

Coping with the Cold: An Ecological Context for the Abundance and Distribution of Rock Sandpipers during Winter in Upper Cook Inlet, Alaska

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ABSTRACT. Shorebirds are conspicuous and abundant at high northern latitudes during spring and summer, but as seasonal conditions deteriorate, few remain during winter. To the best of our knowledge, Cook Inlet, Alaska (60.6° N, 151.6° W), is the world's coldest site that regularly supports wintering populations of shorebirds, and it is also the most northerly nonbreeding location for shorebirds in the Pacific Basin. During the winters of 1997–2012, we conducted aerial surveys of upper Cook Inlet to document the spatial and temporal distribution and number of Rock Sandpipers (*Calidris ptilocnemis*) using the inlet. The average survey total was 8191 ± 6143 SD birds, and the average of each winter season's highest single-day count was 13 603 ± 4948 SD birds. We detected only Rock Sandpipers during our surveys, essentially all of which were individuals of the nominate subspecies (*C. p. ptilocnemis*). Survey totals in some winters closely matched the population estimate for this subspecies, demonstrating the region's importance as a nonbreeding resource to the subspecies. Birds were most often found at only a handful of sites in upper Cook Inlet, but shifted their distribution to more southerly locations in the inlet during periods of extreme cold. Two environmental factors allow Rock Sandpipers to inhabit Cook Inlet during winter: 1) an abundant bivalve (*Macoma balthica*) food source and 2) current and tidal dynamics that keep foraging substrates accessible during all but extreme periods of cold and ice accretion. *C. p. ptilocnemis* is a subspecies of high conservation concern for which annual winter surveys may serve as a relatively inexpensive population-monitoring tool that will also provide insight into adaptations that allow these birds to exploit high-latitude environments in winter.

Key words: Alaska, *Calidris ptilocnemis*, cold adaptations, Cook Inlet, *Macoma balthica*, Rock Sandpiper, winter distribution

RÉSUMÉ. Le printemps et l'été, les oiseaux de rivage abondent et sont bien en vue dans les latitudes de l'extrême nord, mais au fur et à mesure que les conditions saisonnières se détériorent, peu d'entre eux hivernent dans ces régions. Au meilleur de nos connaissances, l'anse Cook, en Alaska (60,6° N, 151,6° O), est l'endroit le plus froid du monde où l'on trouve régulièrement des populations d'oiseaux de rivage l'hiver. Il s'agit aussi de l'emplacement le plus nordique du bassin du Pacifique à ne pas être consacré à la reproduction des oiseaux de rivage. Au cours des hivers allant de 1997 à 2012, nous avons réalisé des levés aériens de la partie supérieure de l'anse Cook afin d'être en mesure de répertorier la répartition spatiale, la répartition temporelle et le nombre de bécasseaux des Aléoutiennes (*Calidris ptilocnemis*) dans l'anse. Le total moyen des levés a permis de repérer 8 191 ± 6 143 (DS) oiseaux, tandis que la moyenne du dénombrement le plus élevé au cours d'une seule journée d'hiver était de 13 603 ± 4 948 (DS) oiseaux. Dans le cadre de nos levés, nous n'avons détecté que des bécasseaux des Aléoutiennes, dont tous étaient essentiellement des individus de la sous-espèce désignée (*C. p. ptilocnemis*). Au cours de certains hivers, les totaux des levés se rapprochaient beaucoup des estimations de population de cette sous-espèce, ce qui laisse entrevoir l'importance de cette région en tant que ressource de non-reproduction pour cette sous-espèce. La plupart du temps, ces oiseaux ne se retrouvaient qu'à quelques endroits de la partie supérieure de l'anse Cook, bien qu'ils se répartissent plus au sud de l'anse pendant les périodes de froid extrême. Deux facteurs environnementaux permettent aux bécasseaux des Aléoutiennes d'évoluer dans l'anse Cook l'hiver : 1) une source abondante de nourriture acéphale (*Macoma balthica*) et 2) une dynamique de courants et de marées qui a constamment pour effet d'alimenter les oiseaux en substrat pendant toutes les périodes, sauf celles de froid extrême et d'accrétion de glace. *C. p. ptilocnemis* est une sous-espèce dont la conservation présente de grandes inquiétudes et pour laquelle les levés hivernaux annuels peuvent constituer un outil de surveillance de population relativement abordable qui permettra également d'en savoir plus sur les adaptations qui permettent à ces oiseaux d'exploiter les milieux de haute latitude l'hiver.

Mots clés : Alaska, *Calidris ptilocnemis*, adaptations au froid, anse Cook, *Macoma balthica*, bécasseau des Aléoutiennes, répartition hivernale

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INTRODUCTION

Birds exemplify many of the adaptations that have enabled animals to inhabit high-latitude regions year-round. Many species have evolved behavioral and physiological adaptations that promote survival during winter at high northern latitudes when food becomes scarce and environmental conditions are extreme. For example, marine birds (e.g., Spectacled Eider *Somateria fischeri*, Thick-billed Murre *Uria lomvia*) occupy isolated but seasonally predictable areas free of sea ice, where they feed on lipid-rich prey (Gaston and Hipfner, 2000; Lovvorn et al., 2003), while frugivorous and granivorous passerines (e.g., Pine Grosbeak *Pinicola enucleator*, Black-capped Chickadee *Poecile atricapillus*) exhibit behavioral adaptations such as irruptive movements in search of food (Newton, 2006), food caching (Hitchcock and Sherry, 1990), and communal cavity roosting (Cooper, 1999).

Such adaptations are the exception, however. Most northern-breeding birds instead migrate south in response to the onset of deteriorating conditions in autumn. This pattern is particularly evident in Arctic-nesting shorebirds (order Charadriiformes, suborders Scolopaci and Charadrii), which have relatively high daily energy requirements and mostly forage by probing in soft substrates (Kersten and Piersma, 1987; Piersma et al., 1996, 2003). The onset of winter at high latitudes greatly reduces food resources, and freezing conditions preclude shorebirds from probing for food in preferred wetland and estuarine habitats.

A few species of small sandpipers, however, have overcome these limitations, most notably the Purple Sandpiper (*Calidris maritima*), which in Norway occurs in winter as far as 71° N (Summers et al., 1990) under prolonged periods of complete darkness, cold temperatures, and steady wind (Summers et al., 1998). Because of advection patterns and the moderating influence of the Gulf Stream current (Seager et al., 2002), marine intertidal substrates along the northeast Atlantic coast seldom freeze, allowing Purple Sandpipers predictable access to intertidal food resources (Summers et al., 1998).

In the North Pacific, the counterpart to the Purple Sandpiper is the closely related Rock Sandpiper (*C. ptilocnemis*; Conover, 1944; Pruett and Winker, 2005). Rock Sandpipers have the most northerly nonbreeding distribution of any shorebird in the Pacific Basin, and the species is common in Alaska throughout the winter as far north as 61° N (Gill et al., 2002). These nonbreeding sites, though farther south than sites used by Purple Sandpipers in Norway, experience more severe winter conditions, including periods of extreme cold, persistent sea ice, as well as snow and ice that regularly cover intertidal habitats (Poole and Hufford, 1982; Gallant et al., 1995).

Given such conditions, it was not until relatively recently that Rock Sandpipers were even suspected of occurring in south-central Alaska in winter. In February 1976, Erikson (1977:14) observed “several large flocks of...probably Rock Sandpipers” in Tuxedni Bay, Cook Inlet. A decade passed

before biologists again observed small sandpipers on partially frozen mudflats during aerial surveys in late fall and early spring (Butler and Gill, 1987; W. Eldridge, pers. comm. 1996). Building on these observations, work was initiated in the late 1990s to determine the seasonal status of shorebirds occurring in upper Cook Inlet, Alaska (Gill and Tibbitts, 1999). These studies involved aerial surveys and ground observations of birds and sampling of potential foods (consisting primarily of the bivalve *Macoma balthica*) on intertidal areas (Gill and Tibbitts, 1999; Gill et al., 2002).

In this paper we summarize data collected over a 16-year period (1997–2012) to assess the seasonal distribution and abundance of Rock Sandpipers during winter in upper Cook Inlet. We also summarize benthic invertebrate collections and long-term climatological information to describe the behavioral, biotic, and abiotic factors that influence the occurrence of Rock Sandpipers at the northern extreme of their wintering range.

METHODS

Study Area and Winter Setting

We studied Rock Sandpipers in Cook Inlet, Alaska (60.6° N, 151.6° W; Fig. 1), a ~280 km long by 20–70 km wide estuary fed by glacially derived rivers. The Inlet is characterized by extensive mudflats interspersed with rocky coastline and high bluffs, and tidal amplitudes that can exceed 10 m (Oey et al., 2007). Circulation patterns in Cook Inlet are driven by river runoff (Kyle and Brabets, 2001). Currents of up to 1 m s⁻¹ sweep strongly south along the western edge of the Inlet and flow more gently to the north along the eastern shores, inducing a general counterclockwise flow (Johnson, 2008).

Average daily high temperature for the city of Anchorage, in upper Cook Inlet (Fig. 1), is at or below 0°C between early November and mid-March (Fig. 2). The daily temperature in January, the coldest month, averages -9.4°C (National Climatic Data Center, 2012). The coldest period of winter also coincides with the period of shortest day lengths (U.S. Naval Observatory, 2012; Fig. 2): at the winter solstice, the day length at 61° N is 5 hours and 27 minutes (Fig. 2). The formation of sea ice is driven primarily by air temperature. In upper Cook Inlet, sub-zero temperatures typically cause significant sea ice to form beginning in late November (Poole and Hufford, 1982). Shore-fast ice and stranded bergs can persist through mid-April in upper Cook Inlet.

Data Collection

We assessed the seasonal distribution and abundance of Rock Sandpipers using aerial surveys. We conducted surveys each year from February 1997 to March 2012, typically flying at least one survey per month between October

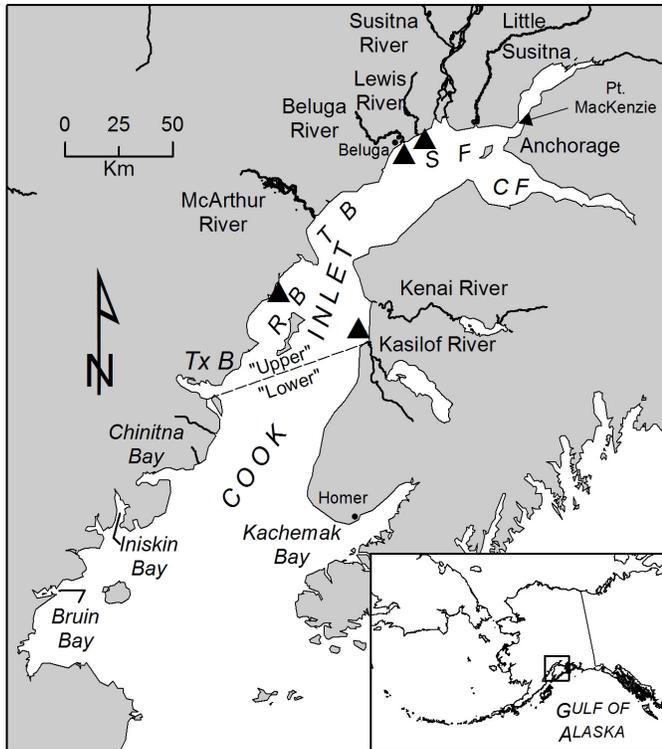


FIG. 1. Primary survey sites of Cook Inlet, Alaska. Upper Cook Inlet was the location of aerial shorebird surveys conducted during winters from 1997 to 2012. Abbreviated site names (clockwise, from top): SF = Susitna Flats, CF = Chickaloon Flats, Tx B = Tuxedni Bay, RB = Redoubt Bay, TB = Trading Bay. Sites of benthic sampling are marked by triangles; place names are mentioned in the text.

and April. We routinely surveyed six segments of the upper Cook Inlet shoreline: 1) the Susitna Flats from Point MacKenzie to Beluga (~58 km of shoreline), 2) Trading Bay (~28 km), 3) Redoubt Bay (~41 km), 4) Tuxedni Bay (~37 km), 5) the mouths of the Kasilof and Kenai Rivers, and 6) Chickaloon Flats (~23 km; Fig. 1). These segments are composed primarily of intertidal mudflats and sandflats connected to adjacent segments by steep bluffs, with rocky cobble intertidal habitats. Because we never detected shorebirds on these rocky connecting sections during the initial years of the study, we often overflowed these areas in later years. On 19 December 2001, we also conducted a survey of Bruin, Chinitna, and Iniskin Bays in lower Cook Inlet (Fig. 1). The importance to Rock Sandpipers of certain sites (e.g., the mouths of the Kasilof and Kenai Rivers) did not become known to us until 2006, but these sites were surveyed regularly thereafter.

We were unable to survey all segments of the main study area on all occasions because of unsafe flying conditions. We conducted surveys during diurnal periods and timed our route on the basis of the tide cycle to maximize observation conditions; however, other factors also affected survey timing, including the marked change in day length during winter and the varying length and breadth of mudflats among segments. We nevertheless tried to fly surveys when mudflats were only partially exposed to minimize search time and increase the likelihood of detecting shorebirds. Surveys

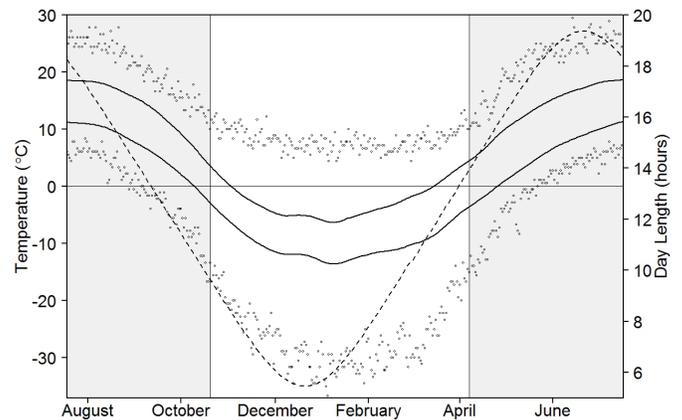


FIG. 2. Average daily high and low temperatures (solid lines) and extreme values (dots) recorded from 1952 to 2012 in Anchorage, Alaska. Day length (dotted line) is plotted on the right axis. The non-shaded portion depicts the approximate period of occurrence of Rock Sandpipers in upper Cook Inlet, Alaska.

were conducted by one observer in single-engine, fixed-wing aircraft flown at 185 km/h indicated air speed and at an altitude of about 50 m above sea level; pilots assisted with detecting birds, but only observers estimated flock sizes. Observers recorded the size and location of each flock on a gridded topographic map (cell width 1 km), and took photographs of large flocks whenever possible in order to correct flock-size estimates. After surveys, flock locations were transferred to a geospatial database, and flock size estimates were photo-corrected. For the sake of our summaries, single birds constituted flocks of one bird.

We opportunistically conducted ground-based observations independently of aerial surveys to determine the identification of birds recorded on aerial surveys. Because it was difficult to access most sites in winter, on-ground assessment was limited to the mouths of the Beluga, Kasilof, and Kenai Rivers and portions of Kachemak Bay near Homer (Fig. 1). To distinguish subspecies of Rock Sandpipers seen on the ground we followed criteria described in Gill et al. (2002) to separate the lighter nominate form (*C. p. ptilocnemis*) from the two darker forms (*C. p. couesi* and *C. p. tschuktschorum*) that might also occur in the area (Gill et al., 2002). The nonbreeding distributions of these three subspecies had not previously been well defined (Gill et al., 2002), and subspecies may overlap at the extremes of their ranges.

We also assessed the potential foods available to Rock Sandpipers. We sampled the diversity and abundance of intertidal benthos along transects at four sites in upper Cook Inlet. At each site we randomly spaced a series of transects (0.18–1.80 km) parallel to each other and oriented perpendicular to shore; these included three transects each near the Beluga and Lewis Rivers at Susitna Flats, three at Redoubt Bay, and two at the Kasilof River (Fig. 1). We divided the mudflats into 250 m wide parallel zones that extended seaward from the vegetated shoreline (four zones at Susitna Flats and Redoubt Bay, three zones at the smaller

Kasilof River). Along each transect, we randomly allocated five sampling locations per zone. At each location, we collected a core sample (10 cm diameter × 20 cm deep) from the substrate. Samples were stored in plastic bags and sorted as soon as possible after collection by flushing the contents with water over a 1 mm sieve.

Aerial Survey Analysis

We summarized the survey results to determine the winter residency period of shorebirds in upper Cook Inlet, as well as their seasonal, interannual, and geographic patterns of occurrence. The minimum period of residency was defined as the first and last surveys on which birds were detected during each winter period.

We assumed that observers detected all flocks in the surveyed areas and correctly counted the numbers of individuals in flocks of 100 or fewer birds ($n = 713$ flocks, 57% of all flocks). However, we assumed that errors likely occurred in estimating the sizes of large flocks. To estimate the magnitude of observer bias, the two primary observers in this study each photographed a subsample of flocks (R.E. Gill, $n = 70$; D.R. Ruthrauff, $n = 26$) during several surveys to compare with their estimated flock sizes. Using these photographs, we constructed a no-intercept linear model of actual photo-counts as a function of estimated flock size and observer, after first log-transforming actual and estimated flock sizes to meet the assumptions of normality and constancy of error variances. Because estimation bias differed significantly between observers ($p < 0.05$), we derived separate models for the two observers. Actual flock sizes were typically larger than those estimated: the ratios were 1.0005 ± 0.0035 SE for Gill and 1.02 ± 0.01 SE for Ruthrauff. To derive model-corrected values for flocks of more than 100 birds that were not photographed, we multiplied log-transformed estimates by these observer-specific parameters and back-transformed the results. T.L. Tibbitts conducted one survey on which no photo-verification images were collected, so that survey's estimates were not adjusted. Unless otherwise noted, reported values represent mean \pm SD.

Climatological and Environmental Analyses

We identified benthic specimens to the lowest practical taxonomic level and measured the length of all bivalve shells to the nearest 1.0 mm (see DeKinga and Piersma, 1993). We determined the density (individuals/m² \pm SE) of prey items per transect for each site and calculated the site's overall mean using a two-stage sampling estimator. Because we made our benthic collections during four different months over 11 years, we did not compare invertebrate densities between sites using formal statistical analyses.

To describe the winter environment of the upper Cook Inlet region, we summarized temperature information from Anchorage, Alaska, over the period 1952–2012.

We deployed temperature loggers in two winter seasons (1998–99 and 1999–2000) at the Ivan River and Trading Bay (Fig. 1) to determine how Anchorage winter temperatures compared to those at sites where shorebirds were detected. Average daily temperatures recorded by data loggers at the Ivan River and Trading Bay during those two winters were highly correlated with average daily temperatures in Anchorage ($R \geq 0.94$ for both sites), and temperatures were slightly colder in Anchorage. The average temperature difference between Anchorage and the Ivan River was $0.1 \pm 2.8^\circ\text{C}$; between Anchorage and Trading Bay, it was $0.9 \pm 2.8^\circ\text{C}$.

We calculated the extent of mudflat at survey sites in upper Cook Inlet using National Oceanic and Atmospheric Administration (NOAA) Environmental Sensitivity Index (ESI) geographic information system (GIS) shapefiles (NOAA, 2012). During aerial surveys, we noted the presence of sea ice and shore-fast ice and used these observations to delimit the period of sea ice presence in the study area. We used digitized NOAA/National Ice Center (NIC) ice analysis GIS products derived from satellite imagery of Cook Inlet to estimate the extent of shore-fast ice that had accreted on mudflats (NIC, 2012). We restricted our analysis to the period from 27 January 2006 to 16 March 2012 (the date of our last survey) to coincide with a period of methodological consistency and greater accuracy of the NIC products. We have assumed that data from this period are representative of average annual ice dynamics in upper Cook Inlet throughout the study period. We used the last (i.e., latest in month) image from each month to estimate the areal extent of shore-fast ice for each year, and we compared site-specific monthly values of shore-fast ice during winter to ice-free totals calculated from the NOAA ESI shapefiles to determine the proportion of ice-covered mudflat unavailable to sandpipers.

RESULTS

Aerial Surveys and Ground Observations

We conducted 99 aerial surveys over 16 winter seasons from February 1997 to March 2012. Surveys were conducted as early as 28 August and as late as 1 May. We flew an average of 6.2 ± 3.6 SD surveys (range 1–14) during each of the 16 winters. Seasonal survey effort was similarly comprehensive, averaging 6.2 ± 2.8 SD surveys (range 1–10) during each two-week period across all years combined (Fig. 3). The earliest shorebird detection on surveys was on 6 October (2001), while the latest detection occurred on 13 April (2002). We did not detect any birds on 11 surveys (11.1%), nine of which occurred either early ($n = 3$) or late ($n = 6$) in the winter season when we were trying to determine periods of arrival and departure (Fig. 3). The two mid-season surveys during which no birds were detected (19 January 2004 and 22 February 2006) were unavoidably conducted during high tides. The lack of birds on these

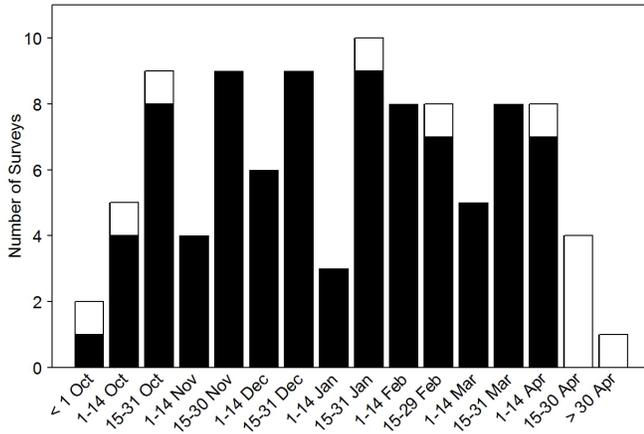


FIG. 3. Timing of aerial shorebird surveys ($n = 99$) of upper Cook Inlet, Alaska, during winter, by two-week intervals. The open portion of bars represents the number of surveys on which no birds were detected; the filled portion shows surveys on which one or more birds were detected.

surveys was likely due to suboptimal survey conditions (i.e., birds may have been roosting along shore and gone undetected) and not necessarily to their absence from the study area. In order to focus our findings on the period of winter residency in upper Cook Inlet, all results presented below (unless otherwise noted) concern surveys during which one bird or more was detected.

Birds were detected primarily on mudflats and sandflats, or, less commonly, roosting along shores or on sea ice. We did not detect any birds along rocky or cobble shorelines. On the basis of their size, flight behavior, and dorsal wing patterning, all birds seen on aerial surveys were tentatively identified as Rock Sandpipers. Ground observations confirmed that only Rock Sandpipers occurred in upper Cook Inlet during winter and that nearly all belonged to the nominate subspecies, *C. p. ptilocnemis* (Table 1). Farther south (e.g., Homer; Fig. 1), dark-plumage birds (*C. p. couesi* or *C. p. tschuktschorum*) predominated (Table 1).

Rock Sandpiper Abundance

Model corrections increased Gill's flock size estimates by an average of $0.31 \pm 0.05\%$ and Ruthrauff's by an average of $12.7 \pm 2.5\%$. Hereafter, all results report model-corrected

counts. We detected 1258 flocks of Rock Sandpipers during the surveys. The average flock size was 573 ± 1311 birds (range 1–12904; median = 75). The highest single-day count (22913 birds) occurred on 4 March 1998, and the lowest season-high count (4453 birds) occurred on 23 January 2010 (Fig. 4). Across the entire study period, the average survey total (not including surveys when no birds were detected) was 8191 ± 6143 Rock Sandpipers, and the average highest single-day count for each winter season was 13603 ± 4948 Rock Sandpipers.

Site Preference and Movements

Rock Sandpipers consistently used specific locations both between and within seasons (Fig. 5). Rock Sandpipers were most often encountered at Susitna Flats (on 85.2% of all surveys conducted there), Trading Bay (71.2%), and the Kasilof River (44.4%; Fig. 5). The greatest proportion of birds recorded during surveys occurred at Susitna Flats (mean of survey totals = 58.9%), followed by the Kasilof River (29.5%), and Trading Bay (28.6%; Fig. 5). Birds were also detected on a high proportion of surveys at Redoubt Bay (45.8%), but typically their overall numbers were low (average proportion of survey total = 9.0%; Fig. 5).

Rock Sandpipers also exhibited preferential use of sites within each of the major survey segments. For example, of the 416188 total birds recorded at Susitna Flats, most (56.8%) were detected along a 7 km long stretch of intertidal flats (~12% of the segment total) between the Lewis and Beluga Rivers (Fig. 1). The same stretch, when assessed in terms of the overall proportion of surveys on which birds were recorded, revealed a similar rate of occurrence (65.9%). The next most used site was a 5 km long portion (~18% of the segment total) near the mouth of the McArthur River in Trading Bay (Fig. 1), where 46.3% of all Rock Sandpipers observed at Trading Bay ($n = 190891$ birds total) were detected. Birds were observed at this site on 37.5% of surveys.

On two occasions the occurrence and distribution of Rock Sandpipers in upper Cook Inlet appeared to be influenced by prolonged periods of deep cold. In the first instance, documented over five consecutive surveys from December 1998 to March 1999, numbers of birds fluctuated from 12595 birds on 21 December 1998 to a low of 3194

TABLE 1. Ground-based identification of Rock Sandpiper subspecies sampled in winter at sites in Cook Inlet, Alaska.

| Site | Date | Percent dark-plumage Rock Sandpipers ¹ | # Birds in sample pool |
|---------------|------------------|---|------------------------|
| Beluga River | 26 February 2004 | 3.2 ± 0.4 SE ² | 5000 |
| Kasilof River | 18 December 2007 | $\leq 1^3$ | 7500 |
| | 19 December 2007 | $\leq 1^3$ | 4400 |
| | 5 February 2009 | $\leq 1^3$ | 3884 |
| | 18 March 2011 | 81.6 ± 1.7 SE ⁴ | 3648 |

¹ See Gill et al. (2002) for plumage characteristics used to distinguish subspecies.

² Value represents average of 52 subsamples from flock (group size 8–50 Rock Sandpipers).

³ Five or fewer dark-plumage individuals observed each day.

⁴ Value represents average of 13 subsamples from flock (group size 9–69 Rock Sandpipers).

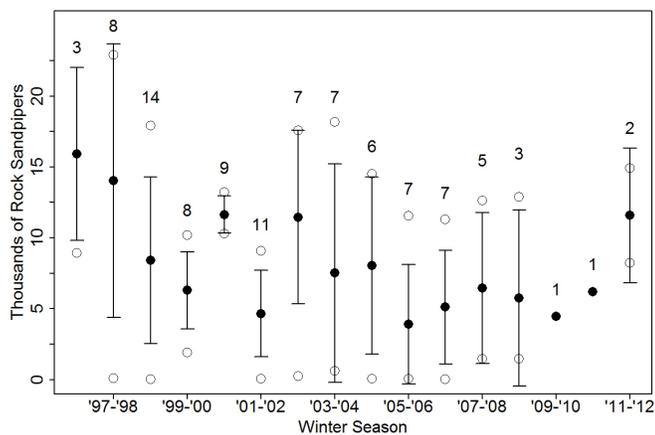


FIG. 4. Winter aerial survey results, upper Cook Inlet, Alaska, 1997–2012. Filled circle is the average number of Rock Sandpipers detected per winter season, whiskers are SD, and open circles represent seasonal maximum and minimum counts. Plotted values include only surveys on which Rock Sandpipers were detected, but numbers represent the total number of surveys flown each winter season, including those on which no birds were detected. Values are corrected for errors in observer estimation of flock size (see Methods).

on 2 February 1999 and returned to late-December levels of 11 938 birds on 4 March 1999. The mean high (-17.9°C) and low (-26.5°C) temperatures from 29 January to 13 February 1999, the period when the fewest birds were recorded, represented deviations of as much as 20°C from long-term average temperatures. The lowest temperature recorded during this period was -33.3°C . The second occasion, on 19 December 2001, also coincided with a period of unusual cold, with temperature deviations as much as 13°C below normal. As in the first case, survey numbers declined in concert with the period of deep cold and rebounded as temperatures normalized. We also surveyed sites on the east side of the lower portion of Cook Inlet (e.g., Bruin, Chin- itna, and Iniskin Bays, Fig. 1) on 19 December. We did not detect any shorebirds in this region, indicating that many Rock Sandpipers had likely departed the Cook Inlet region entirely.

Rock Sandpipers also appeared to move from north to south within upper Cook Inlet during these two cold periods. Across the five surveys encompassing December 1998–March 1999, the percent of survey totals comprised by Susitna Flats and Trading Bay dropped from 100% (21 December 1998) to 0% (8 February 1999), and increased back to 100% once temperatures normalized (4 March 1999). Concordantly, the percent of survey totals at Redoubt and Tuxedni Bays rose from 0% on 21 December 1998 to 99.2% (36.7% at Redoubt and 62.5% at Tuxedni) on 8 February 1999 and then declined to 0% (4 March 1999). The 19 December 2001 survey was characterized by a similar displacement of birds from Susitna Flats and Trading Bay to Redoubt and Tuxedni Bays. These two periods of unusual cold were the only times when we detected more than 1000 Rock Sandpipers in Tuxedni Bay.

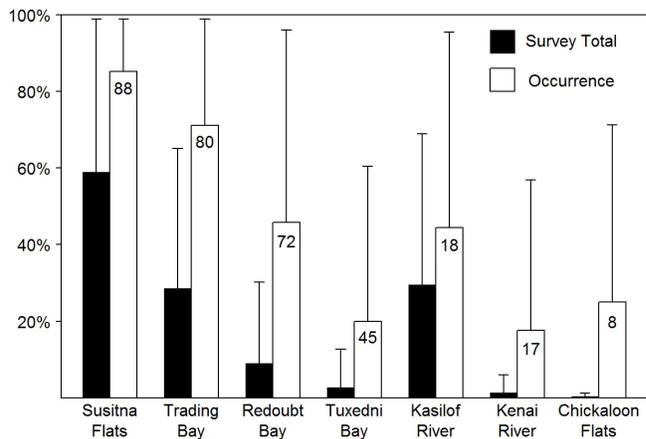


FIG. 5. Occurrence of Rock Sandpipers at primary winter aerial survey sites in upper Cook Inlet, Alaska, 1997–2012. The figure depicts only frequently surveyed sites and only surveys when birds were detected ($n = 88$ out of 99 total surveys). Numbers in the white bars represent the number of times each site was surveyed, including surveys when birds were not detected at that particular site. Not all sites were visited during each survey (see text). For each site, the black bar represents the mean (\pm SD) percentage of survey total, and the white bar, the mean (\pm SD) percent occurrence of birds. For example, Susitna Flats was surveyed 88 times, and Rock Sandpipers were detected on 85% of those surveys. On average, birds at this site constituted 59% of survey totals.

Benthic Prey Diversity and Abundance

We collected benthic samples along transects at 60 locations at Drift River, 57 at Beluga River, 49 at Lewis River, and 30 at Kasilof River ($n = 196$ total; Table 2). About 7% ($n = 14$) of selected sample locations could not be accessed because of tide or ice conditions. The bivalve *Macoma balthica* was the dominant prey item in all samples, present at 169 (86.2%) locations. Polychaete worms occurred in 137 samples (81.1%), but specimens were minute and fragile and were typically destroyed in the sieving process, precluding accurate species identification or measurement. *Macoma* ($n = 2087$) ranged in size from 0.8 to 20.0 mm (Table 2). Across all sampling periods, the average density of *Macoma* ranged from 424.4 ± 68.3 (SE) individuals/ m^2 at the Kasilof River to 3145.1 ± 201.6 (SE) individuals/ m^2 at the Beluga River (Table 2). Average *Macoma* ranged in size from 4.4 ± 0.1 (SE) mm at the Beluga River to 12.2 ± 0.4 (SE) mm at the Kasilof River (Table 2).

Mudflat Extent and Winter Ice Formation

The upper Cook Inlet study area included approximately 610 km^2 of intertidal habitat (primarily mudflats, but also sandflats). Prior to the formation of sea ice, Rock Sandpipers roosted on shoreline habitats, but once sea ice had formed, birds were more commonly detected roosting on sea ice. Persistent cold slowly caused shore-fast ice to accrete across the study area. Estimates of the extent of shore-fast ice derived from remote imagery indicated that as much as 82% (e.g., March 2007) of intertidal habitats

TABLE 2. Density (individuals/m²) and size (mm) of the bivalve *Macoma balthica* collected at sites in upper Cook Inlet, Alaska, 1998–2009.

| Segment | Site ¹ | No. Transects (Samples) | Density (mean ± SE) | Shell Length (mean ± SE; n) |
|---------------|-------------------|-------------------------|---------------------|-----------------------------|
| Susitna Flats | Beluga River | 3 (57) | 3145.1 ± 201.6 | 4.4 ± 0.1; 1408 |
| | Lewis River | 3 (49) | 511.9 ± 56.2 | 7.5 ± 0.2; 197 |
| Redoubt Bay | Drift River | 3 (60) | 810.6 ± 128.8 | 9.1 ± 0.3; 382 |
| Kasilof River | Kasilof River | 2 (30) | 424.4 ± 68.3 | 12.2 ± 0.4; 100 |

can be covered by accreted shore-fast ice. The mean extent of shore-fast ice covering intertidal habitats in upper Cook Inlet exhibited a marked seasonal flux. Shore-fast ice began forming in November (101.8 ± 136.4 km²; 16.7% of total), peaked in January (353.9 ± 102.3 km²; 58.0% of total), declined through March (250.2 ± 141.5 km²; 41.0% of total), and was gone by April each year.

Shore-fast ice was less prevalent at certain sites, and these sites overlapped with the occurrence of Rock Sandpipers. For example, the commonly occupied 7 km long section between the Beluga and Lewis Rivers (see *Site Preference and Movements* above) did not consistently accrete shore-fast ice. We analyzed 28 GIS shapefiles that documented shore-fast ice in upper Cook Inlet, and this region accumulated shore-fast ice on 11 occasions (39.2%). In contrast, an adjacent 20 km long section running from the mouth of the Susitna River to the Little Susitna River (Fig. 1) accreted shore-fast ice on 26 occasions (92.9%), and we detected only half as many Rock Sandpipers (108 322 birds, 26.0% of the Susitna Flats total) along this nearly three times longer section.

DISCUSSION

To the best of our knowledge, the environmental conditions in upper Cook Inlet, Alaska, are the coldest documented within the nonbreeding range of any shorebird, demonstrating the ability of shorebirds to tolerate extreme cold. Our previous understanding of cold tolerance in shorebirds came from Purple Sandpipers wintering in the Atlantic Basin (Summers et al., 1998), where birds occur at more northerly latitudes and days are shorter compared to conditions experienced by Rock Sandpipers in upper Cook Inlet. However, the average temperature during January, the coldest month at each location, is appreciably warmer in Norway (-2.7°C at Vardo, Norway; Summers et al., 1998) than in Anchorage, Alaska (-9.4°C ; this study). Moreover, because of the Gulf Current, Purple Sandpipers at high northern latitudes in the Atlantic Basin use ice-free rocky intertidal habitats (Summers et al., 1998), while Rock Sandpipers in upper Cook Inlet forage exclusively on mudflats and sandflats, habitats that diminish in extent as the accretion of shore-fast ice progresses through the winter. In addition to shore-fast ice, sea ice accumulates annually in upper Cook Inlet and deposits bergs and floes along mudflats at low tide, further reducing foraging habitat. Finally, the

upper layers of the Inlet's mudflats often freeze upon exposure to sub-freezing air temperatures during low tides.

Spending the winter at cold northern latitudes places high energetic demands on shorebirds (Wiersma and Piersma, 1994). Ruthrauff et al. (2013) estimated that the maintenance metabolism of Rock Sandpipers in upper Cook Inlet during December was 2.55 Watts, more than three times their basal metabolic rate at normothermic temperatures. High metabolic rates likewise require high rates of energy intake, and Rock Sandpipers thus avail themselves of an abundant food resource, the bivalve *Macoma balthica*. Although access to *Macoma* is restricted by the accretion of shore-fast ice, and less commonly, by stochastic periods of deep cold when the top surface of mudflats flash-freezes, this food resource is evidently so abundant that Rock Sandpipers can satisfy their energetic demands during winter. Our benthic sampling documented high *Macoma* densities (424–3145 *Macoma*/m²; Table 2) at all sites, and field observations and analysis of stomach contents (Gill et al., 2002) indicate that Rock Sandpiper diets in upper Cook Inlet during winter are composed almost exclusively of *Macoma*. Thus, *Macoma* are a critical winter food resource for Rock Sandpipers, as they are for other molluscivorous shorebirds such as Common Redshank (*Tringa totanus*), Bar-tailed Godwit (*Limosa lapponica*), and Red Knot (*C. canutus*) (Goss-Custard et al., 1977; Piersma et al., 1993).

The consistent occurrence of Rock Sandpipers at certain discrete sites provides insight into how abiotic conditions facilitate the reliable exploitation of upper Cook Inlet's abundant *Macoma* resources. We regularly observed Rock Sandpipers near the mouths of the Beluga and McArthur Rivers (Figs. 1, 5; see RESULTS), and we attribute their presence to an overlap between areas of high *Macoma* density and little or no shore-fast ice accretion. Ice formation in Cook Inlet is primarily a function of air temperature (Poole and Hufford, 1982), but shore-fast ice accretion and berg deposition are strongly affected by currents and tides. The region between the Beluga and Lewis Rivers is strongly swept by freshwater outflow (Johnson, 2008), which likely inhibits the accumulation of shore-fast ice. Similarly, Cook Inlet's great tidal fluctuations also probably flush sea ice from high tide regions adjacent to areas with strong currents. In contrast, regions like those between the Susitna and Little Susitna Rivers receive less current scouring (Johnson, 2008), and these regions more frequently accrete shore-fast ice. This ice in turn limits foraging access to mudflats and ultimately inhibits Rock Sandpiper occupancy at such sites.

Thus, an interaction of biotic factors (high *Macoma* abundance) and abiotic factors (ice-inhibiting currents and tides) enables Rock Sandpipers to occupy upper Cook Inlet during winter. Rock Sandpipers also exhibit unusual behavioral adaptations to the region. For instance, we frequently observed Rock Sandpipers roosting on sea ice, a behavior that likely decreases the risk of attack by both avian and mammalian predators. Additionally, Gill and Tibbitts (Gill, 1997) have observed Rock Sandpipers foraging during falling tides on freshly exposed *Macoma* turned over by the scouring action of receding icebergs. And given that day lengths in upper Cook Inlet decrease to less than 5.5 h at the winter solstice (Fig. 2), Rock Sandpipers must undoubtedly forage outside of daylight periods.

Nearly all Rock Sandpipers within upper Cook Inlet belong to the nominate subspecies (Table 1), and their reliance on upper Cook Inlet during winter has important conservation implications. The nominate subspecies of Rock Sandpiper is considered a species of high conservation concern in numerous conservation planning documents (e.g., Brown et al., 2001; Butcher et al., 2007; Alaska Shorebird Group, 2008). Surveys conducted across the subspecies' breeding range during the summers of 2001–03 yielded a population estimate of 19 832 individuals (95% confidence interval 17 853–21 930) (Ruthrauff et al., 2012). Maximum counts for the winter periods 2001–02, 2002–03, and 2003–04 were 9084, 17 586, and 18 186 birds (Fig. 4), respectively, indicating that in at least some winters nearly the entire population of the subspecies occurs in upper Cook Inlet. Although survey totals varied within each of these winter seasons, upper Cook Inlet annually serves as a critical wintering area for the subspecies. This is further emphasized by the long-term average annual maximum count (13 603 birds), which encompasses nearly 70% of the population estimate. Since *C. p. pitlocnemis* breeds only on remote islands in the Bering Sea (Gill et al., 2002) that are difficult and costly to survey, winter surveys in upper Cook Inlet may serve as an informative and cost-effective population monitoring tool (e.g., Brown et al., 2005). Determining the patterns and causes of within-region movements, as well as documenting the subspecies' winter distribution outside of upper Cook Inlet, would strengthen the inferential power of future surveys.

Our surveys document the unusual occurrence of Rock Sandpipers at sites in Cook Inlet, Alaska, during winter. Their high metabolic rates (Kersten and Piersma, 1987) and reliance on aquatic food resources (Piersma, 1996) make northerly wintering shorebirds highly susceptible to starvation induced by periods of severe cold (Dugan et al., 1981; Davidson and Evans, 1982; Dietz and Piersma, 2007). Rock Sandpipers, however, stand in contrast to these examples: average winter conditions in upper Cook Inlet surpass the severity of the stochastic conditions described during such starvation events. Roosting on sea ice, foraging in ice scours, the likely occurrence of nocturnal foraging, novel observations of body- and plumage-icing (Ruthrauff and Eskelin, 2009), and recent physiological experiments

revealing a less severe metabolic response to extreme cold than other shorebird species (Ruthrauff et al., 2013) are evidence that Rock Sandpipers are adapted to regularly exploit sites in upper Cook Inlet during winter. The unanticipated discovery of Rock Sandpipers at these sites during winter extends the known environmental limits to which shorebirds are adapted and makes the species a unique addition to the winter avifauna of high northern latitudes.

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