POTENTIAL NORTHWARD EXPANSION OF THE BREEDING RANGE OF RED-LEGGED KITTIWAKE *RISSA BREVIROSTRIS*

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ABSTRACT

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We report observations of *ca*. 200 Red-legged Kittiwakes *Rissa brevirostris* occupying cliff habitat on northern St. Matthew Island, and behaviors that indicate the kittiwakes were attempting to breed. This is the first documentation of Red-legged Kittiwake breeding activity on St. Matthew Island, which represents a potential northward expansion of this species' breeding range by nearly 400 km. During a month-long expedition to St. Matthew and Hall islands in June–July 2018, we observed Red-legged Kittiwakes conducting courtship behaviors, nest building and stamping, and sitting on nests at two locations on the northwest side of St. Matthew Island. We discuss our observations with respect to past observations of the species at this location, and with respect to breeding activities at the nearest known breeding locations on St. Paul and St. George islands.

Key words: Red-legged Kittiwake, distribution, Bering Sea, St. Matthew Island

INTRODUCTION

Shifting distributions of higher trophic level consumers, such as birds, provide some of the most obvious evidence of the effects of global climate change on the biota, and serve as signals for impacts across trophic levels (Valiela & Bowen 2003, Illán *et al*. 2014, Paprocki *et al*. 2014, Billerman *et al*. 2016). The Bering Sea represents an ecotone between Arctic and Subarctic marine ecosystems that is largely governed by sea-ice extent, an environmental factor that varies among years (Stabeno *et al*. 2001, Ohashi *et al*. 2013, Wu & Chen 2016). Currently, sea-ice is experiencing a substantial overall reduction in distribution and thickness related to climate change (Wang & Overland 2009, Comiso 2012, Mueller *et al*. 2018). Because this region faces a range of climate change impacts, an overall northward shift in the biogeographic distribution of the region's fauna has followed these decreases in sea-ice distribution and the concomitant northward shift in the ecotone between Arctic and Subarctic biomes (Mueter & Litzow 2008). These changes are likely to influence distributions and population dynamics of taxa at all trophic levels (Hunt *et al*. 2002, Hunt *et al*. 2011, Ohashi *et al*. 2013), but they may be most conspicuous when they result in changes to ecosystem members at high trophic levels—such as seabirds (Springer *et al*. 2007, Renner *et al*. 2016, Hunt *et al*. 2018).

Birds are distributed throughout the Bering Sea along gradients of sea surface temperature, salinity, ocean depths, and currents (Iverson *et al*. 1979, Hunt *et al*. 2014, Santora *et al*. 2018). Because of their association with sea ice, these gradients are likely to change as the extent of sea ice changes (Hunt *et al*. 2018). The Red-legged Kittiwake *Rissa brevirostris* is a Beringean endemic that remains in the Bering Sea during winter and feeds at the margins of sea-ice (Orben *et al*. 2015, 2018). Although sea-ice coverage is correlated with higher stress levels and may limit the ability of kittiwakes to obtain food (Will *et al*. 2018), Red-legged Kittiwake presence at the ice-edge likely reflects the presence of good foraging conditions and the opportunity to employ energy conservative techniques such as perching and foraging. Because fluctuations in sea-ice distribution in the Bering Sea influence reproductive success and productivity for surface feeding consumers such as kittiwakes (including the Black-legged Kittiwake *R. tridactyla*; Byrd *et al*. 2008, Zador *et al*. 2013), recent trends and projections of future sea-ice distributions may impact kittiwake populations.

The Red-legged Kittiwake is thought to feed on a low diversity of prey and possesses physical characteristics such as relatively large eyes and a short bill, indicating the importance of low-light foraging on a specific resource as a life-history strategy (Storer 1987). During the breeding season, Red-legged Kittiwakes feed on a range of prey types (Sinclair *et al.* 2008). In many years, myctophids (Family: Myctophidae), a diel species that is available to surface feeding kittiwakes at night, are the primary prey (Kokubun *et al*. 2015, Guitart *et al*. 2018). This narrow diet niche seems to be maintained throughout their annual cycle (Orben *et al*. 2015). Although geolocator data from the non-breeding season indicate higher diurnal activity levels, with low activity during darkness (Orben *et al*. 2015), this does not necessarily indicate a lack of nocturnal foraging. Rather, it may suggest a more energetically conservative nocturnal winter foraging strategy (Jodice *et al*. 2003) that highlights the importance of prey landscapes in this region during the winter months.

The Red-legged Kittiwake has a breeding distribution restricted to four major breeding locations, all within the Bering Sea (Fig. 1): the Pribilof Islands (St. George, St. Paul, and Otter: 235 624 individuals; Thomson *et al*. 2014, Goyert *et al*. 2017), the Bogoslof Islands

(Bogoslof and Fire: 918 individuals; Byrd *et al*. 2002), the Buldir Islands (Buldir, Outer Rock, Middle Rock: 9350 individuals; Byrd *et al*. 1997), and the Commander Islands, Russia (Bering, Toporkov, Mednyi, Arij Kamen: 32344 individuals; Byrd & Williams 1993, Vyatkin & Artukhin 1994, Byrd *et al*. 1997). Smaller breeding colonies are located on Amak and Chagulak Islands (16 and 18 individuals, respectively; Byrd *et al*. 2001, 2004) and Koniuji and Unalga Islands (eight and nine individuals, respectively; J. Williams unpubl. data), in the Aleutian Archipelago. Historically, the Red-legged Kittiwake was thought to be more widespread in the Aleutian Archipelago and elsewhere in the Bering Sea region (Byrd & Williams 1993); however, there is no existing historical evidence of breeding north of their present, northernmost breeding location on St. Paul Island (57°N). Although some Red-legged Kittiwakes winter in the northern Bering Sea (i.e., in waters off mainland Alaska and near St. Lawrence and St. Matthew islands, and Cape Navarin, Russia; Orben *et al*. 2018), they are rarely observed in this region during the breeding season (Swarth 1934, Faye & Cade 1959, Sealy *et al*. 1971, Winker *et al*. 2002); however, in recent years, they have been observed in low densities in waters around St. Matthew and St. Lawrence islands (Kuletz & Labunski 2017).

Here, we provide the first documentation of a Red-legged Kittiwake colony on St. Matthew Island. We report unprecedented numbers and behaviors of Red-legged Kittiwakes for this location, and provide evidence that these birds are likely breeding, which would represent a northern extension of the breeding distribution of this species by *ca*. 400 km. We discuss the status of colonies on St. George and St. Paul islands, and how breeding trends at these locations and other factors may relate to the discovery of the St. Matthew Island colony.

METHODS

The St. Matthew Island archipelago is part of the Bering Sea Unit of the Alaska Maritime National Wildlife Refuge, administered by the US Fish and Wildlife Service. The archipelago consists of three main islands: St. Matthew (60°24′N, 172°42′W), Hall (60°39′N, 173°05′W), and Pinnacle (60°12′N, 172°45′W). All three islands are uninhabited by humans and designated as Federal Wilderness. These islands are volcanic in origin and located on the Bering Sea Shelf, *ca*. 230 km east of the shelf break in a roughly central position between the coasts of Russia and Alaska. Because of their position in the Bering Sea, the islands support a mixture of northern Palearctic and Nearctic avifaunas.

During a 31-d visit, from 06 June–07 July 2018, we conducted population counts and productivity monitoring for McKay's Bunting *Plectrophenax hyperboreus* and Pribilof Rock Sandpiper *Calidris ptilocnemis ptilocnemis* on St. Matthew Island. During our fieldwork, we collected data on all noteworthy bird and mammal sightings.

We conducted observations by land-based and boat-based methods. On 19 June, 01 July, and 04 July, we conducted land-based observations above a known seabird colony at cliffs on the northwest side of the island (Location A [60°29′N, 173°3′W], Fig. 2). We checked all visible cliff faces for the presence of Red-legged Kittiwakes, and noted locations where birds were sitting on nests. During land-based observations on 01 and 04 July, conditions were foggy with marginal visibility; however, the fog cleared intermittently on these dates, and we were able to make limited observations. On 06 July, we conducted a boat-based survey along the north and northwest sides of St. Matthew Island, looking for kittiwake breeding habitat and additional Red-legged Kittiwakes. We conducted boat-based observations starting north from camp and continuing around the north end of the island and south towards location A. Our survey platform was a 4.5 m-long inflatable skiff employed by a three-person crew (two observers and one skiff operator). During boat-based observations, we maintained a maximum distance of 100 m from the shoreline to best observe potential Red-legged Kittiwake nesting habitat that we could not see from land-based observation points.

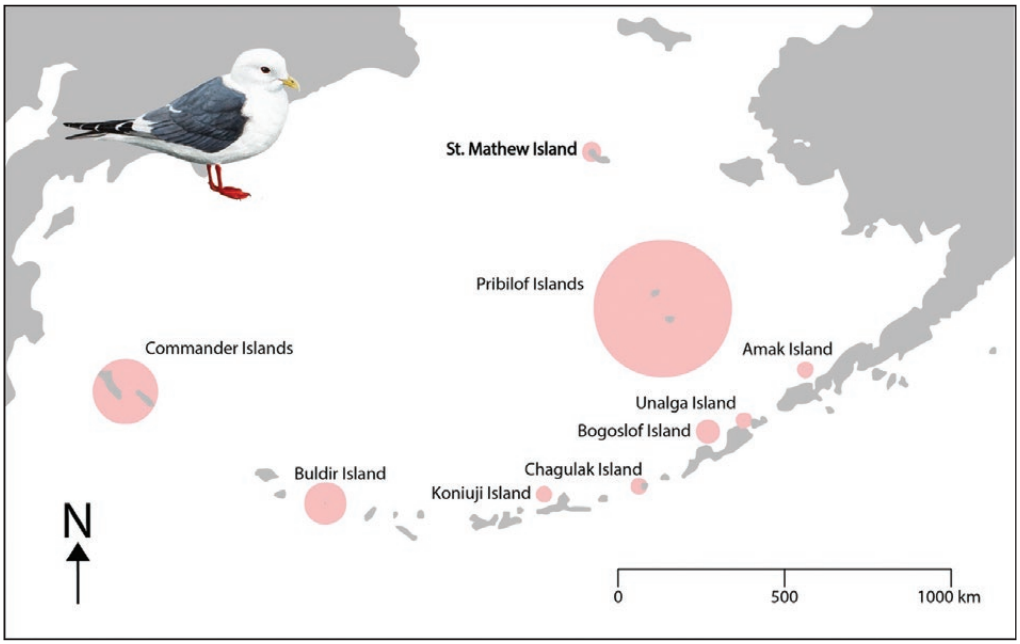

Fig. 1. Red-legged Kittiwake breeding distribution. Colonies are indicated by red circles representing relative colony size (range: 235624 individuals on the Pribilof Islands to eight individuals on Koniuji Island). St. Matthew Island is located *ca*. 400 km north of St. Paul Island.

OBSERVATIONS

During land-based observations on 19 June, we noted two Red-legged Kittiwakes on the water in mixed flocks with *ca*. 18 Black-legged Kittiwakes (Location A, Fig. 2). In the same vicinity, we observed Red-legged Kittiwakes both in flight and perched on sea cliffs (*ca*. 130 individuals) amidst Black-legged Kittiwakes and Common Murres *Uria aalge*. Our count for this day reached *ca*. 150 Red-legged Kittiwakes across the 1.5 km sea-cliff colony. At this time, we did not observe behaviors that indicated breeding, apart from pairs perched together on the cliffs.

On 01 July, we visited the sea-cliff colony (Location A, Fig. 2) and observed *ca*. 100 Red-legged Kittiwakes. Of these birds, we observed individuals conducting courtship behaviors, carrying nest material, and building and stamping nests. Unfortunately, visibility on this date was restricted by dense fog and we were unable to fully count birds attending ledges throughout the sea-cliff colony. However, we intermittently obtained views and were able to photograph the kittiwakes on the cliff (e.g., Fig. 3). When conditions permitted, we observed *ca*. 10 Red-legged Kittiwakes sitting on nests. On one occasion, we observed two individuals for *ca*. 30 min until they stood and revealed empty nests.

On 06 July, we successfully surveyed the north end of the island, where we found only Black-legged Kittiwakes on the cliffs; however, we found *ca*. 30 Red-legged Kittiwakes on the west side at a cliff face where they had not been seen previously (Location B [60°32′N, 173°03′W], Fig. 2), *ca*. 5.8 km north of Location A. At Location B, we observed pairs nest stamping, as well as standing and sitting on nests (Fig. 4). Unfortunately, owing to rough seas, we were unable to reach Location A to survey, from the water, the *ca*. 3 km of cliff habitat that was mostly not visible from our land-based observations.

Based on our combined high counts at Locations A and B, we conservatively estimate that there are *ca*. 200 adult Red-legged Kittiwakes present at the locations we visited (representing only *ca*. 12 % of potential kittiwake nesting habitat on St. Matthew, Hall, and Pinnacle islands; World Seabird Union 2019). At the time of our departure from St. Matthew Island on 07 July, we were unable to confirm Red-legged Kittiwake egg-laying.

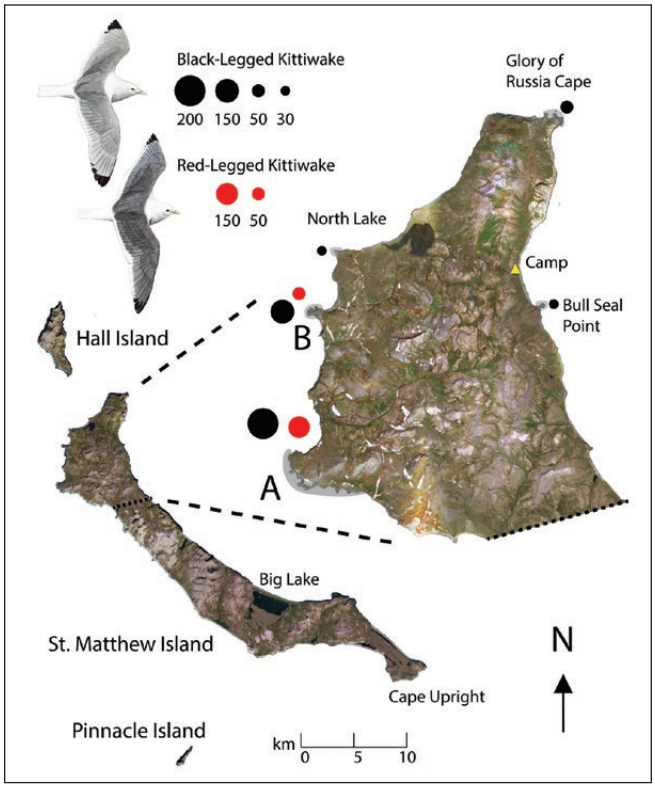

Fig. 2. The St. Matthew Islands including St. Matthew, Hall, and Pinnacle islands, along with an inset of the north end of the island where our observations were focused. Black circles indicate locations and approximate numbers of Black-legged Kittiwake, and red circles indicate location and approximate numbers of Red-legged Kittiwake.

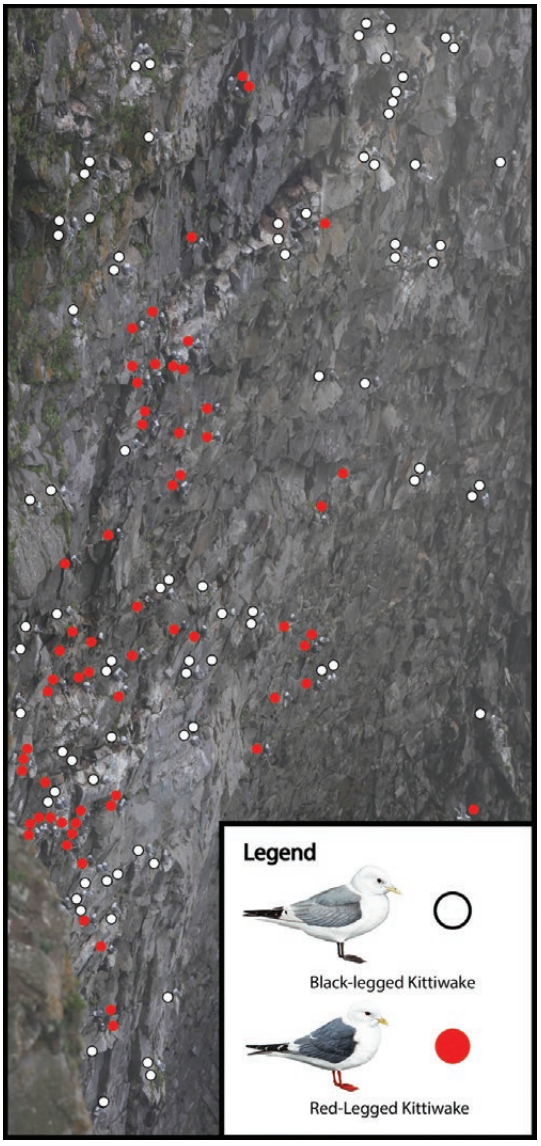

Fig. 3. Kittiwake cliff nesting habitat at a portion of the cliff faces at Location A (Fig. 1). Dots illustrate the abundance and distribution of Red-legged Kittiwake from this observation point. Other habitat where kittiwakes could be heard at Location A were out of view from land-based observers.

DISCUSSION

We document substantial numbers (*ca*. 200) of Red-legged Kittiwakes on St. Matthew Island, along with observations of copulation and nest building that likely indicate that this species is breeding there. Although we provide the first documentation for this species occupying cliffs on St. Matthew Island, it is possible that the birds have been present on the island for some time and have gone unnoticed. Previously, the species' status at St. Matthew has been considered casual or accidental in summer, with the earliest known record of one adult observed in August 1985 (Winker *et al*. 2002). The species has since been observed near the island on a few other occasions, including an eBird report listing two individuals seen in waters south of the island on 01 October 2006 (ML S9104078, www.ebird.org) and a single individual sighted in 2012 near Cape Upright, on the southern tip of St. Matthew Island (T. DeGange *in litt*.). More recently, one individual was observed at Pinnacle Island and two individuals were observed at Hall Island on 18 August 2018 by a tour group (Scott Schuette pers. comm; ML S47934195, S47921944; www.ebird.org). In the broader region of the north Bering Sea, Red-legged Kittiwakes have been documented in low numbers during the breeding season since 2006 (Kuletz & Labunski 2017).

Because of its remote location and challenging weather, very few targeted avian studies have been conducted on St. Matthew Island (Winker *et al*. 2002). Despite this, several notable previous expeditions to the area failed to document Red-legged Kittiwake (Hanna 1917, Gabrielson 1944, Goetzman & Sloan 1982). The failure to record the species was not due to lack of observer effort, as the topic is explicitly addressed in Gabrielson (1944, pg. 130): "We also looked carefully over the kittiwakes on St. Matthew and Hall islands for [Red-legged Kittiwake] but found none." More recently, several expert research teams have visited the islands to conduct standardized seabird monitoring, and none recorded the species (DeGange & Sowls 1978, Byrd & Early 1985, Murphy *et al*. 1987, Mendenhall 1994, Renner & Sowls 2005, Romano & Renner 2012). The absence of previous observations of Red-legged Kittiwakes by so many different teams of trained observers who were familiar with this species supports the scenario that it has only recently begun to occupy St. Matthew Island. However, our land-based observations were made in a very remote part of the island, well away from the usual camp locations of previous expeditions. It is unclear whether previous observers visited Locations A and B, or looked closely over the cliffs for Red-legged Kittiwake. Additionally, most previous observers were conducting their work from land-based sites. The boat-based aspect of our survey helped confirm our land-based observations and allowed us to survey areas inaccessible to land-based crews, which increased our estimate for the number of Red-legged Kittiwakes conducting nesting activities on the island.

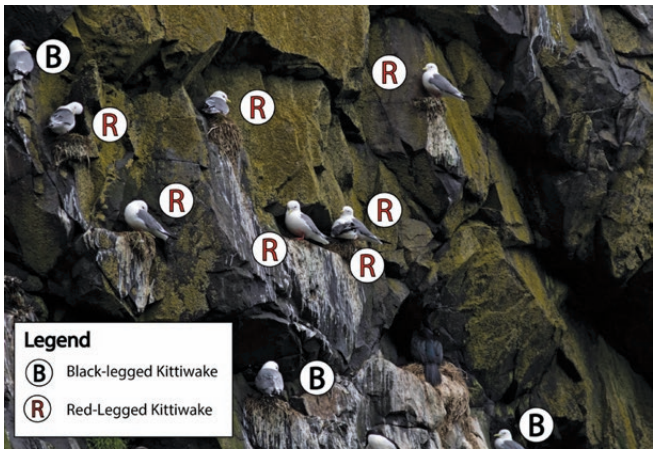

Fig. 4. Example of distribution of kittiwakes on nests at Location B (Fig. 1) as seen from boat-based observations on 06 July 2018. At this location, *ca*. 30 Red-legged and *ca*. 150 Black-legged Kittiwakes were mixed in appropriate habitat, with pairs and single birds perched at nest locations.

Although our survey occurred during the early part of the seabird nesting cycle and we did not observe eggs or young, our observations of nest building and breeding behavior (courtship behavior, birds in incubation posture) provide strong evidence that Red-legged Kittiwakes attempted to breed on St. Matthew Island. The closest Red-legged Kittiwake colony with breeding phenology data for 2018 is located on St. George Island, *ca*. 470 km south of St. Matthew Island. During 2018, laying success of Red-legged Kittiwakes at St. George was very low, and breeding was delayed (Guitart *et al*. 2018). Mean hatch of Red-legged Kittiwakes there occurred on 16 August (n = 2), 32 d later than the long-term mean from 1975–2017. Assuming a *ca*. 30-d incubation period (Byrd & Williams 1993), mean laying on St. George occurred on 17 July (Guitart *et al*. 2018). Given the late breeding on St. George in 2018, it is possible that that the Red-legged Kittiwakes that we observed on St. Matthew Island may have initiated clutches following our departure from the island on 07 July. This possibility is further supported by our lack of observations of eggs or young of Black-legged Kittiwakes, which we also observed conducting courtship behaviors and nest building. Black-legged Kittiwake is a locally abundant species with a mean laying date that occurs later at higher latitudes (Dragoo *et al*. 2018) and has very similar breeding phenology to Red-legged Kittiwakes when in sympatry (Guitart *et al*. 2018).

Our observations suggest a substantial extension of the Red-legged Kittiwake breeding distribution during a time of great change in the Bering Sea. If their presence at this location continues, it provides an opportunity to understand mechanisms involved in the capacity of this regional endemic to shift its breeding range northward. For instance, it is possible that Red-legged Kittiwake presence at St. Matthew Island was facilitated through prospecting movements, much like those documented in Black-legged Kittiwake (Ponchon *et al*. 2015). Methods such as satellite telemetry on St. Paul and St. George islands may reveal the role of such mechanisms in shifting breeding distribution in response to climatic changes in the Bering Sea region (Ponchon *et al*. 2012).

In some ways, St. Matthew is a surprising location for Red-legged Kittiwakes to colonize. This species is thought to specialize on food resources such as *Stenobrachius leucopsarus* (Family: Myctophidae), which are generally found in waters deeper than 200 m (Beamish *et al*. 1999). St. Matthew Island is located on the Bering Sea Shelf in an area where ocean depth is generally less than 200 m; therefore, deep-water myctophids may not be available as food resources to Red-legged Kittiwakes in close proximity to this breeding location. However, deep water at the shelf break may be within foraging range, although trips to obtain such food resources would be longer than those at breeding locations such as at the Pribilof Islands (*ca*. 230 km from St. Mathew Island compared to *ca*. 100 km from St. Paul). For instance, Black-legged Kittiwakes have been documented making extended foraging trips to access

resources during the brood-rearing period, across distances as large as 201.4 ± 6.9 km (n = 18; Paredes *et al.* 2014). Further focus on the breeding status, movements, and diet of St. Matthew Island Red-legged Kittiwakes may provide insight into the species' capacity to shift its range northward through their ability to utilize alternate food resources, or to extend foraging trips to deep water where resources are available.

The Red-legged Kittiwake is listed as vulnerable by the IUCN, a cautionary designation owing to its restricted breeding range and past population decrease (IUCN 2017). Given this status, our finding of Kittiwakes on St. Matthew Island may provide some clarity around downward trends in population and productivity on the Pribilof Islands (Guitart *et al*. 2018). Throughout their annual cycle, continued changes to the oceanographic regime in this region will likely have important implications for Red-legged Kittiwake distribution and population status (Orben *et al.* 2015). Thus, our observations underscore the need for continued focus on Red-legged Kittiwake occupancy at St. Matthew Island, as well as the multitude of other seabirds that breed at this remote Bering Sea location.

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REFERENCES

BEAMISH, R.J., LEASK, K.D., IVANOV, O.A., BALANOV, A.A., ORLOV, A.M. & SINCLAIR, B. 1999. The ecology, distribution, and abundance of midwater fishes of the Subarctic Pacific gyres. *Progress in Oceanography* 43: 399–442.

BIRDLIFE INTERNATIONAL. 2017. *Rissa brevirostris*. The IUCN Red List of Threatened Species 2017: e.T22694502A118920892. Cambridge, UK: International Union for the Conservation of Nature. [Available online at: http://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T22694502A118920892.en. Accessed 07 August 2018.]

BILLERMAN, S.M., MURPHY, M.A. & CARLING, M.D. 2016. Changing climate mediates sapsucker (Aves: Sphyrapicus) hybrid zone movement. *Ecology and Evolution* 6: 1–15.

BYRD, G.V. & EARLY, T.J. 1985. *Trip report to St. Matthew Island.* Unpublished report. Homer, AK: US Fish and Wildlife Service.

BYRD, G. V. & WILLIAMS, J.C. 1993. Red-legged Kittiwake (*Rissa brevirostris*), version 2.0. In: POOLE, A. F. & GILL, F. B. (Eds.) *The Birds of North America*. Ithaca, NY: Cornell Lab of Ornithology. [Available at: https://birdsna.org/Species-Account/bna/species/relkit/introduction]. doi:10.2173/bna.60

BYRD, G.V., WILLIAMS, J.C., ARTUKHIN, Y.B. & VYATKIN, P.S. 1997. Trends in populations of red-legged kittiwake *Rissa brevirostris*, a Bering Sea endemic. *Bird Conservation International* 7: 167–180.

BYRD, G.V., WILLIAMS, J.C., ROSENEAU, D. & KETTLE. A.B. 2001. *Wildlife Surveys at Amak Island, Alaska, in June 2001.* Unpublished report. Homer, AK: US Fish and Wildlife Service.

BYRD, G.V. 2002. *A comparison of breeding kittiwakes at Bogoslof and St. George islands.* Unpublished report. Homer, AK: US Fish and Wildlife Service.

BYRD, G.V., WILLIAMS, J.C. & RENNER, H.M. 2004. *Ledge-nesting seabirds at Chagulak Island in 2004.* Unpublished report. Homer, AK: US Fish and Wildlife Service.

BYRD, G.V., SYDEMAN, W.J., RENNER, H.M. & MINOBE, S. 2008. Responses of piscivorous seabirds at the Pribilof Islands to ocean climate. *Deep-Sea Research Part II* 55: 1856–1867.

COMISO, J.C. 2012. Large decadal decline of the Arctic multiyear ice cover. *Journal of Climate* 25: 1176–1193.

DEGANGE, A.R. & SOWLS, A.L. 1978. *A faunal reconnaissance of the Bering Sea National Wildlife Refuge, 26 June–27 July 1977*. Unpublished report. Anchorage, AK: US Fish and Wildlife Service.

DRAGOO, D.E., RENNER, H.M. & KALER, R.S.A. 2018. *Breeding status and population trends of seabirds in Alaska, 2017.* Unpublished report. Homer, AK: US Fish and Wildlife Service.

FAYE, F.H. & CADE, T.J. 1959. An ecological analysis of the avifauna of St. Lawrence Island Alaska. *University of California Publications in Zoology* 63: 73–150.

GABRIELSON, I.N. 1944. Some Alaskan notes. *The Auk* 61: 105–130, 270–287.

GOETZMANN, W.H. & SLOAN, K. 1982. *Looking Far North: The Harriman Expedition to Alaska, 1899.* Princeton, NJ: Princeton University Press.

GOYERT, H.F., GARTON, E.O., DRUMMOND, B.A., & RENNER, H.M. 2017. Density dependence and changes in the carrying capacity of Alaskan seabird populations. *Biological Conservation* 209: 178–187.

GUITART, S.R., CARVEY, S.B., WHITE, L.M. & ROMANO M.D. 2018. *Biological monitoring at St. George Island, Alaska in 2018.* Unpublished report. Homer, AK: US Fish and Wildlife Service.

HANNA, G.D. 1917. The summer birds of the St. Matthew Island Bird Reservation. *The Auk* 34: 403–410.

HUNT, G.L., STABENO, P., WALTERS, G. ET AL. 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep-Sea Research Part II* 49: 5821–5853.

HUNT, G.L., COYLE, K.O., EISNER, L.B. ET AL. 2011. Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis. *ICES Journal of Marine Science* 68: 1230–1243.

HUNT, G.L., RENNER, M. & KULETZ, K. 2014. Seasonal variation in the cross-shelf distribution of seabirds in the southeastern Bering Sea. *Deep-Sea Research Part II* 109: 266–281.

HUNT, G.L. JR., RENNER, M., KULETZ, K.J. ET AL. 2018. Timing of sea-ice retreat affects the distribution of seabirds and their prey in the southeastern Bering Sea. *Marine Ecology Progress Series* 593: 209–230.

ILLÁN, J.G., THOMAS, C.D., JONES, J.A., WONG, W.-K., SHIRLEY, S.M. & BETTS, M.G. 2014. Precipitation and winter temperature predict long-term range-scale abundance changes in Western North American birds. *Global Change Biology* 20: 3351–3364.

IVERSON, R.L., COACHMAN, L.K., COONEY, R.T. ET AL. 1979. Ecological significance of fronts in the southeastern Bering Sea. In: LIVINGSTON, R.J. (Ed.) *Ecological Processes in Coastal and Marine Systems.* Boston, MA: Springer, pp. 437–466.

JODICE, P.G.R., ROBY, D.D., SURYAN, R.M. ET AL. 2003. Variation in energy expenditure among black-legged kittiwakes: effects of activity-specific metabolic rates and activity budgets. *Physiological and Biochemical Zoology* 76: 375–388.

KOKUBUN, N., YAMAMOTO, T., KIKUCHI, D.M., KITAYSKY, A. & TAKAHASHI, A. 2015. Nocturnal foraging by Red-legged Kittiwakes, a surface feeding seabird that relies on deep water prey during reproduction. *PLoS One* 10: e0138850.

KULETZ, K.J. & LABUNSKI, E.A. 2017. *Seabird Distribution and Abundance in the Offshore Environment, Final Report.* OCS Study BOEM 2017-004. Herndon, VA: US Department of the Interior, Bureau of Ocean Energy Management, Alaska OCS Region. [Available online at: https://www.boem.gov/2017-004/].

MENDENHALL, V.M. 1994. *Monitoring of populations and productivity of seabirds at St. Matthew Island, Bluff, Little Diomede Island, and Cape Thompson, Alaska, 1991*. Minerals Management Service Report, 93-0067. Anchorage, AK: US Fish and Wildlife Service.

MUELLER, B.L., GILLETT, N., MONAHAN, A.H. & ZWIERS, F.W. 2018. Attribution of Arctic sea ice decline from 1953 to 2012 to influences from natural, greenhouse gas, and anthropogenic aerosol forcing. *Journal of Climate* 31: 7771–7787.

MUETER, F.J. & LITZOW, M.A. 2008. Sea ice retreat alters the biogeography of the Bering Sea continental shelf. *Ecological Applications* 18: 309–320.

MURPHY, E.C., COOPER, B.A., MARTIN, P.D. ET AL. 1987. *The population status of seabirds on St. Matthew and Hall islands, 1985 and 1986*. Minerals Management Service Report, 87-0043. Anchorage, AK: US Fish and Wildlife Service.

OHASHI, R., YAMAGUCHI, A., MATSUNO, K. ET AL. 2013. Interannual changes in the zooplankton community structure on the southeastern Bering Sea shelf during summers of 1994-2009. *Deep-Sea Research Part II* 94: 44–56.

ORBEN, R.A., IRONS, D.B., PAREDES, R., ROBY, D.D., PHILLIPS, R.A. & SHAFFER, S.A. 2015. North or south? Niche separation of endemic red-legged kittiwakes and sympatric black-legged kittiwakes during their non-breeding migrations. *Journal of Biogeography* 42: 401–412.

ORBEN, R.A., KOKUBUN, N., FLEISHMAN, A.B. ET AL. 2018. Persistent annual migration patterns of a specialist bird. *Marine Ecology Progress Series* 593: 231–245.

PAPROCKI, N., HEATH, J.A. & NOVAK, S.J. 2014. Regional distribution shifts help explain local changes in wintering raptor abundance: Implications for interpreting population trends. *PLoS One* 9: e86814.

PAREDES, R., ORBEN, R.A., SURYAN, R.M. ET AL. 2014. Foraging responses of Black-Legged Kittiwakes to prolonged food-shortages around colonies on the Bering Sea shelf. *PLoS One* 9: e92520.

PONCHON, A., CHAMBERT, T., LOBATO, E., TVERAA, T., GRÉMILLET, D. & BOULINIER, T. 2015. Breeding failure induces large scale prospecting movements in the black-legged kittiwake. *Journal of Experimental Marine Biology and Ecology* 473: 138–145.

PONCHON, A., GRÉMILLET, D., DOLIGEZ, B. ET AL. 2013. Tracking prospecting movements involved in breeding habitat selection: insights, pitfalls and perspectives. *Methods in Ecology and Evolution* 4: 143–150.

RENNER, H.M. & SOWLS, A.L. 2005. *Marine bird population and productivity surveys on Hall Island, Alaska in 2005.* Unpublished report. Homer, AK: US Fish and Wildlife Service.

RENNER, M., SALO, S., EISNER, L.B. ET AL. 2016. Timing of ice retreat alters seabird abundances and distributions in the southeast Bering Sea. *Biology Letters* 12: 20160276.

ROMANO, M.D. & RENNER, H.M. 2012. *Marine bird population and productivity surveys on Hall and St. Matthew islands, Alaska, in 2012.* Unpublished report. Homer, AK: US Fish and Wildlife Service.

SANTORA, J.A., EISNER, L.B., KULETZ, K.J., LADD, C., RENNER, M. & HUNT, J. L. JR. 2018. Biogeography of seabirds within a high-latitude ecosystem: Use of a data-assimilative ocean model to assess impacts of mesoscale oceanography. *Journal of Marine Systems* 178: 38–51.

SEALY, S.G., BEDARD, J., UDVARDY, M.D.F. & FAY, F.H. 1971. New records and zoogeographical notes on the birds of St. Lawrence Island, Bering Sea. *The Condor* 73: 322–336.

SINCLAIR, E.H., VLIETSTRA, L.S., JOHNSON, D.S., ET AL. 2008. Patterns in prey use among fur seals and seabirds in the Pribilof Islands. *Deep-Sea Research Part II* 55: 1897–1918.

SPRINGER, A.M., BYRD, G.V. & IVERSON, S.J. 2007. Hot oceanography: planktivorous seabirds reveal ecosystem responses to warming of the Bering Sea. *Marine Ecology Progress Series* 352: 289–297.

STABENO, P.J., BOND, N.A., KACHEL, N.B., SALO, S.A. & SCHUMACHER, J.D. 2001. On the temporal variability of the physical environment over the south-eastern Bering Sea. *Fisheries Oceanography* 10: 81–98.

STORER, R.W. 1987. The possible significance of large eyes in the Red-legged Kittiwake. *The Condor* 89: 192–194.

SWARTH, H.S. 1934. Birds of Nunivak Island Alaska. *Pacific Coast Avifauna* 22: 1–65.

THOMSON, G., DRUMMOND, B.A. & ROMANO, M.D. 2014. *Biological monitoring at St. Paul Island, Alaska in 2014.* Unpublished report. Homer, AK: US Fish and Wildlife Service.

VALIELA, I. & BOWEN, J.L. 2003. Shifts in winter distributions in birds: Effects of global warming and local habitat change. *Ambio* 32: 476–480.

VYATKIN, P.S. & ARTYUKHIN Y.B. 1994. Seabird Counts on the Commander Islands in 1993. *Beringian Seabird Bulletin* 2: 36–40.

WANG, M. & OVERLAND, J.E. 2009. A sea ice free summer Arctic within 30 years? *Geophysical Research Letters* 36: L07502. doi:10.1029/2009GL037820

WORLD SEABIRD UNION 2019. *North Pacific Seabird Data Portal.* [Accessed online at http://axiom.seabirds.net/portal.php on 20 May 2019.]

WILL, A.P., KITAISKAIA, E.V. & KITAYSKY, A.S. 2018. Red-legged Kittiwake feathers link food availability to environmental changes in the Bering Sea. *Marine Ecology Progress Series* 593: 261–274.

WINKER, K., GIBSON, D.D., SOWLS, A.L. ET AL. 2002. The Birds of St. Matthew Island, Bering Sea. *Wilson Bulletin* 114: 491–509.

WU, R. & CHEN, Z. 2016. An interdecadal increase in the spring Bering Sea ice cover in 2007. *Frontiers in Earth Science* 4: 26.

ZADOR, S., HUNT, G. L. JR., TENBRINK, T. & AYDIN, K. 2013. Combined seabird indices show lagged relationships between environmental conditions and breeding activity. *Marine Ecology Progress Series* 485: 245–258.