ARCTIC
VOL. 73, NO. 4 (DECEMBER 2020) P. 450–460
https://doi.org/10.14430.arctic71533

Effects of Fish Populations on Pacific Loon (*Gavia pacifica*) and Yellow-billed Loon (*G. adamsii*) Lake Occupancy and Chick Production in Northern Alaska

Brian D. Uher-Koch,[1,2] Kenneth G. Wright,[1] Hannah R. Uher-Koch[1,3] and Joel A. Schmutz[1]

(*Received 5 February 2020; accepted in revised form 24 June 2020*)

ABSTRACT. Predator populations are vulnerable to changes in prey distribution or availability. With warming temperatures, lake ecosystems in the Arctic are predicted to change in terms of hydrologic flow, water levels, and connectivity with other lakes. We surveyed lakes in northern Alaska to understand how shifts in the distribution or availability of fish may affect the occupancy and breeding success of Pacific (*Gavia pacifica*) and Yellow-billed Loons (*G. adamsii*). We then modeled the influence of the presence and abundance of five fish species and the physical characteristics of lakes (e.g., hydrologic connectivity) on loon lake occupancy and chick production. The presence of Alaska blackfish (*Dallia pectoralis*) had a positive influence on Pacific Loon occupancy and chick production, which suggests that small-bodied fish species provide important prey for loon chicks. No characteristics of fish species abundance affected Yellow-billed Loon lake occupancy. Instead, Yellow-billed Loon occupancy was influenced by the physical characteristics of lakes that contribute to persistent fish populations, such as the size of the lake and the proportion of the lake that remained unfrozen over winter. Neither of these variables, however, influenced chick production. The probability of an unoccupied territory becoming occupied in a subsequent year by Yellow-billed Loons was low, and no loon chicks were successfully raised in territories that were previously unoccupied. In contrast, unoccupied territories had a much higher probability of becoming occupied by Pacific Loons, which suggests that Yellow-billed Loons have strict habitat requirements and suitable breeding lakes may be limited. Territories that were occupied had high probabilities of remaining occupied for both loon species.

Key words: Arctic Coastal Plain; Arctic lakes; bottom-up process; fish community; food web; *Gavia adamsii*; *Gavia pacifica*; lake habitat; occupancy modeling; territory occupancy

RÉSUMÉ. Les populations de prédateurs sont vulnérables aux changements de répartition ou de disponibilité des proies. En raison du réchauffement des températures, on prévoit que les écosystèmes lacustres de l'Arctique changeront pour ce qui est du régime hydrologique, des niveaux d'eau et de la connectivité avec d'autres lacs. Nous avons examiné des lacs du nord de l'Alaska pour comprendre comment les changements en matière de répartition ou de disponibilité des poissons peuvent avoir des incidences sur le taux d'occupation et sur le succès de reproduction du huart du Pacifique (*Gavia pacifica*) et du huart à bec blanc (*G. adamsii*). Ensuite, nous avons modélisé l'influence de la présence et de l'abondance de cinq espèces de poissons de même que les caractéristiques physiques de lacs (comme la connectivité hydrologique) par rapport au taux d'occupation lacustre des huarts et à la production d'oisillons. La présence du dallia (*Dallia pectoralis*) avait une influence positive sur l'occupation et la production d'oisillons chez le huart du Pacifique, ce qui suggère que les espèces de poissons au petit corps constituent une proie importante pour les oisillons. Aucune caractéristique de l'abondance des espèces de poissons n'a eu d'influence sur l'occupation lacustre du huart à bec blanc. L'occupation du huart à bec blanc a plutôt été influencée par les caractéristiques physiques des lacs qui contribuent aux populations de poissons persistantes, comme la taille du lac et la proportion du lac qui ne gelait pas en hiver. Toutefois, aucune de ces variables n'a exercé d'influence sur la production d'oisillons. La probabilité qu'un territoire inoccupé devienne occupé par le huart au bec blanc au cours d'une année subséquente était faible, et aucun oisillon huart n'a été élevé avec succès dans des territoires d'oisillons anciennement inoccupés. En revanche, les territoires inoccupés avaient une beaucoup plus grande probabilité de devenir occupés par les huarts du Pacifique, ce qui suggère que les huarts à bec blanc ont des exigences strictes en matière d'habitat et que le nombre de lacs convenant à la reproduction risque d'être limité. Les territoires qui étaient occupés avaient de fortes probabilités de rester occupés par les deux espèces de huarts.

Mots clés : Plaine côtière de l'Arctique; lacs de l'Arctique; processus ascendant; communauté de poissons; réseau trophique; *Gavia adamsii*; *Gavia pacifica*; habitat de lac; modélisation de l'occupation; occupation du territoire

Traduit pour la revue *Arctic* par Nicole Giguère.

---

[1] U.S. Geological Survey Alaska Science Center, 4210 University Drive, Anchorage, Alaska, USA
[2] Corresponding author: buher-koch@usgs.gov
[3] Department of Geography and Environmental Studies, University of Alaska Anchorage, 3211 Providence Drive, Anchorage, Alaska, USA

INTRODUCTION

Understanding the relationship between animals and the habitats they select is a fundamental issue in ecology. In general, organisms select the highest-quality habitat available to maximize fitness. Many factors may influence habitat quality, however, habitat selection is an adaptive process and is often based on the distribution of resources (Jones, 2001). Variations in the quality or reliability of these resources can promote territoriality to ensure sufficient resources for oneself (Krebs, 1971). Territoriality can be a response to competition for resources and therefore result from habitat limitations (Brown, 1964). Identifying what constitutes a high-quality territory is important for prioritizing what habitats to protect and informing management decisions.

Loons (family Gaviidae) are territorial, piscivorous diving birds that use freshwater lakes as feeding, nesting, and chick-rearing areas. Pacific (*Gavia pacifica*) and Yellow-billed Loons (*G. adamsii*) breeding on the Arctic Coastal Plain (ACP) in northern Alaska overlap in distribution and compete for territories. The larger Yellow-billed Loon is uncommon and typically breeds on large, deep lakes (Earnst et al., 2006). Yellow-billed Loons are behaviorally dominant and exclude the smaller more abundant Pacific Loon from breeding lakes (Haynes et al., 2014a; Schmidt et al., 2014). Competition may shape the distribution and resource use of breeding loons on the ACP, thus Pacific Loons either choose or are limited to comparatively smaller, shallower, less-connected lakes (Haynes et al., 2014a; Jones et al, 2017). Interspecific competition can be the result of resource limitation (Kodric-Brown and Brown, 1978) and, since the overall productivity of Arctic lakes is low (Hobbie, 1984) and waterbirds can impact the abundance of fish in lakes (Britton et al., 2003), this extreme territoriality of loons is likely driven by the limited amount of high-quality breeding sites and the need to ensure a sufficient food base within a lake to raise their young (Haynes et al., 2014a; Uher-Koch et al., 2019).

Lake and nest site selection may be important factors determining the breeding success of loons (Alvo et al., 1988; Eberl and Picman, 1993; Haynes et al., 2014b; Uher-Koch et al., 2018). Lake area, lake depth, proportion of shoreline in aquatic vegetation, hydrologic connectivity, and percent of the lake that remains unfrozen over winter all influence Yellow-billed Loon lake occupancy (Earnst et al., 2006; Haynes et al., 2014a, b; Jones et al., 2017; Johnson et al., 2019; Uher-Koch et al., 2019). These factors are similar to the factors that influence persistent fish populations. Work on the closely related Common Loon (*G. immer*) suggests that breeding loons are more likely to be present on large, deep lakes containing large-bodied fish species (Ruggles, 1994; Gingras and Paszkowski, 1999), and that breeding success is related to these characteristics (Alvo et al., 1988; Piper et al., 2012). Pacific and Yellow-billed Loon chicks take a long time to fledge (> 50 days; Russell, 2020; Uher-Koch et al., 2020) and are mostly reliant on their natal lake for resources during this period. Chick survival is likely driven by resource availability as adult loons must select lakes for nesting and brood rearing that contain an adequate supply of fish for themselves and their chicks. Although fish availability may be a critical factor for breeding loon territory selection (Jackson, 2003, 2005), no studies have addressed the relationship between fish populations and loon lake occupancy and breeding success in the Arctic.

Fish species on the ACP exhibit a variety of life history traits. In general, fish communities on the ACP, which we define as the assemblage of fish species within a lake, are dictated by the ecology of the species, adult size, lake size, and colonization potential (Hershey et al., 2006; Haynes et al., 2014c; Laske et al., 2016, 2019). Shallow (< 1.6 m; Jones et al., 2017), unconnected lakes likely constitute poor loon habitat as they may be prone to overwintering fish die-offs and have less predictable sources of prey fish. For large-bodied fish species, lake occupancy is related to stream connectivity and overwintering fish habitat (Haynes et al., 2014c; Laske et al., 2016). Small-bodied fish, which are used as loon prey items and to provision chicks, occupy a variety of niches. Certain fish species may be better suited for recolonizing lakes or can survive harsh winter conditions, such as Alaska blackfish (*Dallia pectoralis*), and their presence early in the nesting season may make them a valuable species to loons. Other fish species, such as least cisco (*Coregonus sardinella*) and ninespine stickleback (*Pungitius pungitius*), are ubiquitous on the ACP (Haynes et al., 2014c) and have high energy densities (Ball et al., 2007), which suggests that they would be important prey items for loons. The fact that individual fish species may play a role in loon habitat selection and influence chick survival (Jackson, 2003) demonstrates the need to understand the relationships between loon habitat selection and the fish communities they rely on.

Identifying Pacific and Yellow-billed Loon habitat requirements is of interest given potential changes to Arctic lake ecosystems, which include continued warming, changes in hydrologic patterns (Prowse et al., 2006; Wrona et al., 2016), and ongoing interest in oil and gas development in the National Petroleum Reserve-Alaska (NPR-A) where high densities of nesting loons occur (Amundson et al., 2019). Loon breeding habitat assessment is also important because loons are considered bioindicators of environmental health (Dickson, 1992; Evers, 2006) and are sensitive to changes in environmental conditions (Evers et al., 2008; Schmutz, 2014), including prey abundance (Alvo et al., 1988; Gingras and Paszkowski, 1999). Declines in fish populations can have large impacts on piscivorous birds (Furness, 2007); therefore, changes in Arctic fish populations and distributions would have implications throughout the food web. We hypothesize that Pacific and Yellow-billed Loon lake occupancy and productivity on the ACP will be dictated by the fish populations on the ACP. Because prior studies on the ACP have addressed loon lake occupancy (North and Ryan, 1989; Earnst et al., 2006; Haynes et al., 2014a; Jones et al., 2017; Johnson et al., 2019), fish detection probabilities (Haynes et al., 2013; Bradley et al., 2016), and fish occupancy (Haynes et al., 2014c; Laske et al., 2016), we were interested in how fish populations relate to loon lake occupancy and breeding success. Our goal for this study was to examine the potential impact of prey fish availability on loon habitat selection during the breeding season. Specifically, we evaluated the relationship between loon lake occupancy, chick production and relative fish species abundance within lakes in Arctic Alaska. We use chick production as a measure of habitat quality because loons must choose a lake to support their chicks, and there may be differences between lakes occupied by loons versus lakes suitable for breeding (e.g., hydrologic connectivity; Ruggles, 1994). Finally, we determine the variability of lake use by loons and contrast this between coastal and inland strata and if it is related to the physical characteristics of lakes.

METHODS

Study Area

We conducted this study at two 64 km^2 study sites on the ACP from 2011 to 2014. The region consists of a low-relief tundra landscape, dominated by many shallow lakes. Chipp North (70.686˚ N, −155.305˚ W) is near the coast, while our other site, Chipp South (70.395˚ N, −155.408˚ W) is ~50 km inland and has greater diversity of surface elevation profiles (Fig. 1). Lakes in our study areas fall into three main categories that influence the fish communities within: 1) large, deep lakes containing multiple fish species and fish species from the Salmonidae family, 2) small, seasonally connected lakes that have small-bodied fish species (often ninespine stickleback are the only species present), and 3) disconnected fishless lakes (Laske et al., 2016). We obtained Light Detection and Ranging (LIDAR) data for each of these study sites, which gave us a precise three-dimensional watershed profile among all the water bodies in these plots, thus allowing more accurate modeling of the hydrologic relation among these water bodies. Almost every lake in each study area was occupied by at least one pair of Pacific or Yellow-billed Loons (e.g., only three unoccupied lakes [> 7 ha] out of 44 lakes at Chipp North and 33 lakes at Chipp South; Uher-Koch et al., 2019).

Lake Surveys

We systematically surveyed each lake in the study area (n = 93) by foot beginning in mid-June from 2011 to 2014 to identify loon territories, determine lake occupancy, and to find loon nests. Researchers walked the perimeter of each lake and all islands and noted the number of loons of each species present on the lake. We recorded coordinates of nest locations using handheld Global Positioning System (GPS) units. Lakes (or portions of lakes for those with multiple territories) were classified as one of three types: unoccupied by loons, occupied by territorial loons, or occupied with a chick present. Because loon nest initiation can occur throughout the breeding season, we revisited each lake periodically throughout the summer, and all lakes were visited at least twice during the breeding season. Yellow-billed Loons occasionally build their nest on small lakes or channels near larger lakes that are part of their territory (Uher-Koch et al., 2018). We considered the adjacent larger lake as their territory when performing occupancy analyses. Following hatch, territories were visited at least once per week to determine chick survival. Loon survey data are publicly available and described in (Uher-Koch, 2020).

Fish Sampling

We sampled fish from 93 lakes between our two study areas over two summers (in 2013 and 2014). Fish sampling followed similar methods employed by Haynes et al. (2013); sampling began once lakes were open following ice breakup (July) and continued through mid-August. Lakes selected for fish sampling were based on size, loon species present, and loon breeding status to get a variety of lakes sampled with different uses by both loon species. We sampled for fish on every lake over 7 ha within both study areas (the minimum size typically used by Yellow-billed Loons; Stehn et al., 2005; Earnst et al., 2006), but also sampled lakes less than 7 ha to account for lakes used by Pacific Loons. Lakes were prioritized if loons had been captured so that we could collect loon prey samples for diet determination using fatty acid and stable isotope analyses (Haynes et al., 2015).

We used three gear types to sample lakes for fish: gill nets, minnow traps, and hoop nets. Following each replicate for each gear type, fish species were identified and counted. We deployed two 24.8 m × 1.8 m variable mesh gill nets (eight mesh sizes ranging from 19 mm to 64 mm) per sample lake. Gill nets were set in 1.8 m water so the lead line of the net sat on the bottom of the lake and the float line was on the surface of the water to sample the entire water column. We attempted to place gill nets perpendicular to the shoreline on opposite sides of the lake. Gill nets were pulled after three hours, and all species of fish caught were recorded and measured.

We deployed two baited galvanized steel minnow traps (2.5 cm opening, 6 mm mesh) in shallow water along the shoreline at opposite ends of each lake. Minnow traps were removed after three hours and all species of fish caught were recorded and measured. We set a single 0.6 m diameter hoop net (2 throats, 6 mm mesh, two 4.6 m wings with a float and lead line) in the lake adjacent to a stream if the lake had a hydrologic connection. We attempted to place the hoop net in water less than 1 m deep. The hoop net was removed after three hours and placed in the same location on the following day.

Gill net and minnow trap sampling were replicated spatially and temporally as we deployed multiple sets per lake at the same time. Most lakes were sampled on consecutive days to get four samples per lake (i.e., two sets of both gear

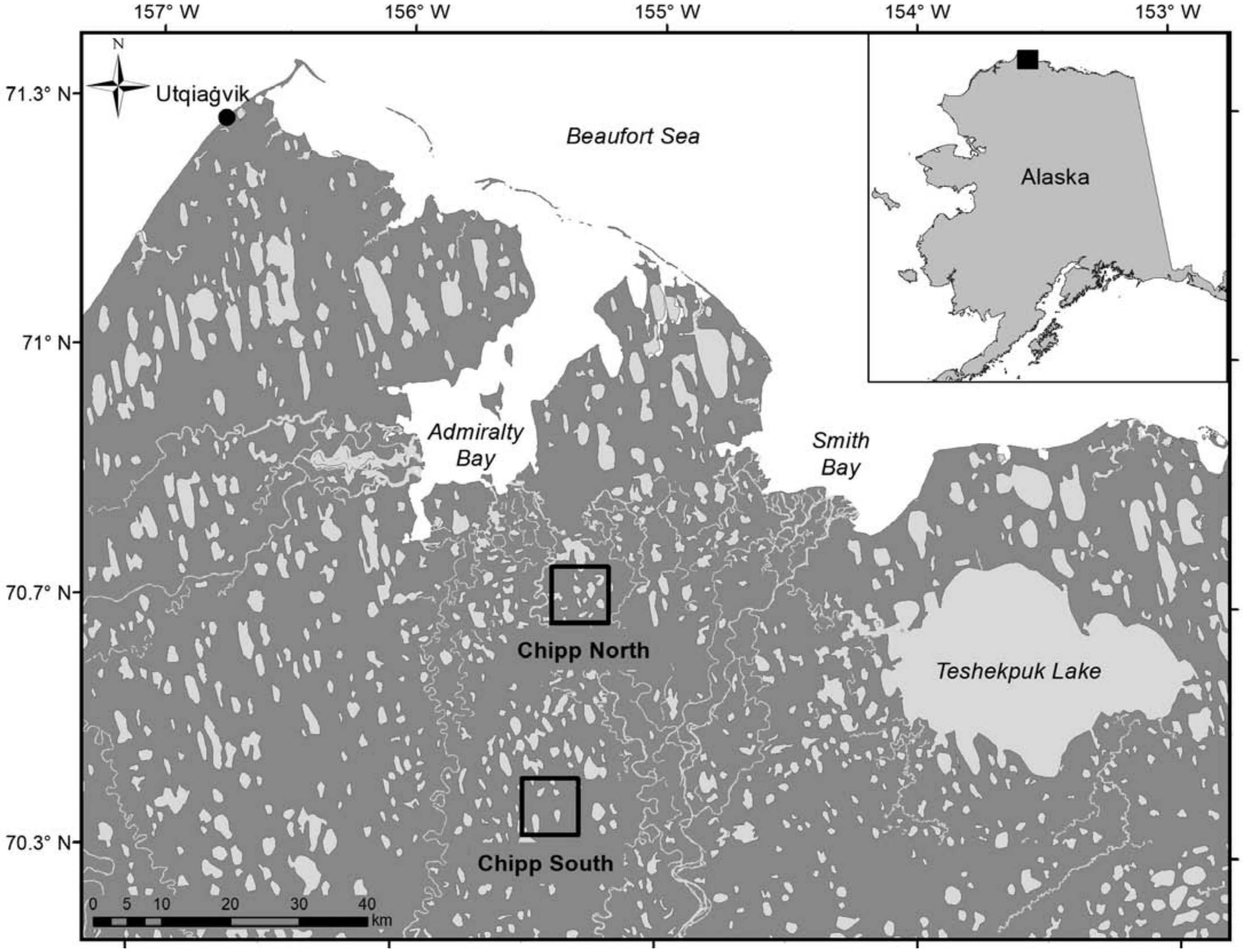

FIG. 1. Locations of study sites used to evaluate fish populations and loon lake occupancy on the Arctic Coastal Plain in northern Alaska from 2011 to 2014.

types [gill nets and minnow traps] for three hours per day). Hoop net sets were only replicated temporally because of the difficulty of transport; thus, hoop nets were placed in the same location the following day (i.e., one set of three hours each day). Nets were not systematically deployed at certain times during the day (most sets were in the afternoon or evening) since there is 24-hour sunlight in the Arctic in the summer and time of day does not influence detection probabilities of lakes on the ACP (Haynes et al., 2013). For a subset of lakes, we only sampled fish on a single day (n = 11). On these days, nets were checked after three hours and then set for an additional three hours. We did not evaluate fish detection probabilities because our fish sampling methods were based on previous work, and detection probabilities for fish species on the ACP have been addressed elsewhere (Haynes et al., 2013; Bradley et al., 2016).

Loon Occupancy Analyses

To investigate patterns of loon lake occupancy and breeding status, we developed an a priori candidate set of 16 models and evaluated the same set of models for both Pacific and Yellow-billed Loons. Loon lake occupancy and breeding status were modeled across four years (2011–14). We collapsed loon territory occupancy into three states: unoccupied (state 0), occupied by territorial loons (state 1), and occupied by territorial loons with reproduction (e.g., chicks at least three weeks old; state 2). We defined reproduction as territories with chicks that reached three weeks of age because loon chicks have a high probability of fledging if they survive the 2-week high-mortality period following hatch and chick survival to two to four weeks is often used as an estimate of fledging rates and productivity (Titus and Van Druff, 1981; McIntyre, 1983; North and Ryan, 1988; Parker, 1988). Because the focus of our study was on the influence of fish populations on loon lake occupancy and breeding status, and dynamics between Pacific and Yellow-billed Loons have been addressed elsewhere (North, 1986, Haynes et al., 2014a; Schmidt et al., 2014), we ran separate analyses for the two loon species. We included 120 loon territories (of either species) or unoccupied lakes in our analyses from the 93 total lakes that were surveyed for fish (i.e., some lakes had multiple loon territories). To account for potential interactions between the two species, we included parameters for lakes with multiple loon nests and lakes with both species present.

We did not examine potential influences on loon detection probabilities (i.e., constant with no covariates) and do not report loon detection probabilities because the focus of our study was to examine the relationship between loons and fish, loon initiation is asynchronous, and all lakes were visited multiple times per season. Further, asynchrony in initiation dates made it difficult to correctly identify occupancy state (e.g., the first time a territory was visited it may have been occupied but the adults had not begun nesting yet). Loons can have high detection probabilities given their large size and territorial nature (Hammond et al., 2012), and because we walked the entire shoreline of each lake including the islands, the probability of detecting a nest, if present, was very high. We only included two surveys in our analyses because the status of the territory could change over the course of the season, and we were unable to evaluate loon breeding success until late in the season. If a territory successfully produced chicks, the territory was considered successful for both encounters, so we did not bias the probability of correctly identifying the breeding state.

To determine the potential influence of fish populations on loon lake occupancy and breeding status we included five covariates for the presence or non-detection of the individual fish species. We only included fish species with naïve occupancy over 10% in our analyses: least cisco, broad whitefish (*Coregonus nasus*), Arctic grayling (*Thymallus arcticus*), Alaska blackfish, and ninespine stickleback. Most adult broad whitefish were too large to be candidate prey for loons, but we included them in analyses as their presence may reflect other factors that are important to loons, such as lakes that support overwintering fish habitat. Because fish abundance can influence loon occupancy and breeding success (Jackson, 2005), we also calculated catch-per-unit effort (CPUE) of fish caught in each lake. We included two models using CPUE as rough estimates of fish abundance to evaluate if fish abundance has a larger impact than the presence or absence of individual fish species. These covariates included the CPUE of large-bodied fish species presence (e.g., broad whitefish) and CPUE for small-bodied fish species presence (e.g., ninespine stickleback). We combined the set times and catches for gill nets and hoop nets to determine the CPUE for large-bodied fish and combined the hoop net and minnow trap set times and catches to determine the CPUE for small-bodied fish. Some fish species in our study areas (e.g., slimy sculpin [*Cottus cognatus*]) had a low naïve occupancy probability (< 10%), but we included these data when calculating the fish abundance estimates (e.g., the only large-bodied fish species present on two lakes with breeding Yellow-billed Loons was Arctic char [*Salvelinus alpinus*]). We also included a model for the total number of fish species (fish richness) caught in a lake because we predicted that fish species diversity may play a role in loon occupancy. We did not include a variable representing lakes without fish because almost every lake we surveyed contained at least one fish species (i.e., only six lakes without fish out of 93 surveyed). We included a constant model to evaluate occupancy and breeding status without any covariates.

To evaluate whether loon lake occupancy and breeding status were related to indices of fish populations or to the physical characteristics of lakes, we included four covariates related to the physical characteristic for each lake. These covariates included the surface area of the lake (lake area), the hydrologic connectivity of the lake, the proportion of the lake that remains unfrozen during winter (unfrozen), and our two study sites (site). We used the National Hydrography Dataset (NHD) to determine lake surface area (km^2; U.S. Geological Survey 2013). To determine hydrologic connectivity (i.e., lake order) we used a combination of LIDAR data and ground-based observations. Lakes were given an order (−3, −2, −1, 0, 1, 2) based on their connectivity and relationship to other lakes within their drainage (Riera et al., 2000). We used synthetic aperture data (SAR) to calculate lake depths and the area of the lake that remains unfrozen (Grunblatt and Atwood, 2014).

We used robust design multi-state occupancy estimation conditional binomial procedures (Mackenzie et al., 2009) in Program MARK to model the probability of Pacific and Yellow-billed Loons occurring in each occupancy state, as well as six state transition probabilities (e.g., from occupied to unoccupied, occupied to occupied with reproduction). Yellow-billed Loons are known to exclude Pacific Loons (Haynes et al., 2014a; Schmidt et al., 2014); therefore, we did not evaluate multispecies occupancy models and modeled each loon species separately. Covariates influencing the occupancy state of loons were only included on the initial states, and we did not evaluate temporal variation or covariates influencing transition probabilities, detection probabilities, or probabilities of observing the true state. We evaluated a single variable on each occupancy state in each model and did not include any additive models in our analyses because we wanted to evaluate the influence of each fish species and keep the number of models in our analyses low because of small sample sizes. An information theoretic approach was used to quantify and interpret effects of fish populations and physical lake characteristics on the territory occupancy and breeding status of loons (Burnham and Anderson, 2004). Multiple a priori hypotheses, expressed as candidate models, were ranked by comparing models using Akaike's Information Criterion adjusted for small sample size (AICc) (Burnham and Anderson, 2004). To determine the relative support of each model, ΔAICc scores and AICc weights (w_i) were used. ΔAICc scores were calculated as the difference between each model and the most parsimonious model (i.e., the model with the lowest AICc score). To determine the relative support of each model, AICc weights (w_i) were

TABLE 1. Model selection results for influences on Pacific Loon lake occupancy and production of chicks on freshwater lakes in northern Alaska from 2011 to 2014. Variables included represent the presence or absence of five different fish species, the total number of fish species found in a lake (fish richness), the study site, the proportion of the lake that remains unfrozen overwinter (unfrozen), presence of islands, and hydrologic connectivity. Detection probabilities and probabilities of observing true states were held constant in all models.

Model	ΔAICc[1]	AICc w_i	Likelihood	K	Deviance
Alaska blackfish	0.00	0.45	1.00	13	379.34
Constant	0.89	0.29	0.64	11	384.66
Fish richness	2.62	0.12	0.27	13	381.96
Ninespine stickleback	3.62	0.07	0.16	13	382.96
Large fish abundance	4.16	0.06	0.13	13	383.50
Small fish abundance	12.87	0.00	0.00	13	392.21
Multiple loon nests	13.88	0.00	0.00	13	393.22
Site	13.91	0.00	0.00	13	393.25
Least cisco	15.06	0.00	0.00	13	394.40
Island presence	15.43	0.00	0.00	13	394.77
Multiple loon species	15.51	0.00	0.00	13	394.85
Arctic grayling	15.73	0.00	0.00	13	395.07
Lake size	15.90	0.00	0.00	13	395.24
Unfrozen	16.04	0.00	0.00	13	395.38
Broad whitefish	16.73	0.00	0.00	13	396.07
Hydrologic connectivity	17.02	0.00	0.00	13	396.36

[1] AICc of the highest-ranking model was 406.90.

used. We used model averaging to estimate state transition probabilities.

RESULTS

Pacific Loon Occupancy

We included 64 Pacific Loon territories and three unoccupied lakes in our analyses from the 93 total lakes surveyed for fish. Model-averaged occupancy without reproduction for Pacific Loons in our study areas was high (0.98, 95% CI: 0.75 – 0.99). For Pacific Loons, the model that included the covariate for Alaska blackfish presence received the most support (ΔAICc = 0.00, $w_i = 0.45$, Table 1). Alaska blackfish had a positive impact on Pacific Loon lake occupancy with reproduction ($\beta_{\text{blackfish}} = 1.47$, 95% CI: 0.04 – 2.91). No other models received more support than the null model. The models including covariates for fish species richness ($\beta_{\text{richness}} = 0.14$, 95% CI: −0.16 – 0.46) and ninespine stickleback presence ($\beta_{\text{stickleback}} = 0.35$, 95% CI: −1.99 – 2.69) received moderate support from the data (ΔAICc < 4.0); however, confidence intervals of parameter coefficients overlapped zero. Pacific Loon occupancy and breeding status did not differ between our coastal or inland study sites.

Yellow-billed Loon Occupancy

We included 50 Yellow-billed Loon territories and three unoccupied lakes in our analyses. Model-averaged occupancy without reproduction for Yellow-billed Loons in our study areas was high (0.94, 95% CI: 0.70 – 0.99). In general, the models influencing Yellow-billed Loon lake occupancy that contained variables representing lake physical characteristics received more support than models including fish covariates. The models including lake size (ΔAICc = 0.00, $w_i = 0.41$) and proportion of the lake that remains unfrozen (ΔAICc = 0.30, $w_i = 0.35$) received the most support (Table 2). However, no covariates influenced loon lake occupancy with chick production including lake size ($\beta_{\text{size}} = 0.70$, 95% CI: −0.15 – 1.53) or proportion of the lake that remains unfrozen ($\beta_{\text{unfrozen}} = 0.76$, 95% CI: −0.50 – 2.01). Mean sizes of lakes occupied by Yellow-billed Loons (0.83 km^2 SE ± 0.11) were larger than those occupied by Pacific Loons (0.41 km^2 SE ± 0.06). Similarly, the mean proportion of each lake occupied by Yellow-billed Loons that remained unfrozen (0.57) was larger than for Pacific Loons (0.26).

Individual fish species received little support from the data as all fish species received less support than the null model. Further, the total number of fish species (fish richness), fish abundance variables, and hydrologic connectivity received little support from the data. Multiple loon species occupying a lake or lakes with multiple loon nests also did not influence Yellow-billed Loon occupancy or breeding status. Yellow-billed Loon occupancy and breeding status did not differ between our coastal or inland study sites.

Loon Occupancy State Transition Probabilities

No Yellow-billed Loon territories that produced chicks became unoccupied in subsequent years and the model-averaged probability that a Pacific Loon territory would remain occupied following chick production was high (0.97, 95% CI: 0.81 – 1.00). Similarly, the probability of a territory being occupied in a subsequent year given that the territory was currently occupied but did not produce chicks was high for both Pacific (0.98, 95% CI: 0.93 – 1.00) and Yellow-billed Loons (0.99, 95% CI: 0.97 – 1.00).

TABLE 2. Model selection results for influences on Yellow-billed Loon lake occupancy and production of chicks on freshwater lakes in northern Alaska from 2011 to 2014. Variables included represent the presence or absence of five different fish species, the total number of fish species found in a lake (fish richness), the study site, the proportion of the lake that remains unfrozen overwinter (unfrozen), the presence of islands, and hydrologic connectivity. Detection probabilities and probabilities of observing true states were held constant in all models.

Model	ΔAICc[1]	AICc w_i	Likelihood	K	Deviance
Lake size	0.00	0.41	1.00	13	287.07
Unfrozen	0.30	0.35	0.86	13	287.37
Constant	4.13	0.05	0.13	11	295.75
Island presence	5.48	0.03	0.06	13	292.55
Large fish abundance	5.52	0.03	0.06	13	292.59
Arctic grayling	5.83	0.02	0.05	13	292.90
Small fish abundance	5.95	0.02	0.05	13	293.02
Least cisco	6.80	0.01	0.03	13	293.88
Site	6.84	0.01	0.03	13	293.91
Multiple loon nests	7.01	0.01	0.03	13	294.08
Broad whitefish	7.14	0.01	0.03	13	294.22
Hydrologic connectivity	7.26	0.01	0.03	13	294.34
Fish richness	7.84	0.01	0.02	13	294.92
Alaska blackfish	8.13	0.01	0.02	13	295.20
Ninepsine stickleback	8.35	0.01	0.02	13	295.42
Multiple loon species	8.45	0.01	0.01	13	295.53

[1] AICc of the highest-ranking model was 314.98.

The probability of a Yellow-billed Loon territory becoming occupied in a subsequent year, given that it was not currently occupied was low (0.28, 95% CI: 0.11–0.55), and no loon chicks were successfully raised in territories that were previously unoccupied. In contrast, unoccupied territories had a much higher probability of use by Pacific Loons (0.84, 95% CI: 0.40–0.98).

The probability of successful reproduction occurring in a subsequent year at a territory was slightly higher for territories that were currently occupied with reproduction for both Pacific (0.34, 95% CI: 0.22–0.51) and Yellow-billed Loons (0.30, 95% CI: 0.17–0.47), than for territories that were currently occupied without reproduction (Pacific Loon: 0.21, 95% CI: 0.15–0.29; Yellow-billed Loon: 0.24, 95% CI: 0.17–0.33). The number of successful territories for Pacific (range: 8–21) and Yellow-billed Loons (range: 7–15) varied across the four years of our study.

DISCUSSION

Similar to other studies on the ACP (Haynes et al., 2014a; Jones et al., 2017; Johnson et al., 2019; Uher-Koch et al., 2019), our results provide further evidence that lakes on the ACP in northern Alaska are consistently used by loons every year because of the physical characteristics of lakes rather than chick production or specific forage resources. If a territory was occupied by either species of loon, even if it did not produce chicks, it was highly likely to remain occupied in a subsequent year. The large amount of research showing that Yellow-billed Loons in northern Alaska continuously use the same territories combined with their clustered distribution, multiple pairs per lake, and large nonbreeding population collectively suggest that breeding habitat may be limiting (Earnst et al., 2005, 2006; Schmutz et al., 2014; Uher-Koch et al., 2019). In contrast, we found a much higher probability of unoccupied territories becoming occupied by Pacific Loons and the only instances we found of new Yellow-billed Loon territory formation was by takeover of territories previously occupied by Pacific Loons. Similarly, Pacific Loons have higher territory colonization probabilities than Yellow-billed Loons (Haynes et al., 2014a). We suspect that Pacific Loons have broader habitat requirements and can use a wider range of lakes (North, 1986, Jones et al., 2017, Solovyena et al., 2017), including potentially using lakes without fish. The higher potential for Pacific Loons to occupy new territories may contribute to the difference in breeding population sizes between the two loon species, with Pacific Loon breeding populations being much larger on the ACP (Wilson et al., 2018).

The presence of Alaska blackfish had a positive influence on Pacific Loon lake occupancy with reproduction. Alaska blackfish and ninespine stickleback often occur in the same lake (Laske et al., 2016), and we speculate that these small-bodied fish species provide important prey for Pacific Loons. These fish species occupy lakes with a wide range of physical characteristics and may be well suited for recolonizing lakes because they are tolerant of harsh conditions and can overwinter in lakes where other species cannot (Haynes et al., 2014c). Their presence early in the breeding season may also make them valuable to nesting loons (Haynes et al., 2015). Pacific Loon chicks are typically fed invertebrates from the nesting lake (Bergman and Derksen, 1977; Kertell, 1996; Rizzolo, 2017), and the lack of large fish (i.e., salmonids) in the lakes used by Pacific Loons may allow for the persistence of large invertebrate taxa that are important prey for Pacific Loon chicks (Laske et al., 2019). The diet of adult Pacific Loons has not been evaluated in northern Alaska, and further quantification of diet and chick provisioning for both species of loons would help with identifying habitat preferences.

Surprisingly, neither the presence of certain fish species nor fish abundance influenced Yellow-billed Loon lake occupancy, although prior research has found that fish abundance can influence loon territory selection and chick survival (Barr, 1996; Jackson, 2005; Merrill et al., 2005; Alvo, 2009). These results coincide with preliminary diet results suggesting that Yellow-billed Loons are generalist foragers that do not rely on one specific fish species and feed on whatever is present within the lake (Haynes et al., 2015). Similarly, fish species on the ACP are generalist foragers, which allows them to deal with the harsh environment in northern Alaska (Laske et al., 2018). We recognize that several factors could have reduced our ability to make inferences regarding the impact of fish populations on loon occupancy and productivity. We attempted to sample a large number of lakes with varying physical characteristics across our two study areas. This meant our fish abundance estimates were only based on a maximum of two days of fish sampling, and we suspect that our sampling may have been insufficient to adequately measure fish abundance. This sampling effort also prevented us from evaluating temporal differences in fish presence and abundance. Further, the detection of fish is imperfect (i.e., low detection probabilities of certain fish species), and few territories for either loon species consistently produced chicks, which made it difficult to evaluate the potential influences on loon occupancy and productivity. Based on prior research on the ACP, we used multiple gear types in an attempt to improve overall detection of fish species (Haynes et al., 2013), but future studies should potentially increase overall sampling effort (i.e., spend more days sampling each lake) to get a better understanding of the fish populations within each lake.

Factors influencing Yellow-billed Loon occupancy were similar to those identified from prior research, such as lake size and the amount of overwintering fish habitat (Haynes et al., 2014a; Jones et al., 2017; Johnson et al., 2019; Uher-Koch et al., 2019). These factors contribute to persistent fish populations in lakes. We suspect that fish presence may be more important to nesting loons on the ACP than any particular fish species and, as long as there are sufficient resources within a lake, it will be occupied by breeding loons. Although we did not find support for an influence of hydrologic connectivity, it is important for both fish and loon lake occupancy on the ACP (Earnst et al., 2006; Haynes et al., 2014c; Laske et al., 2016; Jones et al., 2017). Our lack of results on the influences on loon lake occupancy and production may be related to the high density of loons at our study areas, as almost all lakes in our study areas were occupied by loons. Surveying loon lake occupancy and fish communities across a larger scale in northern Alaska (e.g., Earnst et al., 2006), not just in the highest breeding density areas, would likely provide additional insight into loon habitat preferences.

Habitat preferences and occupancy for adult Yellow-billed Loons have been examined extensively in northern Alaska (North and Ryan, 1989; Earnst et al., 2006; Haynes et al., 2014a; Jones et al., 2017; Johnson et al., 2019; Uher-Koch et al., 2019). However, a general understanding of the factors influencing chick production is still lacking as territories are not consistently productive. We found that a territory that is occupied with reproduction in the current year has only about a 30% chance of being used to successfully reproduce chicks the following year. In this study we tried to determine the potential bottom-up processes that influence loon productivity. Chick survival for other loon species is often driven by the abundance of key fish species (Gingras and Paszkowski, 1999), but top-down processes such as egg predation by terrestrial predators (e.g., Arctic foxes [*Vulpes lagopus*] and red foxes [*V. vulpes*]; Rizzolo et al., 2014), or environmental variables (e.g., flooding due to precipitation; Uher-Koch et al., 2018) can also influence loon breeding success. To further understand loon habitat quality on the ACP, research is needed to quantify the environmental factors affecting temporal and spatial variability in productivity.

Food webs within lake ecosystems in the Arctic are sensitive to climate changes (Prowse et al., 2006; Wrona et al., 2006), and the quality of loon habitat may change with shifts in lake water levels, lake geochemistry, and fish distributions. Given specific habitat requirements for some loon species (e.g., large, deep lakes with overwintering fish habitat for Yellow-billed Loons), future projections of loon habitat quality need to account for changes to water bodies, especially factors that may influence fish abundance and water level changes. Many factors influence fish distributions and many of these are ultimately temperature-driven (e.g., increased hydrologic connectivity through permafrost thawing), which suggests that fish with different life histories will respond to climate warming differently thereby leading to changes in fish community composition (Reist et al., 2006; Sharma et al., 2007; Wrona et al., 2016). For example, least cisco production in the Arctic is expected to increase (Carey and Zimmerman, 2014), while climate warming may have a detrimental effect on Arctic grayling (Deegan et al., 1999) and lake trout (*Salvelinus namaycush*; McDonald et al., 1996), which prefer cooler temperatures. Fish are important in Arctic aquatic food webs and, because of differences in habitat use by Pacific and Yellow-billed Loons, identifying the relationships between loons, fish, and hydrologic variables is critical to predicting how these species and Arctic lake ecosystems will respond to climate change or anthropogenic disturbance.

ACKNOWLEDGEMENTS

We thank the following individuals for field assistance: H. Beutler, C. Bishop, B. Braden, R. Buchheit, D. Cummings, N. Docken, G. Evans, J. Fair, T. Fondell, S. Garcia, C. Gray, I. Isler, C. Johnson, A. Larned, S. Laske, G. Meese, K. Overduijn,

T. Ronningen, T. Shoemaker, T Spivey, and C. VanStratt. We thank the Biodiversity Research Institute and the Bureau of Land Management Arctic Office for financial and logistical assistance. We also thank the North Slope Borough Planning and Community Services Department, the Wildlife Management Department, and the NPR-A Subsistence Advisory Panel for their comments and feedback during fieldwork. The manuscript benefited from thoughtful reviews provided by S. Laske, J. Pearce, and three anonymous reviewers. All capture and handling procedures were reviewed and approved by the U.S. Geological Survey Alaska Science Center Animal Care and Use Committee. This project was funded through the Changing Arctic Ecosystems Initiative of the U.S. Geological Survey Ecosystem Mission Area. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

REFERENCES

Alvo, R. 2009. Common Loon, *Gavia immer*, breeding success in relation to lake pH and lake size over 25 years. Canadian Field-Naturalist 123(2):146–156. https://doi.org/10.22621/cfn.v123i2.693

Alvo, R., Hussell, D.J.T., and Berrill, M. 1988. The breeding success of Common Loons (*Gavia immer*) in relation to alkalinity and other lake characteristics in Ontario. Canadian Journal of Zoology 66(3):746–752. https://doi.org/10.1139/z88-110

Amundson, C.L., Flint, P.L., Stehn, R.A., Platte, R.M., Wilson, H.M., Larned, W.W., and Fischer, J.B. 2019. Spatio-temporal population change of Arctic-breeding waterbirds on the Arctic Coastal Plain of Alaska. Avian Conservation and Ecology 14(1): 18. https://doi.org/10.5751/ACE-01383-140118

Ball, J.R., Esler, D., and Schmutz, J.A. 2007. Proximate composition, energetic value, and relative abundance of prey fish from the inshore eastern Bering Sea: Implications for piscivorous predators. Polar Biology 30(6):699–708. https://doi.org/10.1007/s00300-006-0227-1

Barr, J.F. 1996. Aspects of Common Loon (*Gavia immer*) feeding biology on its breeding ground. Hydrobiologia 321(2):119–144. https://doi.org/10.1007/BF00023169

Bergman, R.D., and Derksen, D.V. 1977. Observations on Arctic and Red-throated Loons at Storkersen Point, Alaska. Arctic 30(1):41–51. https://doi.org/10.14430/arctic2682

Bradley, P., Morris, W., and Moulton, L. 2016. Fish and aquatic habitat surveys in the Topagoruk, Chipp, and Meade Rivers, 2012–2016. Technical Report 16-07. Fairbanks: Alaska Department of Fish and Game.

Britton, J.R., Harvey, J.P., Cowx, I.G., Holden, T., Feltham, M.J., Wilson, B.R., and Davies, G.M. 2003. Key factor analysis to assess cormorant depredation on inland fisheries in the UK. In: Cowx, I.G., ed. Interactions between fish and birds: Implications for management. Oxford: Fishing News Books, Blackwell Science. 14–27. https://doi.org/10.1002/9780470995372.ch2

Brown, J.L. 1964. The evolution of diversity in avian territorial systems. Wilson Bulletin 76(2):160–169.

Burnham, K.P., and Anderson, D.R. 2004. Model selection and multimodel inference: A practice information-theoretic approach, 2nd ed. New York: Springer. https://doi.org/10.1007/b97636

Carey, M.P., and Zimmerman, C.E. 2014. Physiological and ecological effects of increasing temperature on fish production in lakes of Arctic Alaska. Ecology and Evolution 4(10):1981–1993. https://doi.org/10.1002/ece3.1080

Deegan, L.A., Golden, H.E., Harvey, C.J., and Peterson, B.J. 1999. Influence of environmental variability on the growth of age-0 and adult Arctic grayling. Transactions of the American Fisheries Society 128(6):1163–1175. https://doi.org/10.1577/1548-8659(1999)128<1163:IOEVOT>2.0.CO;2

Dickson, D.L. 1992. The Red-throated Loon as an indicator of environmental quality. Occasional Paper No. 73. Ottawa: Canadian Wildlife Service.

Earnst, S.L., Stehn, R.A., Platte, R.M., Larned, W.W., and Mallek, E.J. 2005. Population size and trend of Yellow-billed Loons in northern Alaska. The Condor 107(2):289–304. https://doi.org/10.1650/7717

Earnst, S.L., Platte, R., and Bond, L. 2006. A landscape-scale model of Yellow-billed Loon (*Gavia adamsii*) habitat preferences in northern Alaska. Hydrobiologia 567(1):227–236. https://doi.org/10.1007/s10750-006-0042-2

Eberl, C., and Picman, J. 1993. Effect of nest-site location on reproductive success of Red-throated Loons (*Gavia stellata*). The Auk 110(3):436–444. https://doi.org/10.2307/4088408

Evers, D.C. 2006. Loons as biosentinels of aquatic integrity. Environmental Bioindicators 1:18–21. https://doi.org/10.1080/15555270600605402

Evers, D.C., Savoy, L.J., DeSorbo, C.R., Yates, D.E., Hanson, W., Taylor, K.M., Siegel, L.S., et al. 2008. Adverse effects from environmental mercury loads on breeding Common Loons. Ecotoxicology 17:69–81. https://doi.org/10.1007/s10646-007-0168-7

Furness, R.W. 2007. Responses of seabirds to depletion of food fish stocks. Journal of Ornithology 148:S247–S252. https://doi.org/10.1007/s10336-007-0152-2

Gingras, B.A., and Paszkowski, C.A. 1999. Breeding patterns of Common Loons on lakes with three different fish assemblages in north-central Alberta. Canadian Journal of Zoology 77(4):600–609. https://doi.org/10.1139/cjz-77-4-600

Grunblatt, J., and Atwood, D. 2014. Mapping lakes for winter liquid water availability using SAR on the North Slope of Alaska. International Journal of Applied Earth Observation and Geoinformation 27(Part A):63–69. https://doi.org/10.1016/j.jag.2013.05.006

Hammond, C.A.M., Mitchell, M.S., and Bissell, G.N. 2012. Territory occupancy by Common Loons in response to disturbance, habitat, and intraspecific relationships. Journal of Wildlife Management 76(3):645–651. https://doi.org/10.1002/jwmg.298

Haynes, T.B., Rosenberger, A.E., Lindberg, M.S., Whitman, M., and Schmutz, J.A. 2013. Method- and species-specific detection probabilities of fish occupancy in Arctic lakes: Implications for design and management. Canadian Journal of Fisheries and Aquatic Sciences 70(7):1055–1062. https://doi.org/10.1139/cjfas-2012-0527

Haynes, T.B., Schmutz, J.A., Lindberg, M.S., Wright, K.G., Uher-Koch, B.D., and Rosenberger, A.E. 2014a. Occupancy of Yellow-billed and Pacific Loons: Evidence for interspecific competition and habitat mediated co-occurrence. Journal of Avian Biology 45(3):296–304. https://doi.org/10.1111/jav.00394

Haynes, T.B, Schmutz, J.A., Lindberg, M.S., and Rosenberger, A.E. 2014b. Risk of predation and weather events affect nest site selection by sympatric Pacific (*Gavia pacifica*) and Yellow-billed (*Gavia adamsii*) Loons in Arctic habitats. Waterbirds 37(sp1):16–25. https://doi.org/10.1675/063.037.sp104

Haynes, T.B., Rosenberger, A.E., Lindberg, M.S., Whitman, M., and Schmutz, J.A. 2014c. Patterns of lake occupancy by fish indicate different adaptations to life in a harsh Arctic environment. Freshwater Biology 59(9):1884–1896. https://doi.org/10.1111/fwb.12391

Haynes, T.B., Schmutz, J.A., Bromaghin, J.F., Iverson, S.J., Padula, V.M., and Rosenberger, A.E. 2015. Diet of Yellow-billed Loons (*Gavia adamsii*) in Arctic lakes during the nesting season inferred from fatty acid analysis. Polar Biology 38(8):1239–1247. https://doi.org/10.1007/s00300-015-1690-3

Hershey, A.E., Beaty, S., Fortino, K., Keyse, M., Mou, P.P., O'Brien, W.J., Ulseth, A.J., et al. 2006. Effect of landscape factors on fish distribution in arctic Alaskan lakes. Freshwater Biology 51(1):39–55. https://doi.org/10.1111/j.1365-2427.2005.01474.x

Hobbie, J.E. 1984. The ecology of tundra ponds of the Arctic Coastal Plain: A community profile. FWS/OBS 83/25. Washington, D.C.: U.S. Fish and Wildlife Service.

Jackson, D.B. 2003. Between-lake differences in the diet and provisioning behaviour of Black-throated Divers *Gavia arctica* breeding in Scotland. Ibis 145(1):30–44. https://doi.org/10.1046/j.1474-919X.2003.00119.x

———. 2005. Environmental correlates of lake occupancy and chick survival of Black-throated Divers *Gavia arctica* in Scotland. Bird Study 52(3):225–236. https://doi.org/10.1080/00063650509461396

Johnson, C.B., Wildman, A.M., Prichard, A.K., and Rea, C.L. 2019. Territory occupancy by breeding Yellow-billed Loons near oil development. Journal of Wildlife Management 83(2):410–425. https://doi.org/10.1002/jwmg.21592

Jones, B.M., Arp, C.D., Whitman, M.S., Nigro, D., Nitze, I., Beaver, J., Gädeke, A., et al. 2017. A lake-centric geospatial database to guide research and inform management decisions in an Arctic watershed in northern Alaska experiencing climate and land-use changes. Ambio 46(7):769–786. https://doi.org/10.1007/s13280-017-0915-9

Jones, J. 2001. Habitat selection studies in avian ecology: A critical review. The Auk 118(2):557–562. https://doi.org/10.2307/4089822

Kertell, K. 1996. Response of Pacific Loons (*Gavia pacifica*) to impoundments at Prudhoe Bay, Alaska. Arctic 49(4):356–366. https://doi.org/10.14430/arctic1211

Kodric-Brown, A., and Brown, J.H. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. Ecology 59(2):285–296. https://doi.org/10.2307/1936374

Krebs, J.R. 1971. Territory and breeding density in the Great Tit, *Parus major* L. Ecology 52(1):2–22. https://doi.org/10.2307/1934734

Laske, S.M., Haynes, T.B., Rosenberger, A.E., Koch, J.C., Wipfli, M.S., Whitman, M., and Zimmerman, C.E. 2016. Surface water connectivity drives richness and composition of Arctic lake fish assemblages. Freshwater Biology 61(7):1090–1104. https://doi.org/10.1111/fwb.12769

Laske, S.M., Rosenberger, A.E., Wipfli, M.S., and Zimmerman, C.E. 2018. Generalist feeding strategies in Arctic freshwater fish: A mechanism for dealing with extreme environments. Ecology of Freshwater Fish 27(3):767–784. https://doi.org/10.1111/eff.12391

———. 2019. Surface water connectivity controls fish food web structure and complexity across local- and meta-food webs in Arctic Coastal Plain lakes. Food Webs 21: e00123. https://doi.org/10.1016/j.fooweb.2019.e00123

Mackenzie, D.I., Nichols, J.D., Seamans, M.E., and Gutiérrez, R.J. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. Ecology 90(3):823–835. https://doi.org/10.1890/08-0141.1

McDonald, M.E., Hershey, A.E., and Miller, M.C. 1996. Global warming impacts on lake trout in Arctic lakes. Limnology and Oceanography 41(5):1102–1108. https://doi.org/10.4319/lo.1996.41.5.1102

McIntyre, J.W. 1983. Nurseries: A consideration of habitat requirements during the early chick-rearing period in Common Loons. Journal of Field Ornithology 54: 247–253.

Merrill, E.H., Hartigan, J.J., and Meyer, M.W. 2005. Does prey biomass or mercury exposure affect loon chick survival in Wisconsin? Journal of Wildlife Management 69(1):57–67. https://doi.org/10.2193/0022-541x(2005)069<0057:dpbome>2.0.co;2

North, M. R. 1986. Breeding biology of Yellow-billed Loons on the Colville River Delta, Arctic Alaska. MSc thesis, North Dakota State University, Fargo, North Dakota.

North, M.R., and Ryan, M.R. 1988. Yellow-billed Loon, *Gavia adamsii*, breeding chronology and reproductive success in Arctic Alaska. The Canadian Field-Naturalist 102(3):485–490.

———. 1989. Characteristics of lakes and nest sites used by Yellow-billed Loons in Arctic Alaska. Journal of Field Ornithology 60(3):296–304.

Parker, K.E. 1988. Common Loon reproduction and chick feeding on acidified lakes in the Adirondack Park, New York. Canadian Journal of Zoology 66(4):804–810.

Piper, W.H., Grear, J.S., and Meyer, M.W. 2012. Juvenile survival in Common Loons *Gavia immer*: Effects of natal lake size and pH. Journal of Avian Biology 43(3):280–288. https://doi.org/10.1111/j.1600-048X.2012.05633.x

Prowse, T.D., Wrona, F.J., Reist, J.D., Gibson, J.J., Hobbie, J.E., Lévesque, L.M.J., and Vincent, W.F. 2006. Climate change effects on hydroecology of Arctic freshwater ecosystems. Ambio 35(7):347–358. https://doi.org/10.1579/0044-7447(2006)35[347:CCEOHO]2.0.CO;2

Reist, J.D., Wrona, F.J., Prowse, T.D., Power, M., Dempson, J.B., Beamish, R.J., King, J.R., Carmichael, T.J., and Sawatzky, C.D. 2006. General effects of climate change on Arctic fishes and fish populations. Ambio 35(7):370–380. https://doi.org/10.1579/0044-7447(2006)35[370:GEOCCO]2.0.CO;2

Riera, J.L., Magnuson, J.J., Kratz, T.K., and Webster, K.E. 2000. A geomorphic template for the analysis of lake districts applied to the Northern Highland Lake District, Wisconsin, USA. Freshwater Biology 43(3):301–318. https://doi.org/10.1046/j.1365-2427.2000.00567.x

Rizzolo, D.J. 2017. Contrasting diet, growth, and energy provisioning in loons breeding sympatrically in the Arctic. PhD dissertation, University of Alaska Fairbanks, Fairbanks, Alaska, USA.

Rizzolo, D.J, Schmutz, J.A., McCloskey, S.E., and Fondell, T.F. 2014. Factors influencing nest survival and productivity of Red-throated Loons (*Gavia stellata*) in Alaska. The Condor 116(4):574–587. https://doi.org/10.1650/CONDOR-14-25.1

Ruggles, A.K. 1994. Habitat selection by loons in southcentral Alaska. Hydrobiologia 279:421–430. https://doi.org/10.1007/BF00027873

Russell, R.W. 2020. Pacific Loon (*Gavia pacifica*), version 1.0. In: Rodewald, P.G., ed. Birds of the world. Ithaca, New York: Cornell Lab of Ornithology. https://doi.org/10.2173/bow.pacloo.01

Schmidt, J.H., Flamme, M.J., and Walker, J. 2014. Habitat use and population status of Yellow-billed and Pacific loons in western Alaska, USA. The Condor 116(3):483–492. https://doi.org/10.1650/CONDOR-14-28.1

Schmutz, J.A. 2014. Survival of adult Red-Throated Loons (*Gavia stellata*) may be linked to marine conditions. Waterbirds 37(sp1):118–124. https://doi.org/10.1675/063.037.sp114

Schmutz, J.A., Wright, K.G., DeSorbo, C.R., Fair, J., Evers, D.C., Uher-Koch, B.D., and Mulcahy, D.M. 2014. Size and retention of breeding territories of Yellow-billed Loons (*Gavia adamsii*) in Alaska and Canada. Waterbirds 37(1):53–63. https://doi.org/10.1675/063.037.sp108

Sharma, S., Jackson, D.A., Minns, C.K., and Shuter, B.J. 2007. Will northern fish populations be in hot water because of climate change? Global Change Biology 13(10):2052–2064. https://doi.org/10.1111/j.1365-2486.2007.01426.x

Solovyeva, D.V., Paruk, J.D., Tash, J., Vartanayn, S.L., Danilov, G.K., Pospekhov, V.V., and Evers, D.C. 2017. Post-breeding densities, population sizes and lake size partitioning of loon species in western Chukotka, Russia. Contemporary Problems of Ecology 10:621–631. https://doi.org/10.1134/S1995425517060130

Stehn, R.A., Platte, R.M., Larned, W.W., Mallek, E.J., Mills, T.K., and Marks, D.K. 2005. Habitat associations of Yellow-billed Loons on the Arctic Coastal Plain of Alaska. U.S. Fish Wildlife Service Report. Anchorage, Alaska, USA.

Titus, J.R., and Van Druff, L.W. 1981. Response of the common loon to recreational pressure in the Boundary Waters Canoe Area, northeastern Minnesota (*Gavia immer*). Wildlife Monographs 79.

Uher-Koch, B.D. 2020. Survey data for loons in freshwater lakes; National Petroleum Reserve-Alaska, 2011–2014. U.S. Geological Survey Data Release. https://doi.org/10.5066/P9Z3AGXS

Uher-Koch, B.D., Koch, J.C., Wright, K.G., and Schmutz, J.A. 2018. Comparative nest survival of three sympatric loon species breeding in the Arctic. Journal of Avian Biology 49(7): e01671. https://doi.org/10.1111/jav.01671

Uher-Koch, B.D., Wright, K.G., and Schmutz, J.A. 2019. The influence of chick production on territory retention in Arctic-breeding Pacific and Yellow-billed loons. The Condor 121(1):1–11. https://doi.org/10.1093/condor/duy021

Uher-Koch, B.D., North, M.R., and Schmutz, J.A. 2020. Yellow-billed Loon (*Gavia adamsii*), version 1.0. In: Billerman, S.M., ed. Birds of the world. Ithaca, New York: Cornell Lab of Ornithology. https://doi.org/10.2173/bow.yebloo.0

Wilson, H.M., Larned, W.W., and Swaim, M.A. 2018. Abundance and trends of waterbird breeding populations on the Arctic Coastal Plain, Alaska, 1986–2017. Migratory Bird Management Report. Anchorage, Alaska: U.S. Fish and Wildlife Service.

Wrona, F.J., Prowse, T.D., Reist, J.D., Hobbie, J.E., Lévesque, L.M.J., and Vincent, W.F. 2006. Climate change effects on aquatic biota, ecosystem structure and function. Ambio 35(7):359–369. https://doi.org/10.1579/0044-7447(2006)35[359:CCEOAB]2.0.CO;2

Wrona, F.J., Johansson, M., Culp, J.M., Jenkins, A., Mård, J., Myers-Smith, I.H., Prowse, T.D., Vincent, W.A., and Wookey, P.A. 2016. Transitions in Arctic ecosystems: Ecological implications of a changing hydrological regime. Journal of Geophysical Research: Biogeosciences 121(3):650–674. https://doi.org/10.1002/2015JG003133