CHANGES IN DISTRIBUTION AND ABUNDANCE OF KITTLITZ'S MURRELETS BRACHYRAMPHUS BREVIROSTRIS RELATIVE TO GLACIAL RECESSION IN PRINCE WILLIAM SOUND, ALASKA

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SUMMARY

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The Kittlitz's Murrelet is a diving seabird of relatively low abundance found only in Alaska and eastern Siberia. Prince William Sound (PWS), Alaska, is a population center for this species, where it typically occurs near tidewater glaciers. In PWS, marine bird surveys (n = 7 years) indicated that there was an 84% decline in Kittlitz's Murrelets from approximately 6400 birds in 1989 to 1000 birds in 2000. During this period, the distribution in PWS changed from being fairly dispersed to being concentrated in the northwest region. In 2001 we surveyed for Kittlitz's in PWS, targeting 17 fjords and bays where they had been found in the past or with suitable habitat. We estimated 1,969 ± 1,058 (95% C. I.) Kittlitz's Murrelets in PWS, with 78% of the population in two fjords in the northwest corner, and 20% in three other fjords. With one exception, fjords with > 1% of the estimated population of Kittlitz's Murrelet had advancing or stable glaciers, based on glacial accounts from the late 1980s. The fjords where this species disappeared had receding glaciers as of the late 1980s, or had no direct glacial input. These results are consistent with a link between the decline of Kittlitz's Murrelets and glacial recession. More recent data indicate that several glaciers in the northwest region of PWS are now stagnating or retreating, likely due to global warming (Arendt *et al.* 2002), which in turn might result in further declines in the Kittlitz's Murrelet population. Our findings underscore the importance of tidewater glaciers to Kittlitz's Murrelets, and suggest that pagophilic species are sensitive indicators of climate change.

Keywords: Kittlitz's Murrelet Brachyramphus brevirostris, distribution, habitat, population trend, glacial retreat

INTRODUCTION

The Kittlitz's Murrelet Brachyramphus brevirostris, a small diving bird in the family Alcidae, may today be the rarest seabird regularly breeding in Alaska. Current population estimates range from 9000-25 000 birds (USFWS 2003). Most of the world population inhabits Alaskan waters, with an estimated 5% of the remaining birds in eastern Siberia (Day et al. 1999). Anecdotal accounts of birds at sea and standardized surveys in a few areas suggested that Kittlitz's Murrelets were declining in coastal areas of the northern Gulf of Alaska (GOA) at least since the early 1970s (Kendall & Agler 1998, USFWS 2003). Isleib & Kessel (1973) suggested that the Kittlitz's Murrelet population along the northern GOA was probably a few 100 000s birds, and noted that in several PWS fjords and near the Malaspina-Bering icefields, Kittlitz's 'outnumber all other alcids'; in the 1990s, this was no longer the case (USFWS 2003). By 1998, more complete at-sea surveys derived an estimate of 12 130 \pm 8312 (95% C.I.) Kittlitz's for the core population centers in the GOA: Cook Inlet, PWS, and Southeast Alaska (Kendall & Agler 1998). Based on these surveys and scattered records, Day et al. (1999) estimated the Kittlitz's world population to be in the 'thousands or very low tens of thousands'.

Small breeding populations of Kittlitz's Murrelet occur along the Aleutian Islands and as far north as the central Chuckchi Sea (Day *et al.* 1999). However, most of the Alaska population appears to have a quite restricted set of habitat preferences, being primarily found near tidewater glaciers or in nearshore waters with glacial runoff (Islieb & Kessel 1973, Day *et al.* 1999, 2003).

Because Kittlitz's Murrelet tend to associate with coastal glaciers, some authors speculated that their apparent decline is related to the retreat of glaciers in Alaska in recent decades (vanVliet 1993, Day *et al.* 1999, 2003). Changes in Alaskan glaciers, while locally dynamic, are generally associated with changes in atmospheric temperatures during the past 100 years (Molnia 2001, Arendt *et al.* 2002). Species with critical parts of their life histories (for Kittlitz's Murrelet, the breeding season) restricted to ice-associated habitats will be the first to respond to climate change (Walther *et al.* 2002, Root *et al.* 2003). However, for Kittlitz's Murrelet, knowledge of the population trends and their linkages to changes in coastal glaciers is very limited.

Our study area, PWS, is a population center for Kittlitz's Murrelet, supporting roughly 15-20% of the known Alaska population (USFWS 2003). Since 1989 the U.S. Fish and Wildlife Service (USFWS) has conducted standardized at-sea surveys in PWS to

monitor trends in all species of marine birds (Lance *et al.* 2001, Stephensen *et al.* 2001). These surveys comprise the best existing long-term trend data for Kittlitz's Murrelet. We examined these historical data sets for trends in the PWS Kittlitz's Murrelet population and conducted a vessel-based survey specifically to map the current distribution and abundance of the species. Because Kittlitz's Murrelets tend to associate with coastal glaciers, some authors speculate that the recent and continuing retreat of glaciers in Alaska (Lethcoe 1987, Arendt *et al.* 2002) could be detrimental to the murrelets (van Vliet 1993, Day *et al.* 1999, 2003). Here we present evidence that changes observed in this Kittlitz's population are linked to the status of neighboring glaciers.

METHODS

Study area

All surveys were conducted in PWS, a large embayment in southcentral Alaska with about 9000 km² surface water area and over 5000 km of shoreline (Fig. 1). The sound is bordered by the Chugach Mountains, which include several large icefields, each > 800 km² which drain into PWS via > 40 fjords and 20 tidewater glaciers (Molnia 2001). The upper portions of fjords with tidewater glaciers are generally only ice free during summer months, and always contain variable amounts of floating brash ice (Molnia 2001, author's pers. obs.). Weather in PWS is characterized by frequent cloud cover and precipitation (Wilson & Overland 1986). Summer air temperatures during 2001 surveys averaged 12°C (range 4-22).

The fjords and bays are diverse in topography and basin depth, ranging from averages of < 50 m deep (usually classified as bays) to > 400 m deep (usually considered fjords) (Gay & Vaughan 1998). Fjords with tidewater glaciers generally have steep-sided basins and underwater sills which may be 4-60 m deep (Gay & Vaughan 1998). Bays, fjords, and large islands without tidewater glaciers typically have non-tidewater glaciers discharging runoff. Throughout PWS, and particularly in the fjords and bays, water is highly stratified during summer, when snow and ice melt peaks. Local hydrographic conditions, tidewater fjords tend to have cooler,

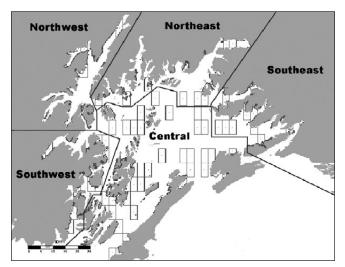


Fig. 1. The Prince William Sound study area for the 1989-2000 sound-wide surveys. Randomly selected shoreline transects (black shoreline) and blocks sampled with pelagic transects are shown within the five regions used to examine spatial population trends.

fresher waters, with stronger, and more shallow (10-15 m) temperature (thermocline) and salinity (halocline) vertical gradients (Gay & Vaughan 1998). Tides are semidiurnal and range up to 6 m.

Data collection

All strip transect surveys were conducted from 8 m fiberglass boats traveling at speeds of 10-20 km hr⁻¹, although observers reduced the cruising speed during sightings to confirm species identification. Two observers recorded all birds < 100 m to either side or ahead of the boat, using binoculars to aid in species identification (Klosiewski & Laing 1994). Most surveys were conducted when wave height was < 0.3 m, and none were done in seas > 0.6 m, to avoid missing birds sitting on the water. The sightings were expressed as an encounter rate (birds km⁻²).

The USFWS sound-wide surveys were each conducted over ≤ 3 weeks of July in 1989-1991, 1993, 1996, 1998 and 2000. Detailed methods for these surveys were described elsewhere (Klosiewski & Laing 1994, Kendall & Agler 1998). USFWS personnel surveyed 347-351 transects each year except during 1989, when 325 transects were surveyed. Transects were randomly selected from two strata – shoreline (< 200 m from shore), and offshore (> 200 m from shore), with the latter based on two parallel bands within 5' latitude x 5' longitude blocks (Fig. 1). Shoreline transects, defined by geographic features, varied in length (mean = 6.6 km) (Fig. 1). Study design and survey methodology were consistent between 1989 and 2000. During these surveys, Kittlitz's Murrelet abundance estimates had an average coefficient of variation of 0.40 (Nielson et al. 2003), which for the sound-wide surveys, results in ~ 65 % probability of detecting a 20 % annual change in population (estimated from Fig. 5, Klosiewski & Laing 1994).

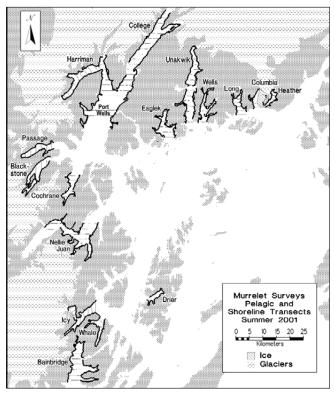


Fig. 2. Surveyed shorelines (black shoreline) and pelagic transects (light, parallel lines) in fjords and bays sampled for the 2001 intensive survey of Prince William Sound.

The sound-wide surveys provided trend data, but did not sample a high proportion of Kittlitz's Murrelet preferred habitat. To solve this problem, we conducted an intensive survey between 22 May and 3 August 2001, targeting 17 fjords and bays in PWS where Kittlitz's have occurred in the past, or that had suitable marine habitat but had not been sampled. Due to time constraints, and because few or no Kittlitz's were observed during sound-wide surveys in the southeastern and central regions since 1993, we did not sample those waters in 2001.

In 2001, we surveyed most of the sites once between late June and late July, during the chick-rearing phase (Day et al. 1999). At this time, both members of breeding pairs are at sea and counts of Kittlitz's Murrelet are highest in PWS (Klosiewski & Laing 1994, Day & Nigro 1999, Kuletz et al. 2003). Each fjord or bay took 1-2 days to survey, using standard USFWS protocol (Klosiewski & Laing 1994). The intensive surveys included a continuous shoreline count in each fjord and a systematic grid of pelagic transects (> 200 m from shore), which ran roughly perpendicular to shore at approximately 2 km intervals (Fig. 2). We used DLOG software (R.G. Ford Consulting, Portland, OR) to enter observations directly into a computer connected to a global positioning system (GPS), so that every observation was geo-referenced. Four of the fjords were surveyed three times, during the early (22 May-9 June), middle (12-30 June), and late (12 -30 July) summer. For these fjords, we included the survey with the highest Kittlitz's Murrelet density in the final PWS population estimate.

Potential sources of error

Variation in species identification and survey conditions forced us to make assumptions when analyzing the survey and trend data. The two Brachyramphus murrelets, the Kittlitz's Murrelet and the Marbled Murrelet B. marmoratus, were not always identified to species and the proportion of unidentified birds declined in later years (Stephensen et al. 2001). We assumed that the probability of being identified was the same for both species and that identification rates did not vary within a survey. Thus, changes in the abundance of identified Kittlitz's Murrelet were assumed to be representative of changes in the actual population. To investigate the potential confounding effect of higher identification rates in later years we examined population trends of both identified Kittlitz's Murrelets only and total Kittlitz's Murrelets. The latter included the identified birds, plus the portion of unidentified birds that were classified as Kittlitz's, based on the annual percentage of identified murrelets that belonged to that species. For the intensive surveys in 2001, observers were trained to distinguish the two Brachyramphus species using photographs, study skins, and onsight practice prior to surveys. Unidentified murrelets comprised 4% of sightings in 2001, usually due to insufficient viewing time, and they were not combined with identified Kittlitz's Murrelets.

Second, we assumed that changes in ice conditions or weather did not bias counts of Kittlitz's Murrelet over time. All of the soundwide surveys and most of the intensive survey, occurred from late June through July, when fast ice near glaciers breaks up, brash ice is reduced, and small vessels can maneuver farther into upper fjords (Kuletz *et al.* 2003). Floating ice could have precluded transects in the upper fjords from being surveyed during sound-wide surveys, so we examined the raw data from 1989-2000 for missed transects. Of the 41 transects in upper fjords surveyed over 7 years (n = 287), 9 were missed due to ice (3%). Five of the missed transects occurred in 1989, when the Kittlitz's Murrelet population estimate was highest (Stephensen *et al.* 2001). The remaining 4 missed transects contained 1 or 2 Kittlitz's Murrelets sighted in at least one other year. Because of the low proportion of missed transects, most of which occurred the year that Kittlitz's Murrelets were most abundant, we did not revise the population estimates to exclude those transects.

Another possible concern was that observers may have missed birds found in waters hemmed in by ice. Most of the sound-wide surveys did not use GPS, so it was not possible to determine at what point ice might have inhibited our surveys. In 2001, however, the hard-hulled whalers (also used during sound-wide surveys) were able to move into open leads and maneuvered through areas of > 50% and up to 80% ice cover. We rarely sighted Kittlitz's Murrelets in waters with ice cover > 50%, supporting previous findings in the literature (Day & Nigro 2000, Day *et al.* 2003). When the vessel's progress was blocked by ice, the observers scanned open water from the cabin top (~ 4 m above water). Because we did not detect Kittlitz's Murrelets in open leads, we believe that negligible numbers of birds were missed during PWS surveys.

Data analysis

For sound-wide surveys, we estimated the Kittlitz's Murrelet population for each year using the ratio of the total sightings to the area surveyed (Cochran 1977), and the 95% confidence intervals from the sum of the variances of each stratum (Kendall & Agler 1998). The population trend was examined by comparing the log-transformed annual estimates over time. The slope of the regression was tested for a significant deviation from zero, at the alpha 0.05 significance level. The per annum percent change in the population was derived from the back-transformed best-fit slope of the regression.

For the 2001 intensive survey, the population estimate for each fjord was derived from the average density among pelagic transects, extrapolated using the total area of the fjord (for waters > 200 m offshore), plus the total number of birds counted along the shoreline. The total population estimate was then derived by summing the individual estimates for each fjord, and calculating the 95% confidence intervals from the sum of the variances of each fjord. The population estimate for the intensive survey can only be applied to the surveyed areas and is thus a minimum estimate for the entire PWS. However, based on the sound-wide surveys since 1996, these areas encompass 86-90% of the PWS population.

We examined the distribution of Kittlitz's Murrelet over time using the sound-wide surveys, as the same transects were surveyed repeatedly every year. To map bird distributions, we used the total number seen on each transect, and the transect centroid as their location. We divided PWS into five geographically defined regions (Fig. 1). Mainland fjords occurred in the southwest, northwest, northeast, and southeast regions, and large islands and remaining pelagic waters comprised the central region. We summed the number of Kittlitz's Murrelets sighted within each region during a given year, and tested for concordance among regions over time, using Friedman's rank sum test. Due to the low counts (including zeros) in some regions and years, we combined the data into three time periods: 'early' (1989 and 1990), 'middle' (1991 and 1993), and 'late' (1996, 1998 and 2000). We tested the null hypothesis of no association among regions and changes over time at the significance level of alpha = 0.05.

To examine the current distribution of Kittlitz's Murrelet relative to glaciers, we used the intensive survey results, where all sightings was mapped using GPS. We quantified glacier status as advancing, stable, or receding, based on data through the mid-1980s (Lethcoe 1987). We tested for association between Kittlitz's Murrelet occupation of a fjord or bay (occupation was defined as > 1% of the estimated population in 2001) and glacial status of the bay, using Fisher's exact test. We contrasted the number of sites with (n = 5) or without (n = 12) Kittlitz's Murrelet occupation and the number of sites with stable or advancing glaciers (n = 4) vs. sites with retreating or no tidewater glacier (n = 13).

RESULTS

Population trends and abundance

From 1989 to 2000, the population of Kittlitz's Murrelet in PWS declined either 18% (identified only; Fig. 3) or 24% (total) per year. For identified birds, the slope of the regression ($r^2 = 0.61$) was significantly different from zero (t = -2.79, P = 0.04). The regression for total birds was similar ($r^2 = 0.57$), and the slope was still significant (t = -2.59, P = 0.05). The population estimate in 2000 was 16% and 10% of the 1989 estimate for identified and for total Kittlitz's Murrelets, respectively.

In 2001, 387 Kittlitz's Murrelets sighted on the water yielded a population estimate for the surveyed fjords of 1969 ± 1058 (95% C.I.) birds. Approximately 98% of the population occurred in five of the 17 fjords, with most (78%) in two adjacent northwest fjords, Harriman and College, with the remainder of the population in Blackstone Bay (6%), Unakwik Inlet (3%), and Icy Bay (11%). Port Nellie Juan, Long Bay, and Heather Bay together contributed only 2% of the total (Fig. 4).

Distribution over time

As the population declined over time, the distribution of Kittlitz's Murrelet in PWS has changed (Fig. 5). In 1989, Kittlitz's Murrelets were most abundant in the northwest and northeast fjords, but occurred throughout PWS, including large numbers in the southeast (Fig. 5; 1989). In 1990 and 1991, low numbers were sighted in the southwest, with most Kittlitz's occurring in the northwest and northeast fjords (Fig. 5; 1990, 1991). In 1993, which was characterized by unusually high numbers of both *Brachyramphus* species (Stephensen *et al.* 2001), there were relatively high numbers of Kittlitz's Murrelet in the central region (Fig. 5; 1993). In 1996 (Fig. 5; 1996), 1998 (which had a distribution similar to 1996 but fewer birds), and 2000 (Fig. 5;

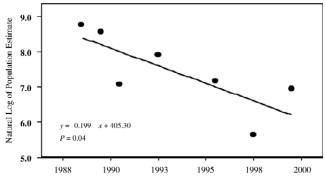


Fig. 3. Population trend of identified Kittlitz's Murrelets in Prince William Sound, based on sound-wide surveys during 1989-2000.

2000), there was a marked absence of Kittlitz's Murrelet throughout most of PWS, except for the northwest region.

The observed changes in Kittlitz's Murrelet abundance were not synchronous across the five regions we surveyed (Friedman's chisquare = 7.2, df = 4, P = 0.13), suggesting that the onset of the decline varied across the study area. Although all five regions showed a decline between the beginning (1989-90) and the end (1996-2000) of our study, numbers in the southeast remained low after 1989-90, while numbers in the southwest and central regions peaked during the middle period (1991-93) (Fig. 6a). The northwest always had the highest numbers, and supported a greater proportion of the total population over time, comprising up to 55% of the PWS population during the late period (1996-2000) (Fig. 6b). The proportion in the northeast remained stable at about 22% of the total, while the proportions in other regions declined or, following temporarily higher proportions during the middle period, declined in the late period.

Distribution relative to glaciers

In 2001, Kittlitz's Murrelets generally occupied the upper regions of fjords, usually near tidewater glaciers or the outflow from recently grounded glaciers (Fig. 4). Among fjords, their distribution was highly correlated with the status of surrounding glaciers. Substantial numbers (> 1% of the PWS population at a given site) were found at all four sites with stable or advancing glaciers and at only one of the 13 sites with retreating or non-tidewater glaciers (n = 17; Fisher's exact test, P = 0.002). The Harriman and College fjords are surrounded by the greatest number of glaciers (Fig. 4),

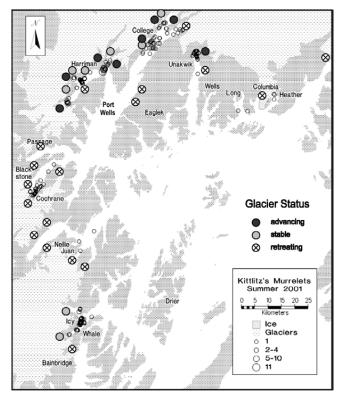


Fig. 4. Distribution of Kittlitz's Murrelets (open circles) during the 2001 intensive survey of Prince William Sound, and the status of tidewater and near-shore glaciers, based on Lethcoe (1987). Each circle represents an observation, with a different number of possible birds (1-11) per sighting.

most of which were classified in the 1980s as stable or advancing. Similarly, advancing or stable glaciers occurred at the terminus of Unakwik Inlet and Icy Bay, where we observed many Kittlitz's Murrelets. In other areas, glaciers were retreating by the 1980s, and of these, only Blackstone fjord retained substantial numbers of Kittlitz's Murrelet.

DISCUSSION

Kittlitz's Murrelets have declined dramatically in PWS during the 12 years of this study, and possibly for the past 30 years (Kendall & Agler 1998). However, little attention was given to this small, non-colonial bird until the 1989 *Exxon Valdez* oil spill, when it was

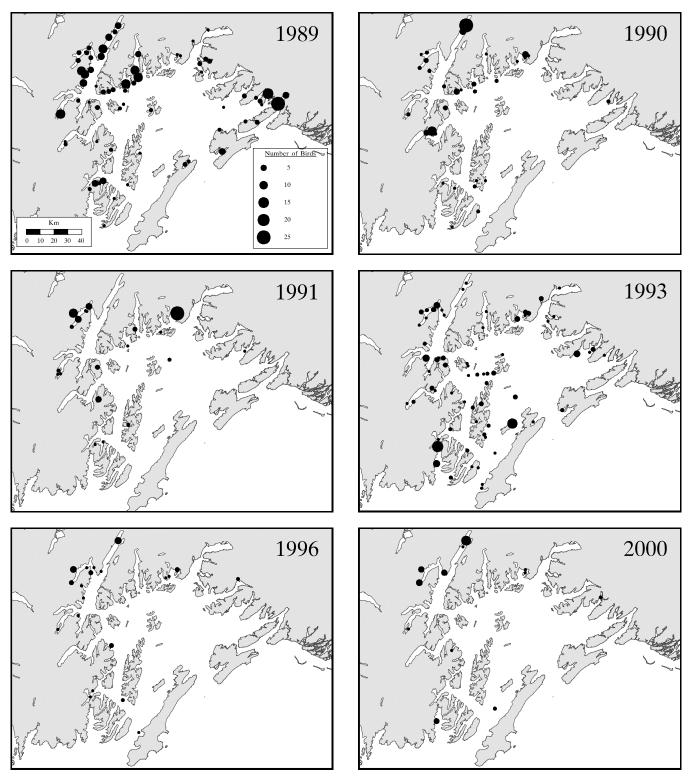


Fig. 5. Distribution of Kittlitz's Murrelets (filled circles) along randomly selected transects during the sound-wide surveys, 1989-2000. Each circle represents the total number of birds sighted on that transect.

suggested that, relative to its small population, it was the most affected species of marine bird (van Vliet & McAllister 1994). Since the oil spill, population trends in the GOA have been assessed in three other regions beyond PWS – the Kenai Fjords west of PWS (Van Pelt & Piatt 2003), the Malaspina Forelands east of PWS (USFWS 2003), and Glacier Bay farther south (Robards *et al.* 2003) – Kittlitz's Murrelets have declined dramatically in all of them. Little is known about their ecology and this paper is a step towards identifying the factors that may be influencing the population declines.

Distribution relative to glaciers

Our results support the observation that Kittlitz's Murrelets associate with tidewater glaciers (Isleib & Kessel 1973, Kendall & Agler 1998, Day et al. 1999, 2003), and more importantly, the hypothesis that their distribution is affected by glacier status. The northwest region of PWS contained ~ 30-45% of the estimated Kittlitz's Murrelet population through the mid-1990s, but today, it supports between 55% (based on 2000 sound-wide surveys) and 84% (2001 intensive survey) of the PWS population. The concentration in northwest PWS, where more glaciers are stable or advancing (Lethcoe 1987, Molnia 2001), suggests a strong association with the phase of advancement or recession exhibited by surrounding glaciers. In particular, Harriman fjord, with eight stable or advancing glaciers, supported ~ 58% of the estimated PWS population in 2001. The high number of 'healthy' (i.e., nonretreating) glaciers in this region is likely a consequence of the local topography, which promotes low atmospheric temperatures and high snow fall (Molnia 2001).

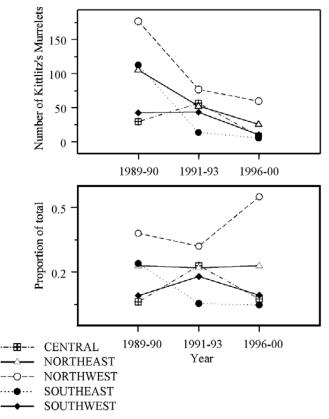


Fig. 6. Total number of Kittlitz's Murrelets (A; top) and proportion of total murrelets (B; bottom) for three time periods in five regions of Prince William Sound. Data are from the 1989-2000 sound-wide surveys.

The reported status of PWS glaciers was based on data from the mid or late 1980s (Lethcoe 1987), just prior to the decrease in the Kittlitz's population documented here. Many of these glaciers, however, have been retreating over at least the past 50 years (Lethcoe 1987, Molnia 2001, Arendt *et al.* 2002), and it is possible that the response of Kittlitz's Murrelet to changes in these glaciers began before our sound-wide surveys were initiated. Indeed, a PWS survey in 1972, using a different study design, revealed a population closer to 60 000 birds (63 229 ± 80 122 95% C.I.; Klosiewski & Laing 1994). The large confidence interval of this estimate requires caution in interpretation, but a population near that size in the early 1970s would suggest that Kittlitz's Murrelet has been declining in PWS over several decades.

The change in distribution of Kittlitz's Murrelet among PWS fjords in recent years may reflect changes in the fjords themselves. Among Alaskan glaciers, those in the Chugach Mountains have exceptionally high rates of volume change (Arendt *et al.* 2002). It is generally recognized that atmospheric temperature is linked to changes in glaciers (Root *et al.* 2003), but the connection is complicated by local topography and weather (Molnia 2001, Arendt *et al.* 2002). Physical and biological differences among the fjords themselves likewise may determine their attractiveness to Kittlitz's Murrelet. Even while only a few kilometers apart, neighboring fjords can vary tremendously because tidal effects, eddies, sediment load, and productivity depend on topography and drainage conditions, which are influenced by the glacier's movements (Svendsen 1995).

Biological link to glaciers

The attraction of Kittlitz's Murrelet to glacial outflow has been well documented (Day et al. 1999, 2003, this study), but the mechanisms responsible for this association remain unknown. In PWS, their near-exclusive use of tidewater glacier fjords suggests strong physical or biological links. The sparse information available on food preferences indicate that macrozooplankton and amphipods may at times comprise a large portion of their diet, but Kittlitz's Murrelets also show a high degree of dietary overlap with Marbled Murrelets (Day et al. 1999, Day & Nigro 2000). Kittlitz's Murrelets in PWS eat a variety of forage fish, including Pacific sandlance Ammodytes hexapterus, Pacific herring Clupea pallasi, and capelin Mallotus villosus (Day & Nigro 2000, Piatt unpublished data, KJK, pers. obs.). These prey species are available in many areas of PWS and rich forage sites outside the fjords attract Marbled Murrelets and other seabirds (Ostrand et al. 1998, Brown 2002, Ainley et al. 2003), suggesting that prey distribution is not entirely dictating the Kittlitz's Murrelet distribution. Day et al. (2003) proposed that Kittlitz's Murrelets, while remaining food generalists, have specialized to better compete for food in a habitat not easily exploited by other seabirds. They appear to select waters with low surface water clarity, and Day et al. (2003) speculated that their proportionately large eyes may be an adaptation to foraging under such conditions.

If Kittlitz's Murrelet is better adapted than other birds to forage in glacial waters with high sediment loads, they may have access to otherwise under-utilized resources. Macrozooplankton can be concentrated in dense patches in inner fjords via advection and entrapment by estuarine and tidally-induced currents (Weslawski *et al.* 2000, Zajaczkowski & Legezynska 2001), which might also attract fish. The undersides of icebergs and pack ice, and the upwelling that often occurs at glacial sills or at the face of a glacier,

are small-scale features that can increase prey abundance or availability for seabirds (Hunt & Schneider 1987). The presence of ice alone, however, does not attract Kittlitz's Murrelet, since both retreating and advancing glaciers calve (Molnia 2001) and brash ice was present in areas without Kittlitz's (KJK, unpublished). Investigating the attributes of this dynamic foraging habitat will be critical to understanding the Kittlitz's ecology.

The mystery of why stable or advancing glaciers attract Kittlitz's Murrelet, while retreating glaciers do not, may require investigating differences in sedimentation rates and associated characteristics among glacier types. Fjords in the North Atlantic with receding glaciers tend to have higher sedimentation rates and lower salinity due to glacial ablation, which can lower primary productivity and diversity of benthos (Weslawski et al. 1995) and reduces the feeding ability and survival of macrozooplankton (Weslawski et al. 2000, Zajaczkowski & Legezynska 2001). The onset of the spring plankton bloom in fjords appears to depend partly on the resuspension of resting spores in the sediment, which might be impaired with increased sedimentation (Hegseth et al. 1995). A working hypothesis behind this physical-biological coupling is that the lack of a phytoplankton bloom and the increased mortality of macrozooplankton reduce the biomass of invertebrates and of forage fish. Kittlitz's Murrelets could thus be affected at multiple trophic levels, since they feed on euphausiids, amphipods, and small crustacea as well as fish. (Day et al. 1999, Day & Nigro 2000). The reduction in water transparency in fjords with retreating glaciers (Weslawski et al. 1995), might also reach a threshold where Kittlitz's Murrelet foraging success, even while adapted for low-visibility foraging, may be detrimentally affected.

Implications for the future

Recent analyses indicated that some PWS glaciers which had been categorized as stable or advancing (Lethcoe 1987), including five in the northwest region, shifted into receding phases in the 1990s (Molnia 2001, & pers. comm.). Our results suggest that continued wastage of these glaciers may precipitate future declines in the PWS Kittlitz's Murrelet population. Similarly, the decline of Kittlitz's Murrelet populations in other regions of the GOA can be expected to continue, particularly if glacial recession lags nearly half a century behind changes in climate (Arendt *et al.* 2002).

Kittlitz's Murrelets inhabit some non-glacial areas of Alaska (Day et al. 1999), but these populations are small and possibly isolated, as indicated by the genetic distinctiveness identified between populations in the Aleutian Islands and the northern GOA (Pitocchelli et al. 1995). Kittlitz's Murrelet is thought to have evolved during the Pleistocene (Pitocchelli et al. 1995, Friesen et al. 1996), and thus to have survived periods of glacial recession. However, Root et al. (2003) noted that for such species the cumulative effects of rapid environmental change, worsened by habitat loss, fragmentation of populations, and other anthropogenic impacts, are unprecedented. In addition to changes in their habitat, Kittlitz's Murrelets are confronted with oil spills and incidental take in gillnets, and possibly, disturbance from increased boat traffic near tidewater glaciers (Day et al. 1999, 2003, USFWS 2003). The cumulative effects of these stressors could impinge on the ability of some Kittlitz's Murrelet populations to adapt to global warming.

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