**
Both Kittlitz's and Marbled murrelets exhibited widely variable niche widths (B), depending on the habitat variable or site (Table 4).  Both Kittlitz's and Marbled murrelets exhibited the narrowest niche widths in ice cover and the widest niche widths in distance to shore and distance to fresh water.  Kittlitz's Murrelets also exhibited the narrowest niche widths in SST, and Marbled Murrelets also exhibited the narrowest widths in habitat type.

As might be expected, the murrelet species exhibited widely variable niche overlap, depending on the habitat variable and site (Table 4).  Marbled Murrelets had the least niche overlap with Kittlitz's Murrelets in water clarity and SST and had the greatest overlap in shoreline substrate and SSS.  Kittlitz's Murrelets had the least overlap with Marbled Murrelets in water clarity and habitat type and had the greatest overlap in distance to shore and ice cover.

Because water clarity represented the least niche overlap between the two species, we investigated patterns of its availability and use (Table 5).  Water clarity differed significantly in availability among habitat types ($F_{3,\ 1008} = 49.640$; $P < 0.001$), with multiple comparisons indicating the pattern marine-sill-affected > glacial-unaffected > glacial-stream-affected > glacial-affected.  Hence, water clarity decreased as the effects of glaciers increased.

Kittlitz's Murrelets occurred in waters that were more turbid than those where Marbled Murrelets occurred, regardless of habitat type (Table 5).  The maximal Secchi depth in which Kittlitz's Murrelets occurred was 5.5 m, whereas the maximal depth for Marbled Murrelets was 13.0 m (the maximal depth measured in this study).  Kittlitz's Murrelets occurred in water substantially more turbid than that available, on average, in glacial-stream-affected and glacial-unaffected habitats and occurred in water clarity approximating availability in glacial-affected and marine-sill-affected habitats.  Marbled Murrelets occurred in water substantially less turbid than that available, on average, in marine-sill-affected habitats and occurred in water clarity approximating availability in the other three habitats.  The similarity between availability and use

of water clarity in glacial-affected habitats for both species probably reflects the low variation in availability, as all of that water was highly turbid (Table 5).  Overall, Kittlitz's Murrelets occurred in waters that were significantly more turbid than Marbled Murrelets did in glacial-affected ($t = -2.343$; df = 644; $P = 0.019$), glacial-stream-affected ($t = -10.900$; df = 561; $P < 0.001$), and glacial-unaffected habitats ($t = -20.340$; df = 594; $P < 0.001$).  Water clarity of the two species did not differ between species in marine-sill-affected habitats ($t = -0.653$; df = 215; $P = 0.515$), probably because of low statistical power caused by the small sample sizes of Kittlitz's Murrelets in that habitat.

**Optical differentiation**
Kittlitz's Murrelets had eyes that were larger than those of Marbled Murrelets in the proportion of both orbit diameter to total head length (Kittlitz's mean = $32.22 \pm 0.18\%$, n = 16; Marbled mean = $30.08 \pm 0.55\%$, n = 9) and orbit diameter to post-bill head length (Kittlitz's mean = $61.94 \pm 0.40\%$, n = 16; Marbled mean = $60.41 \pm 0.55$, n = 12).  The former proportion was 7.1% larger, and the latter was 2.6% larger, in Kittlitz's Murrelets than in Marbled Murrelets.  These proportions were significantly larger in Kittlitz's Murrelets for both total head length (t = 4.517; df = 23; P ≤ 0.001) and post-bill head length (t = 2.342; df = 26; P = 0.027).

**DISCUSSION**
Kittlitz's and Marbled murrelets exhibited several differences in nearshore habitat use.  Both exhibited the strongest deviations from random distribution with respect to habitat type, with the two species preferring essentially nonoverlapping habitat types.  Kittlitz's Murrelets preferred glacial-affected and glacial-stream-affected habitats and avoided marine sills and glacial-unaffected habitats.  In contrast, Marbled Murrelets preferred glacial-unaffected habitats and avoided glacial-affected and marine-sill-affected habitats.  To some extent, differences in ice cover, water clarity, and SST are interdependent with this difference in habitat preferences: Kittlitz's Murrelets preferred water that was considerably icier, more turbid, and colder than that preferred by Marbled Murrelets, especially water that was more turbid.  Kittlitz's Murrelets also occurred in water that was slightly deeper (it often is deep off the faces of tidewater glaciers) and often was closer to freshwater input (common near glaciers, but we noticed an apparent affinity with even small streams) than that preferred by Marbled Murrelets.  There appeared to be little overall separation between the two species in SSS, and patterns in distance to shore were inconsistent enough (even though often significant overall) that we do not believe that there actually was much separation in that variable.

The affinities of both Kittlitz's and Marbled murrelets for particular water turbidity and habitat types seen here likely reflect foraging preferences.  Analyses of feeding rates (Day and Nigro 2000) support this conclusion.  For example, Kittlitz's Murrelets showed a strong preference for turbid water, preferring (~53% of all birds occurring in) waters with <1 m of visibility and avoiding waters with ≥2 m of visibility; because they showed no difference in feeding frequencies among visibility categories (Day and Nigro 2000), they apparently feed preferentially in waters with <1 m of visibility and avoid feeding in waters with ≥2 m of visibility.  In addition, they occurred preferentially in glacial-affected and glacial-stream affected habitats, and they exhibited the highest feeding frequencies in glacial-stream affected habitats; because they also occurred preferentially in glacial-affected habitats and showed no difference from other categories in feeding frequencies there, they also fed preferentially in that habitat type.  Marbled Murrelets, in

contrast, showed a preference for clearer water than Kittlitz's Murrelets did, preferring (~60% of all birds occurring in) waters having 2–4 m of visibility and avoiding waters with <2 m of visibility; because they showed no difference in feeding frequencies among visibility categories, they apparently feed preferentially in waters with ≥2 m of visibility and avoid feeding in waters with <2 m of visibility.  In addition, most fed in glacial-unaffected habitats and fewest fed in glacial-affected habitats, based on abundance; the higher feeding frequency, but low overall occurrence, in marine-sill-affected habitats may reflect episodic feeding opportunities (i.e., tidal fronts).

**Ecological specialization in *Brachyramphus* murrelets**
Wiens (1989) discussed both the nature of competition and the overwhelming lack of evidence for it and explained the numerous difficulties associated with documenting its occurrence.  For example, "simply documenting the fact that two species share a resource says nothing about resource limitation," and "even if resource levels are also measured, limitation can only be inferred at best."  He further listed six criteria that provide various levels of confidence in a conclusion of interspecific competition.  On the other hand, circumstantial evidence of competition in the evolutionary past may be provided by evidence of ecological isolation and morphological differentiation, although such inferences should be cautiously made.  Such evidence of ecological isolation requires that morphological differences be associated with relevant features of ecological isolation and niche overlap (Wiens 1989).

We propose that the evidence presented here indicates ecological and accompanying morphological specialization between these two *Brachyramphus* murrelets, both within these glaciated fjords and range-wide in general.  Kittlitz's Murrelets have a strong affinity for occurring and foraging in turbid, glacial waters.  They do not leave these fjords to forage (Day and Nigro, unpublished data), so they are tied to often-turbid glaciated areas throughout the summer, until they abandon the bays for the winter.  In contrast, Marbled Murrelets that do occur within these fjords are associated with glacial-unaffected areas, occurring primarily in moderately to highly clear water.  Further, they often forage in outer Prince William Sound, outside of these fjords (Day and Nigro, unpublished data; K. J. Kuletz, U.S. Fish and Wildlife Service, unpublished data), so most of the population actually occurs in even clearer waters, with Secchi depths up to 15 m having been recorded (K. J. Kuletz, USFWS, Anchorage, AK, pers. comm.).  In this study, water clarity clearly was an important habitat variable in most analyses, was that variable having the greatest effect on identity of a group of murrelets, and was the one that occurred with the least niche overlap in both directions.  Further, within a habitat type, Kittlitz's Murrelets always occurred in waters more turbid than those used by Marbled Murrelets.

The overall summer distribution of these two species provides additional evidence for habitat specialization by glaciation and water clarity.  At a large scale within Alaska, Kittlitz's Murrelets concentrate in glaciated areas, primarily in Glacier Bay, in glaciated parts of Prince William Sound, along the heavily glaciated Kenai Peninsula, and near glaciated parts of the Alaska Peninsula (Kendall and Agler 1998, Day et al. 1999).  The northernmost extent of this species' breeding range in Alaska also is delineated by the former extent of Pleistocene glaciation (Piatt et al. 1999).  In contrast, Marbled Murrelets exhibit little association with glaciers, instead concentrating near old-growth forest from Alaska to California (Nelson 1997).  Such a difference in range-wide distributions also reflects differences in the two species' nesting habitat use (Day et

al. 1983, Ralph et al. 1995, Nelson 1997), with the nearshore adaptations discussed here being additional forms of specialization.

Accompanying this evidence for ecological specialization by water clarity is evidence of optical differentiation, with Kittlitz's Murrelets having proportionately larger eyes than are those of Marbled Murrelets.  We interpret the pronounced differences between the two species for different water clarity and in eye size to be an adaptation of Kittlitz's Murrelets for foraging in low light-levels in turbid glacial water.  The ability to feed in such areas might allow Kittlitz's Murrelets to take advantage of a food resource that is unavailable to Marbled Murrelets or that occurs in reduced quantities in other habitat types.  Birds generally avoid competition by becoming foraging specialists but remaining food generalists (Hespenheide 1975), a pattern consistent with the habitat specialization documented here and the species' apparently extensive dietary overlap (see Day et al. 1999).

Eye size frequently differs between closely related species that forage in different light levels (Walls 1942, Tansley and Erichsen 1985, Storer 1987).  For example, Red-legged Kittiwakes (*Rissa brevirostris*) forage nocturnally on lanternfishes (Hunt et al. 1981) and have significantly larger sclerotic rings (scleral ossicles; an indicator of pupil size) than do larger but diurnally foraging Black-legged Kittiwakes (*R. tridactyla*; Storer 1987).  Similarly, the Ross' Gull (*Rhodostethia rosea*) and Ivory Gull (*Pagophila eburnea*) forage under low light levels during high-latitude winters and have larger sclerotic rings than do similarly sized but diurnally feeding Bonaparte's (*Larus philadelphia*) and Ring-billed gulls (*L. delawarensis*) of lower latitudes.  Likewise, Red-footed Boobies (*Sula sula*) are the only nocturnally oriented *Sula* and have "eyes" (i.e., pupil sizes) that are visibly larger than those of other species (Murphy 1936), and nocturnally feeding shorebirds have proportionately larger eyes than do diurnally feeding ones (Rojas de Azuaje et al. 1993).  Unfortunately, not enough museum material is available to test whether the inner diameter of sclerotic rings (i.e., pupil size) in the two species of murrelets studied here differ.  The noticeable interspecific difference in eye size, however, is what originally led us to pursue this study and suggests that, in addition to a difference in overall eye size, pupil diameter differs between the two species.

Aquatic birds have developed many other optical adaptations to facilitate vision underwater, where light levels are low (Levenson and Schusterman 1997) and the refractive index of the cornea is greatly reduced (Katzir 1993, Levenson and Schusterman 1997).  Adaptations include possessing a large accommodative ability (Martin 1985, Tansley and Erichsen 1985), a flat cornea (Katzir 1993), a thick retina packed with visual cells, oil droplets on the retinal cones (Martin 1985, Tansley and Erichsen 1985, Begin and Handford 1987), and a high rod:cone ratio (Rojas de Azuaje et al. 1993).  In addition to the larger eye size identified here, one or more of these other adaptations also may be possessed by Kittlitz's Murrelets.

Water clarity has been proposed as an important environmental variable affecting seabird faunas at larger scales.  For example, water clarity is significantly negatively correlated with the incidence of pursuit-diving and directly correlated with the incidence of plunge-diving as a feeding method at a large scale (Ainley 1977).  The association is not complete, however.  In fact, in some locations, plunge-divers actually may increase in abundance in more turbid water, suggesting that water clarity may have little effect on the occurrence of aerially foraging seabirds

(Haney and Stone 1988). Nevertheless, water clarity dramatically affects the detectability of fishes (Eriksson 1985) and probably other prey and appears to limit mesoscale marine distributions of seabird species in some locations (Brown et al. 1975). In the latter location, most bird species avoided the highly turbid Baker and Iceberg inlets of southwestern South America, although King (*Phalacrocorax albiventer*) and Blue-eyed (*P. atriceps*) shags were common there and appeared to be adapted to foraging at the turbidity fronts that were common.

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Table 1. Results of logistic regression comparing random to actual locations for Kittlitz's and Marbled murrelets in nearshore waters of Prince William Sound, Alaska, 1997–1998. In this type of model, one of the categories is the default value and is parameterized with a β of zero with respect to the other categories. SST was excluded because of its collinearity with ice cover.

| Source | Kittlitz's Murrelet | | | | Marbled Murrelet | | | |
|---|---|---|---|---|---|---|---|---|
| | β | df | Likelihood ratio | P | β | df | Likelihood ratio | P |
| Constant | −0.235 | 1 | 1.252 | 0.263 | 0.350 | 1 | 14.884 | <0.001 |
| Habitat type | | 3 | 98.899 | <0.001 | | 3 | 571.301 | <0.001 |
| Glacial-affected | 0.659 | 1 | 28.559 | <0.001 | −0.960 | 1 | 89.644 | <0.001 |
| Marine-sill-affected | −2.342 | 1 | 18.195 | <0.001 | −1.824 | 1 | 439.521 | <0.001 |
| Glacial-unaffected | −0.612 | 1 | 35.716 | <0.001 | −0.163 | 1 | 19.301 | <0.001 |
| ln ice cover | 0.710 | 1 | 5.210 | 0.022 | −0.200 | 1 | 179.799 | <0.001 |
| ln Secchi depth | −0.113 | 1 | 8.403 | 0.004 | 0.190 | 1 | 61.647 | <0.001 |
| SSS | 0.013 | 1 | 2.401 | 0.121 | 0.006 | 1 | 24.316 | <0.001 |
| Water depth | 0.016 | 1 | 35.342 | <0.001 | −0.010 | 1 | 78.994 | <0.001 |
| Distance to shore | −0.005 | 1 | 45.692 | <0.001 | −0.001 | 1 | 30.649 | <0.001 |
| Distance to fresh water | 0.000 | 1 | 0.028 | 0.867 | 0.000 | 1 | 2.982 | 0.084 |

Table 2. Mean environmental attributes used by Kittlitz's (KIMU) and Marbled (MAMU) murrelets in nearshore waters of Prince William Sound, Alaska, 1996–1998.

| Variable | Species | Mean | SE | Range | $n$ |
|---|---|---|---|---|---|
| Ice (%) | KIMU | 8.1 | 0.3 | 0–90 | 1,887 |
| | MAMU | 0.9 | <0.1 | 0–90 | 12,977 |
| Secchi depth (m) | KIMU | 1.0 | <0.1 | 0–5.5 | 1,524 |
| | MAMU | 2.3 | <0.1 | 0–13.0 | 10,016 |
| SST (°C) | KIMU | 6.1 | <0.1 | 1.0–13.0 | 1,852 |
| | MAMU | 8.2 | <0.1 | 2.0–14.1 | 12,895 |
| SSS (‰) | KIMU | 20.0 | 0.1 | 7.2–29.5 | 1,526 |
| | MAMU | 20.3 | <0.1 | 5.0–29.5 | 9,998 |
| Water depth (m) | KIMU | 37 | <1 | 1.6–64.6 | 1,887 |
| | MAMU | 29 | <1 | 1.6–64.6 | 12,977 |
| Distance to shore (m) | KIMU | 86 | 1 | 4–193 | 1,887 |
| | MAMU | 94 | <1 | 1–199 | 12,972 |
| Distance to fresh water (m) | KIMU | 487 | 13 | 4–2,878 | 1,887 |
| | MAMU | 651 | 5 | 12–2,862 | 12,972 |

Table 3.  Results of logistic regression comparing nearshore habitat use by groups of Kittlitz's and Marbled murrelets in Prince William Sound, Alaska, 1997–1998.  SST was excluded because of its collinearity with ice cover.  The dependent variable is species.

| Variable | β | Likelihood ratio | df | *P* |
|---|---|---|---|---|
| Constant | −4.422 | 216.279 | 1 | <0.001 |
| Habitat type | | 91.442 | 3 | <0.001 |
|    Glacial-affected | 1.294 | 61.112 | 1 | <0.001 |
|    Marine-sill-affected | −0.581 | 0.758 | 1 | 0.384 |
|    Glacial-unaffected | −0.376 | 12.231 | 1 | <0.001 |
| ln ice cover | 0.662 | 275.896 | 1 | <0.001 |
| ln Secchi depth | −1.101 | 295.964 | 1 | <0.001 |
| SSS | 0.077 | 33.202 | 1 | <0.001 |
| Water depth | 0.020 | 37.538 | 1 | <0.001 |
| Distance to shore | −0.005 | 26.148 | 1 | <0.001 |
| Distance to fresh water | 0.000 | 0.000 | 1 | 1.000 |
| Year (1997) | 0.135 | 2.030 | 1 | 0.154 |
| Site | | 90.831 | 3 | <0.001 |
|    Unakwik Inlet | 0.915 | 19.281 | 1 | <0.001 |
|    College Fjord | 1.686 | 75.318 | 1 | <0.001 |
|    Harriman Fjord | 1.216 | 38.177 | 1 | <0.001 |
| Season | | 29.111 | 2 | <0.001 |
|    Early summer | 0.642 | 24.946 | 1 | <0.001 |
|    Mid-summer | 0.473 | 8.298 | 1 | 0.004 |

Table 4. Number of categories and estimates of niche width and overlap for Kittlitz's and Marbled murrelets in nearshore waters of Prince William Sound, Alaska, 1996–1998. The top half of the table indicates the overlap of Marbled Murrelets on Kittlitz's Murrelets; the bottom half indicates the reverse; a niche width approaching 4 (the number of categories within each habitat variable) indicates that the species uses all categories within a variable equally, whereas a small niche width indicates specialization in a few categories. In the niche-overlap calculations, 0 indicates no overlap and 1 indicates complete overlap, but the value of $\alpha$ may exceed 1 if niche widths are unequal (Hespenheide 1975).

| Species | Source | Number of categories | Niche width (B) | Niche overlap ($\alpha$) Kittlitz's | Niche overlap ($\alpha$) Marbled |
|---|---|---|---|---|---|
| Kittlitz's Murrelet | Habitat type | 4 | 2.97 | | 1.03 |
| | Ice cover | 4 | 1.46 | | 0.76 |
| | Secchi depth | 4 | 2.50 | | 0.56 |
| | SST | 4 | 2.40 | | 0.72 |
| | SSS | 4 | 3.00 | | 1.04 |
| | Water depth | 4 | 2.69 | | 0.87 |
| | Distance to shore | 4 | 3.54 | | 0.95 |
| | Distance to fresh water | 4 | 3.61 | | 0.98 |
| | Shoreline substrate | 4 | 2.61 | | 1.08 |
| | Site | 4 | 3.14 | | 0.76 |
| Marbled Murrelet | Habitat type | 4 | 1.81 | 0.63 | |
| | Ice cover | 4 | 1.94 | 1.01 | |
| | Secchi depth | 4 | 3.16 | 0.71 | |
| | SST | 4 | 2.67 | 0.80 | |
| | SSS | 4 | 2.30 | 0.80 | |
| | Water depth | 4 | 2.75 | 0.89 | |
| | Distance to shore | 4 | 3.84 | 1.02 | |
| | Distance to fresh water | 4 | 3.29 | 0.89 | |
| | Shoreline substrate | 4 | 2.02 | 0.84 | |
| | Site | 4 | 3.13 | 0.76 | |

*Note:* B = niche width = $1/(\Sigma p_i^2)$; $\alpha$ = niche overlap = $(\Sigma p_i p_j)/(\Sigma p_i^2)$.

TABLE 5. Mean Secchi depths (m) of nearshore waters in which Kittlitz's (KIMU) and Marbled (MAMU) murrelets occurred in four bays in Prince William Sound, Alaska, in 1997–1998, by habitat type. Values for availability are calculated as arithmetic means and for the two murrelet species are calculated as geometric means.

| Habitat type | Category/species | Secchi depth (m) | | | Range | n |
| --- | --- | --- | --- | --- | --- | --- |
| | | Mean | Lower bound | Upper bound | | |
| Glacial-affected | Availability | 0.47 | 0.39 | 0.55 | 0–1.5 | 119 |
| | KIMU | 0.51 | 0.48 | 0.54 | 0–1.5 | 516 |
| | MAMU | 0.60 | 0.55 | 0.65 | 0–1.5 | 130 |
| Glacial-stream-affected | Availability | 1.22 | 1.10 | 1.34 | 0–9.5 | 303 |
| | KIMU | 0.74 | 0.67 | 0.81 | 0–3.5 | 456 |
| | MAMU | 1.27 | 1.23 | 1.30 | 0–9.5 | 2,842 |
| Marine-sill-affected | Availability | 3.24 | 2.84 | 3.64 | 1.0–7.0 | 41 |
| | KIMU | 3.17 | 1.99 | 5.00 | 2.5–4.0 | 2 |
| | MAMU | 3.63 | 3.49 | 3.78 | 1.0–5.5 | 215 |
| Glacial-unaffected | Availability | 2.09 | 1.91 | 2.27 | 0–13.0 | 549 |
| | KIMU | 0.90 | 0.83 | 0.99 | 0–5.5 | 550 |
| | MAMU | 2.19 | 1.86 | 2.57 | 0–13.0 | 6,829 |
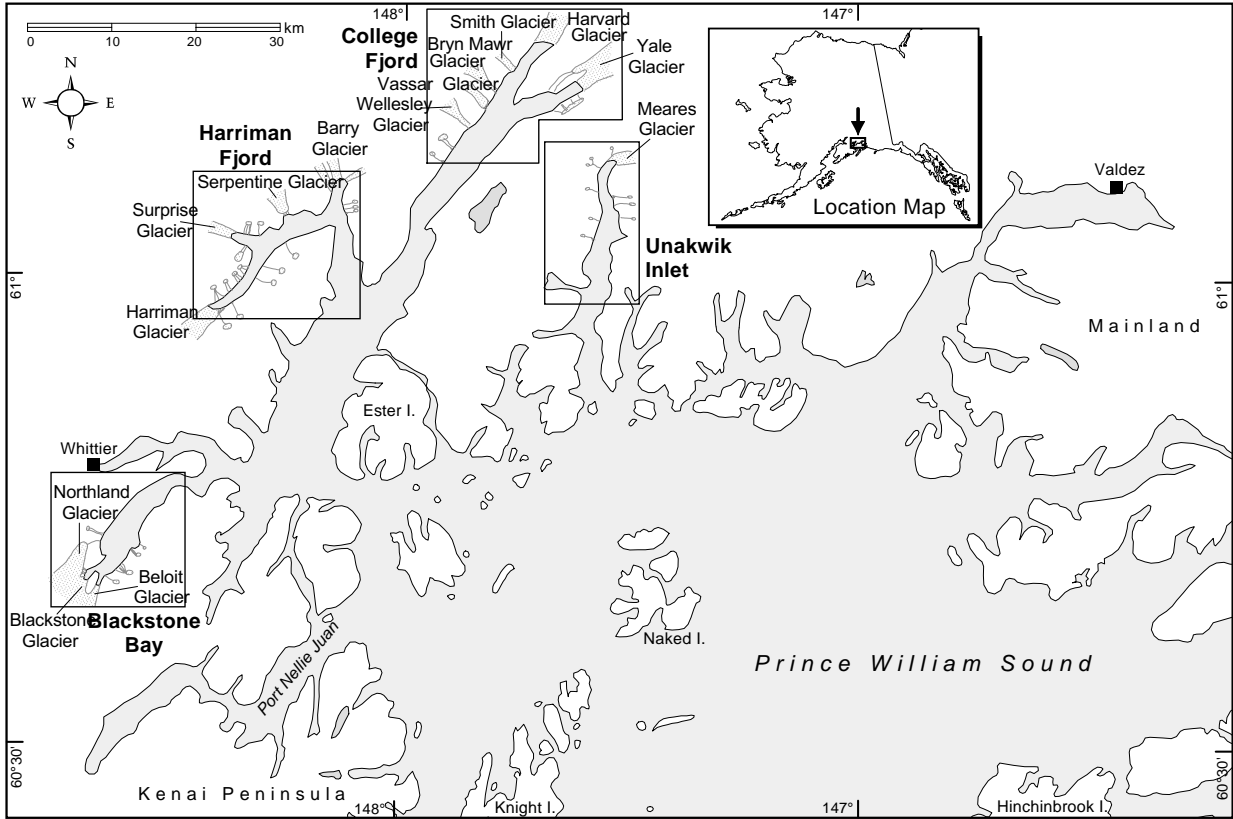
Fig. 1. Locations of study bays in Prince William Sound, Alaska, in 1996–1998.
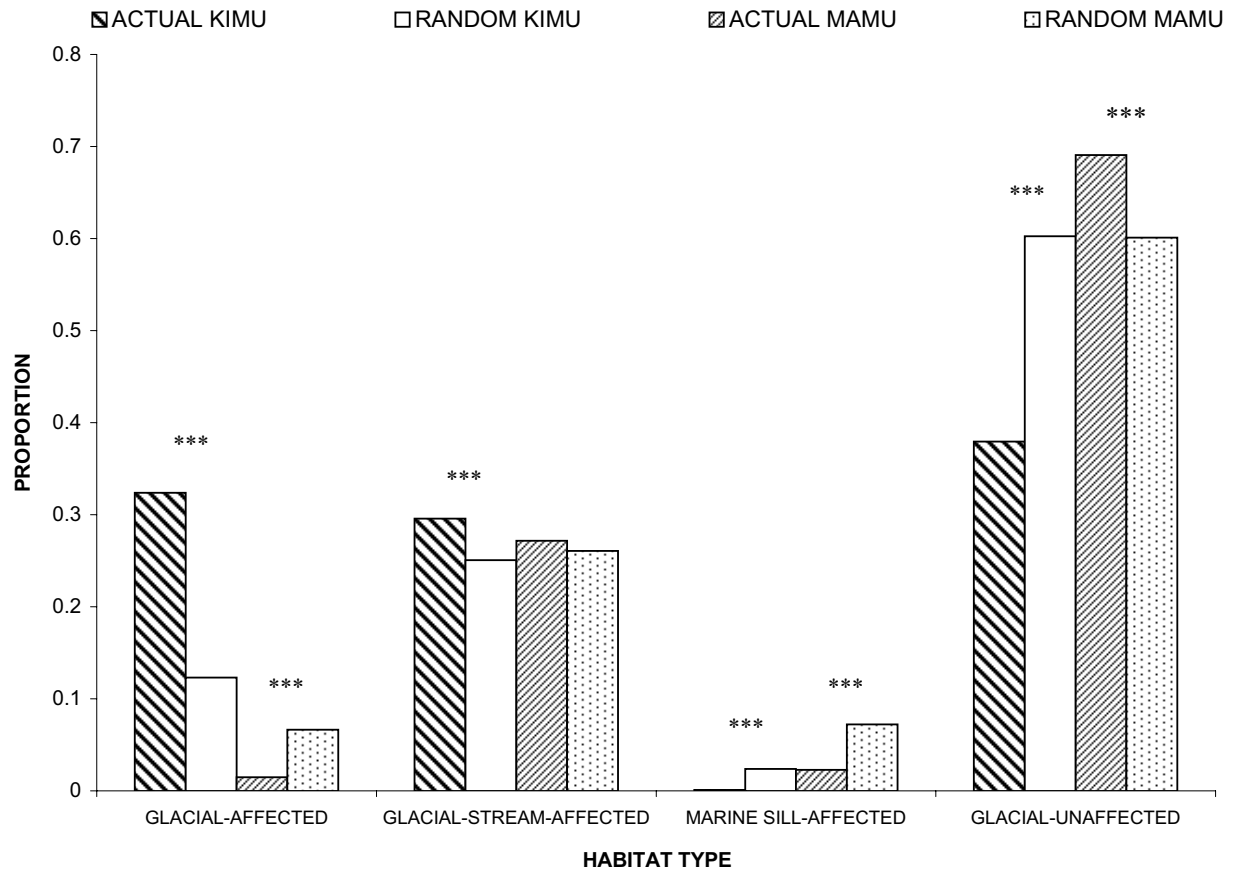
Fig. 2.   Use versus availability of habitat types by Kittlitz's and Marbled murrelets in Prince William Sound, Alaska, in 1996–1998.  Significant differences are indicated by asterisks ($*0.05 \geq P \geq 0.01$; $**0.01 > P \geq 0.001$; $***P < 0.001$).
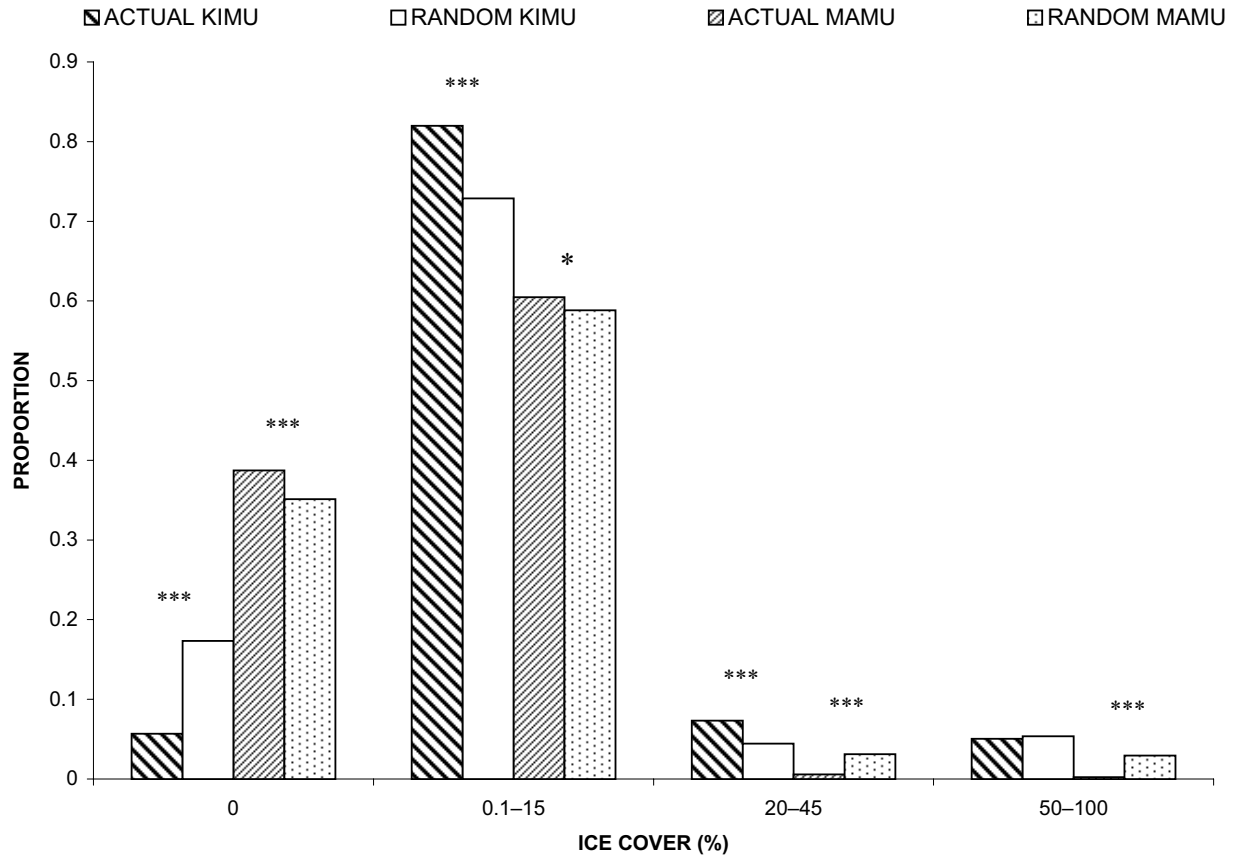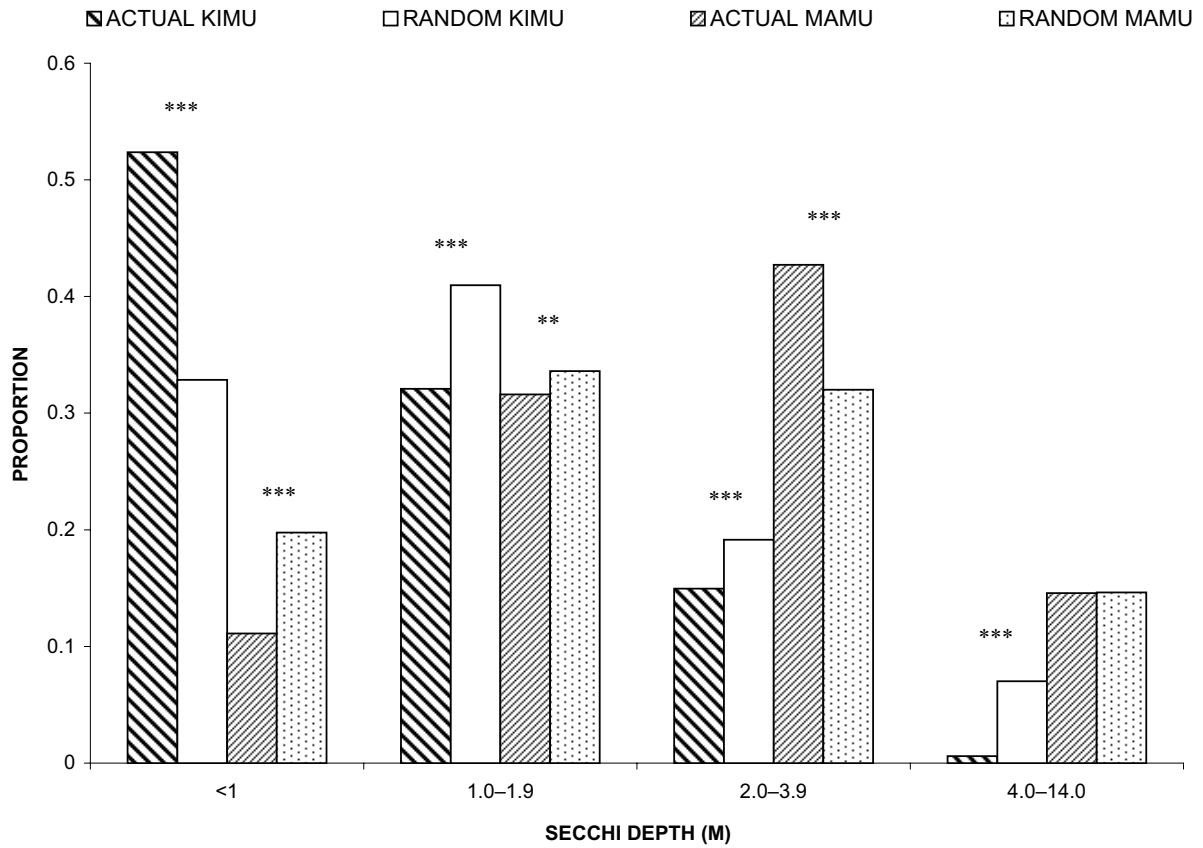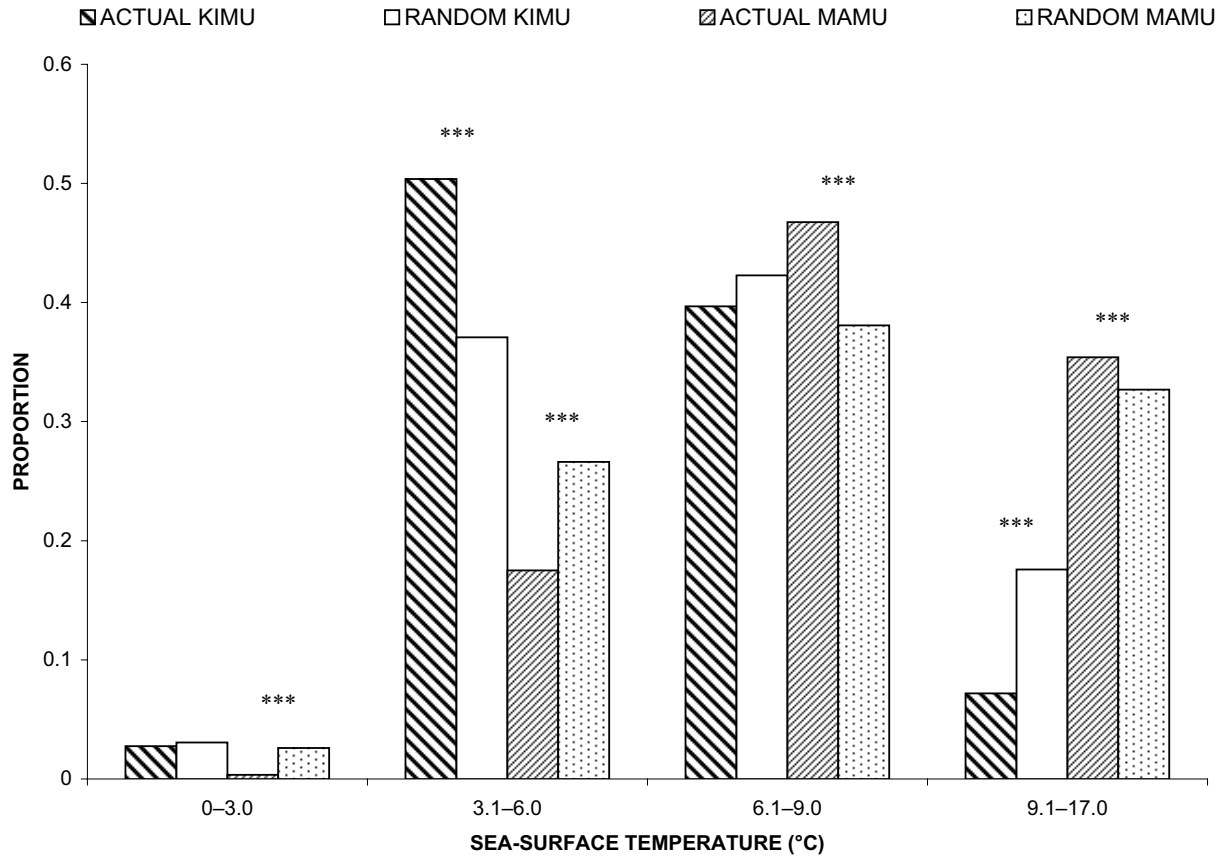
Fig. 3.  Use versus availability of ice cover by Kittlitz's and Marbled murrelets in Prince William Sound, Alaska, in 1996–1998.  Significant differences as in Figure 2.

Fig. 4.   Use versus availability of Secchi depths (water clarity) by Kittlitz's and Marbled murrelets in Prince William Sound, Alaska, in 1996–1998.  Significant differences as in Figure 2.
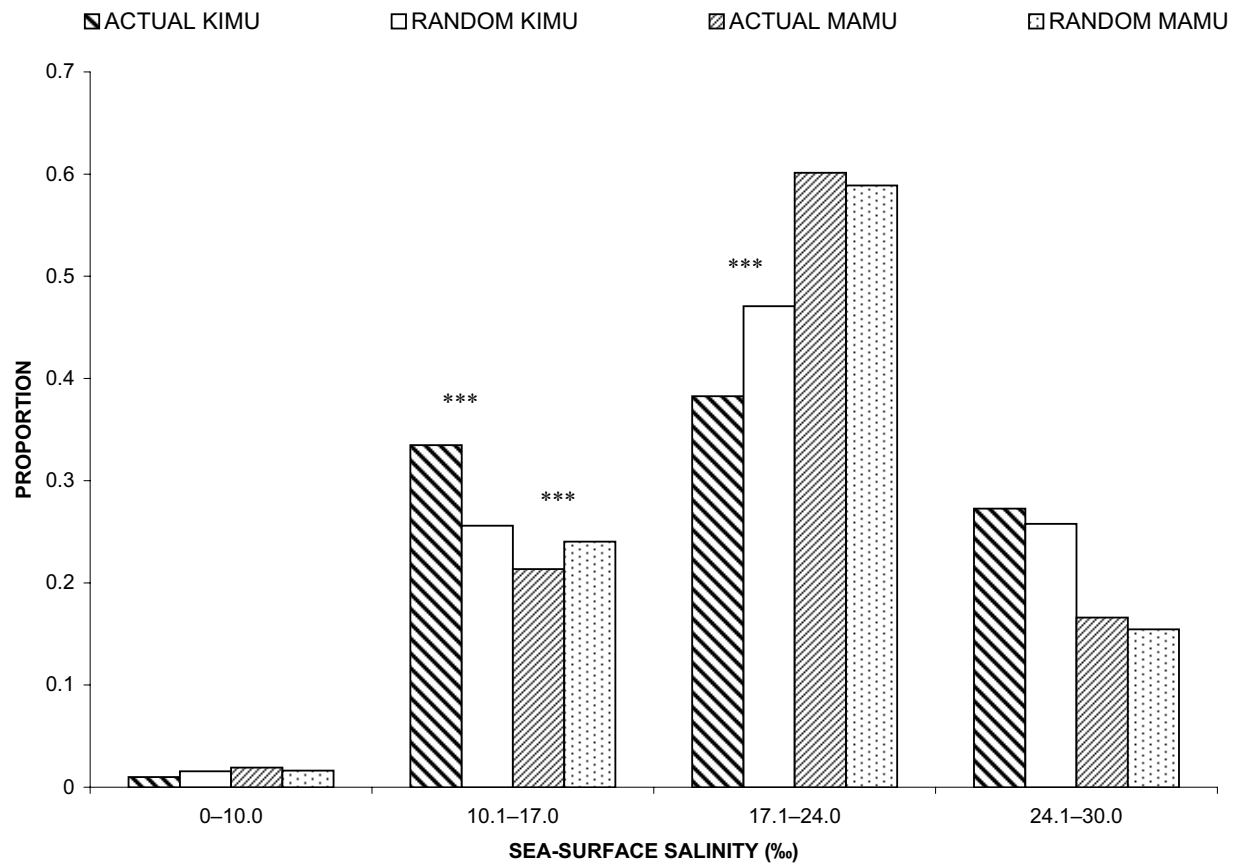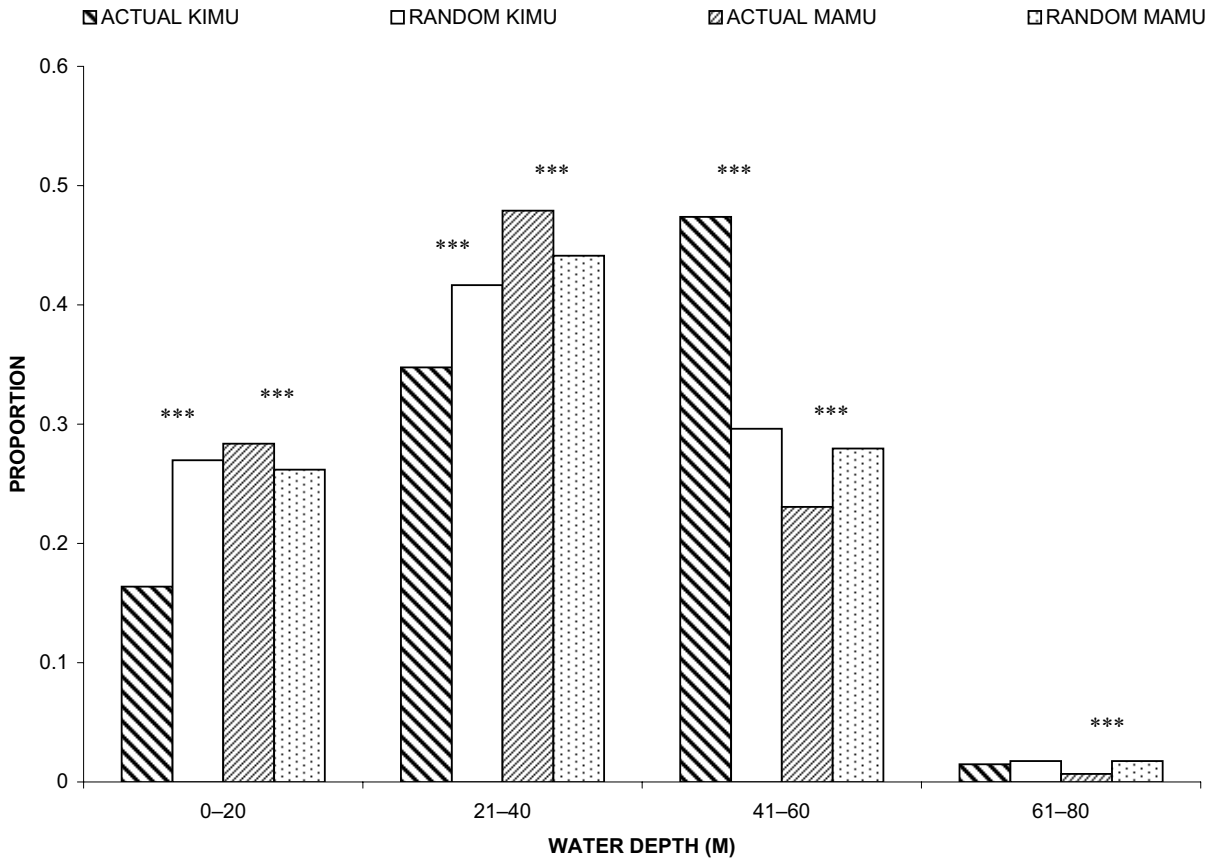
Fig. 5.   Use versus availability of sea-surface temperatures (SST) by Kittlitz's and Marbled murrelets in Prince William Sound, Alaska, in 1996–1998.  Significant differences as in Figure 2.

Fig. 6. Use versus availability of sea-surface salinities (SSS) by Kittlitz's and Marbled murrelets in Prince William Sound, Alaska, in 1996–1998. Significant differences as in Figure 2.

Fig. 7.   Use versus availability of water depth by Kittlitz's and Marbled murrelets in Prince William Sound, Alaska, in 1996–1998.  Significant differences as in Figure 2.
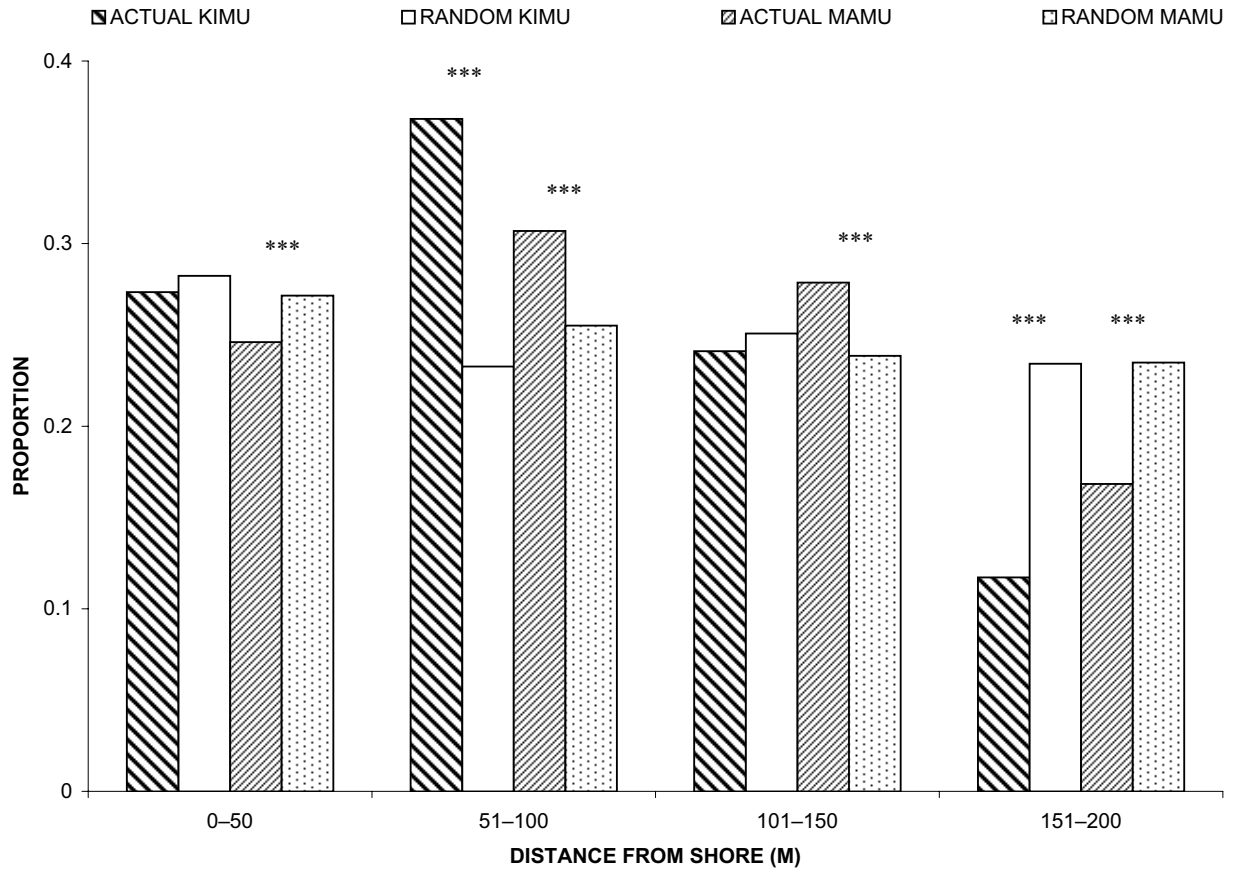
Fig. 8.   Use versus availability of distance to shore by Kittlitz's and Marbled murrelets in Prince William Sound, Alaska, in 1996–1998.  Significant differences as in Figure 2.
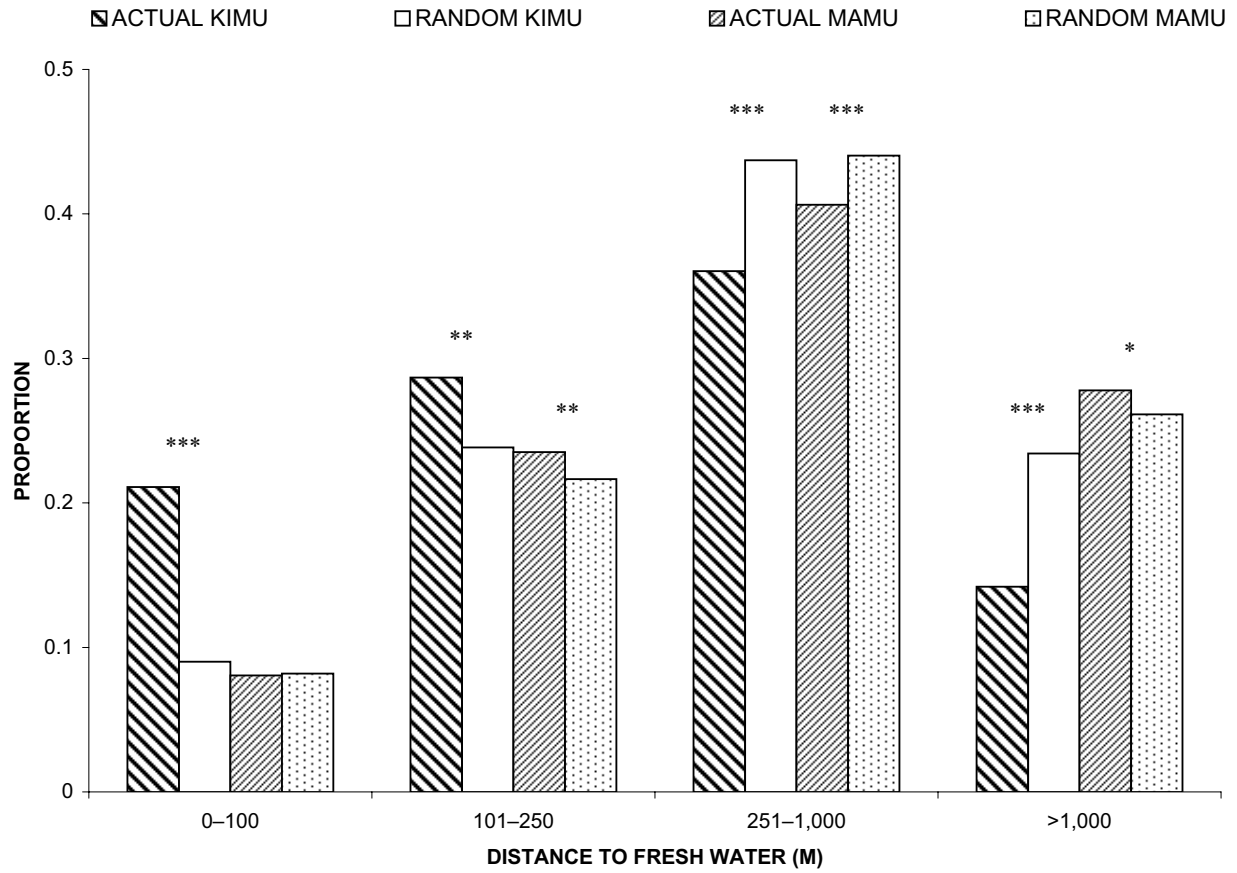
Fig. 9. Use versus availability of distance to fresh water by Kittlitz's and Marbled murrelets in Prince William Sound, Alaska, in 1996–1998. Significant differences as in Figure 2.
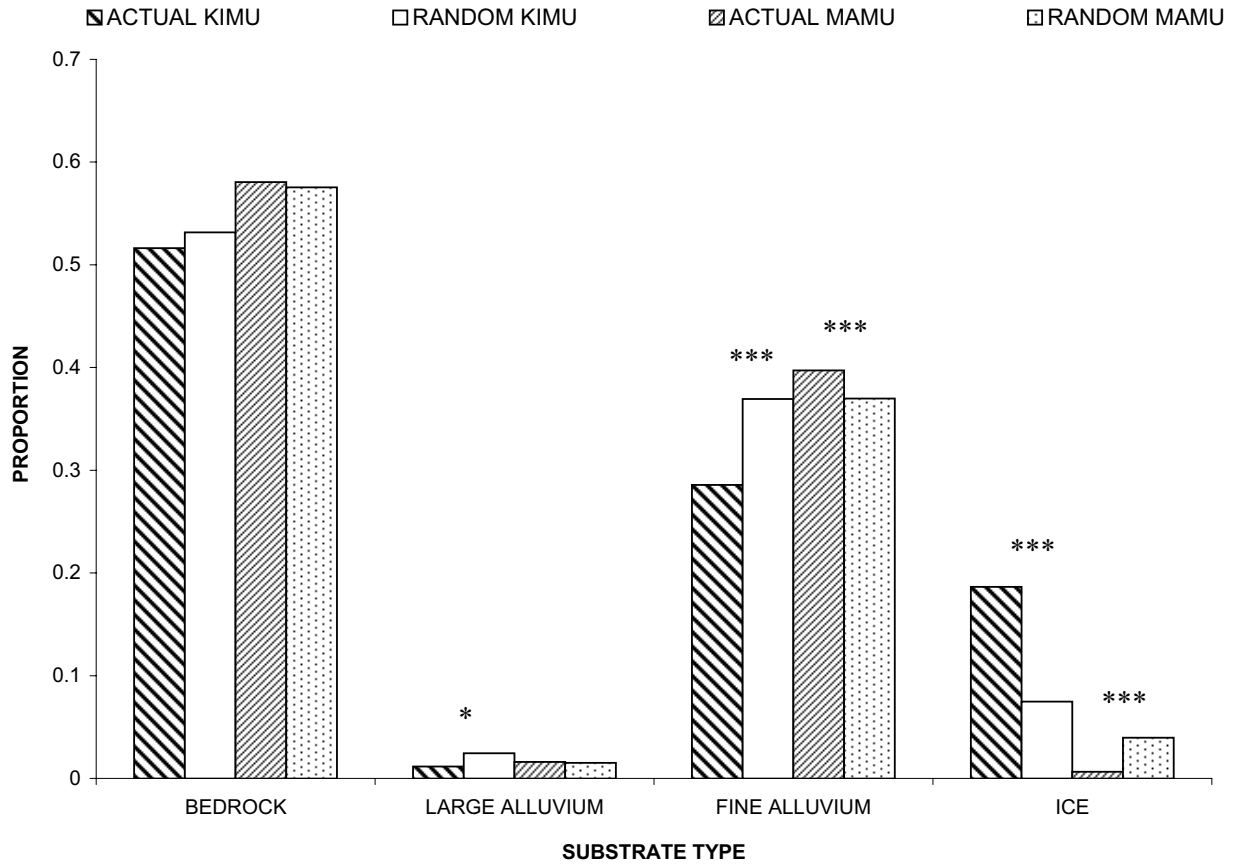
Fig. 10. Use versus availability of shoreline substrate by Kittlitz's and Marbled murrelets in Prince William Sound, Alaska, in 1996–1998. Significant differences as in Figure 2.