BIOTIC AND ABIOTIC INFLUENCES ON THE USE OF ARCTIC LAKES BY FISH AND LOONS

By

Trevor B. Haynes

RECOMMENDED: Joel

Dr. Joel Schmutz

Kim Titus

Dr. Kimberly Titus

Dr. Andrés López

Amanda Rosenberger

Dr. Amanda Rosenberger
Advisory Committee Co-Chair

Dr. Mark Lindberg
Advisory Committee Co-Chair

S. Atkinson

Dr. Shannon Atkinson
Chair, Graduate Program in Fisheries

APPROVED:

Dr. Michael Castellini
Dean, School of Fisheries and Ocean Sciences

John Eichelberger

Dr. John Eichelberger
Dean of the Graduate School

12/8/14

Date

BIOTIC AND ABIOTIC INFLUENCES ON THE USE OF ARCTIC LAKES BY FISH AND LOONS

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Trevor B. Haynes, B.Sc., M.Sc.

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Abstract

The particularly severe effects of climate change anticipated in the Arctic, accompanied by ongoing anthropogenic activities, necessitate proactive and knowledge-based management of the region's aquatic ecosystems. However, the paucity of information on the Arctic's aquatic environments hinders strategic or spatially-explicit management. In this dissertation, I examine the habitat use of poorly studied taxa of the Arctic Coastal Plain (ACP) of Alaska, including freshwater fishes and yellow-billed loons (*Gavia adamsii*). Distribution studies can be biased by false absences; therefore, I began by determining the detection probabilities of six fish species common to Arctic lakes for five gear types (Chapter 2). Variation in gear- and species-specific detection probability was considerable, suggesting a multi-method approach may be most effective for whole-assemblage sampling. Adjusting for detection probability, I then examine how occupancy probabilities of the six fish species were related to lake and landscape scale covariates (Chapter 3). Three large-bodied salmonid species were influenced by factors associated with the probability of fish colonizing lakes, including whether the lakes had a stream connection. Models for small-bodied fish indicated different strategies for persistence among species. Ninespine stickleback (*Pungitius pungitius*) were widespread and captured in lakes that freeze to the bottom, suggesting rapid dispersal after spring freshet (when snow and ice had melted rapidly and caused widespread flooding) and colonization of sink habitats. In contrast, Alaska blackfish (*Dallia pectoralis*) distributions reflect tolerance to harsh conditions, while the slimy sculpin's (*Cottus cognatus*) was indicative of its marine origin. Based on these patterns, I propose a model of primary controls on the distribution of fishes in ACP lakes. Severe winter conditions limit occupancy through extinction events, while lake occupancy in spring and summer is driven by directional migration (large-bodied species) and undirected dispersal (small-bodied species). To provide insight to the relevance of species-specific distributions of prey fish to yellow-billed loons (*Gavia adamsii*), I investigated loon diet on their breeding grounds using quantitative fatty acid signature analysis (Chapter 4). Tissues were collected from 26 yellow-billed loons (shortly after they had moved from coastal staging areas), nine fish species and two invertebrate groups. Results suggest that yellow-billed loons are eating high proportions of Alaska blackfish, broad whitefish (*Coregonus nasus*) and three-spined stickleback (*Gasterosteus aculeatus*). The prominence of blackfish in diets highlights the importance of this species' tolerance to winter conditions that permits its widespread availability during the early stages of loon nesting. Broad whitefish and three-spined stickleback are more likely to be encountered in coastal regions at this time, and their importance may reflect pre-nesting period diet, when loons are staging in coastal and brackish waters before lakes are ice free. Finally, I use the prior chapters to inform an investigation into lake occupancy dynamics of nesting yellow-billed loons and loon chicks (Chapter 5). From a total of four years of data (collected over nine years for nests and seven years for chicks), I examine landscape features that influence the distribution and breeding success of breeding loons on ACP lakes (>7 ha in area), including landscape and lake features, and fish prey occupancy. Over this time, nesting yellow-billed loons exhibited a relatively low (< 30%), but stable to increasing, lake occupancy. Local extinction and colonization rates were also relatively stable, suggesting the nesting population in this region may be near equilibrium. A decreasing rate of change in chick occupancy associated with concomitant increases in nesting occupancy implies density-dependence in chick production. The occupancy probability of a prey fish, least cisco (*Coregonus sardinella)*, had a positive influence on the probability of colonization of unoccupied lakes by nesting loons. I confirm that lake size and lake depth were not only positively associated with nesting occupancy, but also with chick production. Large lakes had occupancy probabilities near one for nesting loons and chicks; this, along with the near equilibrium in breeding loon occupancy and the relative rarity of these large lakes over the landscape, suggests breeding habitat is limiting loon populations in this part of their range. Given the lack of data from the ACP on fish distributions and yellow-billed loons, my findings inform current management practices and provide foundation for future research.

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Chapter 1: Introduction

Water is a dominant feature on Alaska's Arctic Coastal Plain (ACP) - a flat, expansive landscape dotted with tens of thousands of lakes, ponds and wetlands. Its mosaic of diverse waterbodies, which have varying levels of hydrographic connectivity to the streams and rivers that drain to the North Coast, create a vast aquatic ecosystem that provides habitat for a diversity of aquatic organisms. This includes a host of fish species that live in the Arctic throughout the winter and a diversity of migratory birds that only reside in the Arctic during the growing season. Due to the sheer extent of the landscape and the size and range of physical characteristics possible in this area, the aquatic ecosystem of the ACP has an inherent level of complexity. However, in other regards, it can be viewed as relatively simple. Arctic lakes have low species diversity and productivity, and species distributions are limited by a few key environmental drivers (Hershey et al. 1999). Further, the Arctic is removed from major population centers and thus is less affected by anthropogenic influences that complicate ecological study.

The size and inaccessibility of Alaska's ACP has limited studies of its aquatic animals. One such species is the Yellow-billed loon (*Gavia adamsii*) – a waterbird that breeds on Arctic lakes in the low-lying tundra regions of Canada, Alaska and Russia (U.S. Fish and Wildlife Service 2009). Approximately 6,000 adult yellow-billed loons are present on lakes or on adjacent marine waters in Alaska during summer months (Earnst et al. 2005). Of those, approximately 5,000 occur on the ACP, 70% of which attempt to breed (for this dissertation, 'breeding' refers to the process of loon pairs both nesting and rearing chicks). Loons arrive between late May and mid-June, timed with the break-up of ice on breeding lakes. Pairs establish and defend territories on suitable lakes characterized as large, deep, and connected via streams, with suitable nesting habitat on the shoreline (Stehn et al. 2005, Earnst et al. 2006, Haynes et al. 2014a). Pairs of breeding yellow-billed loons aggressively defend the lake territory from other loons, including conspecifics (Sjölander and Ǻgren 1976) and Pacific (*G. pacifica*) and red-throated (*G. stellata*) loons (North 1994, Haynes et al. 2014b). They lay one or two eggs in nests constructed on the lake shore and incubate eggs for 27 - 28 days (North 1994).

Although some basic information on yellow-billed loon exists, knowledge of loon nesting season ecology is limited. For example, during brooding, yellow-billed loons are thought to use fish primarily from the brood lake to feed their chicks (Sjölander and Ǻgren 1976, North 1994);

however, no empirical information is available regarding the diet of adults or chicks for inland areas. Additionally, the distribution and habitat use of yellow-billed loons during the nesting season is not well understood. The U.S. Fish and Wildlife Service conducts annual breeding bird surveys across the North Slope of Alaska; however, yellow-billed loons occur in such low densities that surveys have limited utility for examining their distribution and habitat use (Stehn et al. 2005).

The overarching goal of this dissertation is to examine the habitat use and diet of yellow-billed loons on the ACP. Past models of yellow-billed loon habitat use based on remotely sensed data (Stehn et al. 2005, Earnst et al. 2006) have identified important landscape factors influencing their distribution, but models generally over-predicted loon occupancy. Empirical data, measured in the field, have the potential to enhance past models (Stehn et al. 2005) and our understanding of loon breeding ecology. Because the distribution of fish prey likely is important in determining the distribution of yellow-billed loons, I initially examine how fish species are distributed across the landscape. I first examine the efficacy of fish sampling methods and then create distribution models for key fish species. Using molecular techniques, I investigate which fish species may be important in the diet of breeding yellow-billed loons. Lastly, I examine the occupancy dynamics of breeding loons and loon chicks on Arctic lakes and investigate how habitat features are related to loon distribution, chick production and breeding dynamics.

In Chapter 2, I examine sampling issues related to determining occupancy of fishes in Arctic lakes. Although some efforts have been made to sample Arctic lakes (e.g., Hershey et al. 1999, Hershey et al. 2006), many, if not most, of these waterbodies remain unstudied. This paucity of information on Arctic fish communities, combined with the potential threats due to climate warming, suggests that the Arctic may be an important area for future fish ecology research. Because species are rarely sampled with perfect detection (MacKenzie et al. 2002), it is important to understand efficacy of gear types to avoid bias in sampling efforts. In Chapter 2, I compare the detection probabilities of gear types for sampling fish species and provide unbiased occupancy data for modeling habitat relationships in Chapter 3. Results can be used for future sampling of Arctic lake fish communities by providing information useful in designing future sampling efforts. This is particularly relevant in the Arctic given this is a region where there may be substantial scientific investigation of aquatic ecosystems. Also, because industry on the ACP and other Arctic areas use lake water for ice road construction, lakes are commonly sampled for fish occupancy without a strong understanding of sampling efficacy.

No broad scale habitat models exist for fish species occupying lakes on the ACP. In Chapter 3, I examine the distributions of fish species in lakes to provide a better understanding of the environmental controls on fish distributions. Using modeling efforts from Chapter 2 to account for imperfect detection, I use an occupancy modeling approach to examine how local and landscape characteristics shape species distributions. I examined three large-bodied species: least cisco (*Coregonus sardinella*), broad whitefish (*Coregonus nasus*) and arctic grayling (*Thymallus arcticus*), and three small-bodied species: ninespine stickleback (*Pungitius pungitius*), Alaska blackfish (*Dallia pectoralis*) and slimy sculpin (*Cottus cognatus*). These species vary in their ecological attributes and life histories, which can lead to species-specific responses to spatial and temporal variation in environmental conditions (Winemiller & Rose, 1992) and, ultimately, variation in lake occupancy (Miyazono et al. 2010). Based on the patterns in occupancy, I construct a conceptual model of how these species distributions are shaped by seasonal changes in environmental controls.

In Chapter 4, I use fatty acid analysis to resolve what prey items may be important in the diet of breeding yellow-billed loons. Unlike other loon species, relatively little is known about the diet of yellow-billed loons. Because diet may be a major influence on the distribution of yellow-billed loons and is a key feature of its ecology, this work is an important step for conserving the species. Current information available on yellow-billed loon diet is based on a few anecdotal records of stomach contents from individuals collected on marine waters (North 1994), and essentially no information exists on the diet of loons breeding on Arctic lakes. Recent advances in molecular methods have allowed researchers to describe diet for predators for which it was previously impractical (Barrett et al. 2007). I use fatty acid analysis to determine diet composition of breeding yellow-billed loons. Fatty acids are a large group of molecules which are the main component of lipids found in organisms (Budge et al. 2006). The large diversity in fatty acid types results in different organisms having distinct arrays of fatty acids or fatty acid “signatures”. Fatty acid analysis can take advantage of these distinct signatures by examining predator fat tissues which reflect the distinct fatty acids signatures from prey. Because the physiology of predators’ bodies do not allow most fatty acids to digest, the fatty acid molecules from the prey are incorporated into the tissue of the predator in a predictable fashion, which allows for inference as to what the predator has been consuming and in what proportion.

In Chapter 5, I refine previous nesting season habitat models for yellow-billed loons by incorporating information on fish distributions from Chapter 3 and prey species importance from Chapter 4, with an additional focus on breeding birds in the core area of their range. Previous distribution models for yellow-billed loons on the ACP (Stehn et al. 2005, Earnst et al. 2006) found that loons were more likely to occupy lakes that were larger, deeper, had a more complex shoreline with emergent vegetation present and showed some level of hydrologic connectivity. However, both modeling efforts used remotely sensed explanatory variables. Stehn et al. (2005) suggested that forage fish prey data were likely the most important missing variables in their models. Earnst et al. (2006) reiterated this, suggesting that yellow-billed loon distribution models would be more accurate if models incorporated landscape scale models of fish communities. Also, models from Stehn et al. (2005) and Earnst et al. (2006) were for a broad spatial region of the ACP that included large regions with very few loons. Further, these studies included both breeding and non-breeding loons and did not discriminate between these two states in the analysis. I examine a core region of yellow-billed loon distribution and model lake occupancy dynamics of breeding loons (i.e., lakes with nesting loons or loon chicks). By examining occupancy over time, I can investigate temporal variation in breeding occupancy and chick production and examine key vital rates (e.g., local extinction and colonization probabilities).

In my final Chapter, I summarize the findings of the dissertation, highlight potential management recommendations, and discuss the results in a broader ecological and conservation context.

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Chapter 2: Method- and species-specific detection probabilities of fish occupancy in Arctic lakes: implications for design and management[1]

Abstract

Studies examining species occurrence often fail to account for false absences in field sampling. We investigate detection probabilities of five gear types for six fish species in a sample of lakes on the North Slope, Alaska. We used an occupancy modeling approach to provide estimates of detection probabilities for each method. Variation in gear- and species-specific detection probability was considerable. For example, detection probabilities for the fyke net ranged from 0.82 (SE = 0.05) for least cisco (*Coregonus sardinella*), to 0.04 (SE = 0.01) for slimy sculpin (*Cottus cognatus*). Detection probabilities were also affected by site-specific variables such as depth of the lake, year, day of sampling, and lake connection to a stream. With the exception of the dip net and shore minnow traps, each gear type provided the highest detection probability of at least one species. Results suggest that a multi-method approach may be most effective when attempting to sample the entire fish community of Arctic lakes. Detection probability estimates will be useful for designing optimal fish sampling and monitoring protocols in Arctic lakes.

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[1] Haynes T.B., A.E. Rosenberger, M.S. Lindberg, M. Whitman, J.A. Schmutz. 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.

Introduction

The study of how species' distributions vary over time, space, and environmental heterogeneity has long been a central theme in ecology (e.g., Elton 1927; Krebs 1978). Studies of these kinds generally link species presence-absence data with environmental characteristics to infer how the environment influences a species' distribution (Guisan and Zimmermann 2000). However, concluding a species is absent with 100% certainty is difficult, and "presence-absence" data are more accurately referred to as "detection-nondetection" data (MacKenzie et al. 2006). Studies examining the spatial patterns of species occurrence often incorrectly assume detection-nondetection data to be presence-absence data by failing to account for false absences (i.e., the species is not detected at the site despite being present). Further, detection probability of a species can vary by the sampling method used and features of the habitat or survey (MacKenzie et al. 2006; Nichols et al. 2008). When a species has a detection probability less than one and detection probability is not incorporated into analysis, then information on species distributions will be incomplete and the naïve estimates of occupancy (i.e., the estimate of the probability that a site is occupied, not accounting for detection probability) may be biased (MacKenzie et al. 2002). This bias can affect how we relate species distributional traits with habitat features (Tyre et al. 2001) or estimates of incidence functions when studying metapopulation dynamics (Moilanen 2002.). Further, partial observability, due to imperfect detection, can affect the efficacy of management actions and compromise the decision making process (Martin et al. 2009a).

Recent advances in occupancy estimation (MacKenzie et al. 2002; MacKenzie et al. 2006) have provided the framework with which to incorporate detection probability. In many situations, detection probability might be viewed as a "nuisance variable" if examining occupancy is the main aim of the study. However, when designing sampling and monitoring protocols or developing standardized methodology, determining detection probability is of primary interest (Guillera-Arroita et al. 2010). During the planning phase, detection probability can be used to inform the most efficient sample design given the project goals and the resources available for conducting the study (Bailey et al. 2007; Guillera-Arroita et al. 2010). Understanding of detection probability is especially pertinent in the case of poorly studied systems where rigorous inventories, published information, or expert opinion is lacking or, alternatively, when conducting a pilot study to obtain this information is prohibitively expensive.

With sparse data on Arctic fishes on the North Slope of Alaska (due, in part, to the remoteness of the region and the cost of conducting Arctic research), much of the work that has taken place comes from a few locations such as the Toolik Lake region (e.g., Hershey et al. 1999; 2006), where research facilities and access facilitate field research. Because the region's fish communities are poorly studied and likely to be affected by increasing industrial development and the effects of climate change, a strong impetus exists to develop reliable methods with known sources of error. These methods can be used to set up a reliable sampling framework for ecological research and for monitoring and inventory. For example, current practices of water withdrawal from northern lakes to build ice roads require consideration of potential impacts to aquatic systems, including fish communities (Cott et al. 2008a;b). The State of Alaska permits a decreasing amount of water withdrawal based on whether lakes are unoccupied by fish (withdrawal of up to 20% of lake volume), are occupied only by "resistant" species (ninespine stickleback - *Pungitius pungitius* and Alaska blackfish - *Dallia pectoralis*; withdrawal of up to 30% of calculated volume deeper than 7 feet) or are occupied by any other fish species, which are classified as "sensitive" (withdrawal of up to 15% of calculated volume deeper than 7 feet, Cott et al. 2008b). While several hundred lakes on the North Slope have been sampled for fish to support this permitting process (e.g., MJM Research 2001; 2007), the protocols chiefly aim to identify the presence of any "sensitive" species, at which point the survey is sufficient for water permitting needs. To improve future fish distribution data for scientific and management applications, it is necessary to gain a better understanding of the detection probabilities of common fishing gear used to sample lakes on the North Slope. Further, this knowledge may be applicable to northern regions across Canada and Eurasia with comparable environmental characteristics that face similar issues of climate change and resource development.

We evaluate the detection probabilities of five common fish sampling gear types (fyke net, beach seine, gill net, minnow trap, and dip net) in lakes over a broad region (study extent > 7600 km^2) of the North Slope, Alaska. We investigate the detection probabilities of six fish species that commonly occur over this region, including small-bodied species such as ninespine stickleback, Alaska blackfish, and slimy sculpin (*Cottus cognatus*), and large-bodied species, such as least cisco (*Coregonus sardinella*), broad whitefish (*C. nasus*), and Arctic grayling (*Thymallus arcticus*). Specifically, we 1) compare detection probabilities of different gear types and 2) determine how detection probabilities of gear types varied temporally among species and habitats.

Methods

Sampling

We sampled fish in 86 lakes (sampling units) across the interior North Slope within the National Petroleum Reserve – Alaska (NPRA). We selected lakes > 7 ha in surface area from 7 x 7 km plots that were randomly distributed across the study area (Figure 2.1). Within a plot, we randomly chose lakes with the following caveats: 1) because this was part of a larger study looking at nesting habitat of yellow-billed loons (*Gavia adamsii*), we stratified the random sampling within loon use/non-use designations determined by aerial surveys to accommodate the sampling scheme necessary for modeling loon habitat and 2) four lakes were sampled that were just outside sample plots as a result of logistical coordination with the overall project.

Sampling by two (2009) or three (2010) independent crews began 4 July in 2009 and 23 June in 2010, shortly after spring ice melt, and continued until mid-August. Lakes were accessed by fixed-wing amphibious plane or by helicopter. At each lake, we sampled over 48-72 h using both spatial and temporal replicate sampling to allow detection probability estimation with five gear types including: gill net (2 nets, 3 temporal replicates), minnow trap (8 traps, 2 temporal replicates), fyke net (2 nets, 2 temporal replicates), dip net (8 spatial replicates), and beach seine (2 spatial replicates). After each replicate for each gear type, fish were identified and enumerated.

Gill nets – We used two variable-mesh multifilament gill nets measuring 38 x 1.8 m with five panels ranging in bar mesh size from 1.3 to 6.5 cm. We floated one gill net (“pelagic gill net”) perpendicular to the shoreline at the surface within the littoral zone (Bonar et al. 2009). The bottom of the net closest to shore was just above the lake floor. The second gill net (“benthic gill net”) was weighted so that it floated submerged with the lead line on the lake bottom. We deployed the benthic gill net at the deepest zone of the lake (as determined by depth sounder transects), perpendicular or oblique to the shoreline. Gill nets were checked every two to three hours and removed on the third check.

Minnow Traps – We baited eight Gee-style galvanized steel minnow traps (2.5 cm opening with 6 mm mesh) with preserved salmon eggs. Four traps were deployed individually in shallow water along the shoreline ("shore minnow traps") and four traps were sunk with weights in deepest zone of the lake ("deep minnow traps"). After 12 h, traps were checked for fish, baited again and replaced. Traps were checked for fish and removed after 24 h.

Fyke nets – We sampled shorelines with two fyke nets, each having a hoop net constructed of 0.3 cm sized stretched mesh and had a frame opening of 1.1 x 1.1 m, followed by five sequential hoop frames spaced 0.8 m apart and measuring 0.6 x 0.6 m in size. Attached to the hoop net were two 15.2 x 1.2 m wings and a 30.5 x 1.2 m centerline with 0.6 cm sized stretched mesh. Wings and centerline had float lines and weighted lead lines. The hoop net had three net throats within the frame measuring 15 x 23 cm at the middle of each throat. We set nets either in the morning (8 am – 12 pm) or the evening (8 pm – 12 am) at separate locations within a lake. Nets were checked twice for fish, once after approximately 12 h and again after 24 h when the nets were pulled. If a lake had a stream connection, one fyke net was set adjacent the connection, but did not entirely block it. Centerlines were set perpendicular from the shore except in lakes with very shallow shelf zones (< 0.4 m depth) that exceeded the length of the centerline. At locations with extensive shallow shelves, the centerline was set away from shore (but still perpendicular) such that the fyke net was closer to the drop off and would sample the deeper water.

Dip nets – We used dip nets (3 mm mesh; two opening sizes 28 x 38 x 20 and 41 x 41 x 41 cm) on the lakeshore. We swept nets along the lake bottom adjacent to shore for three eight-minute intervals.

Beach seine – We employed a 3 mm mesh beach seine measuring 15 m in length and tapered in width from 3 m at the middle to 1.2 m at the wings. Two beach seine replicates, covering approximately 10-15 m in length, were conducted at a location with shoreline structure amenable to seining. The second replicate was offset from the first by at least 5 m parallel along the shore.

Multi-Method Analysis

We used the multi-method parameterization described by Nichols et al. (2008) to estimate detection probability (p) of each gear type while simultaneously estimating the probability of occupancy at the sample lake (Ψ), and the probability of occupancy at the sampling location within the lake (θ). The multi-method approach allows direct comparison among methods while incorporating the influences of other covariates (e.g., lake size, species) and uses the combined detection histories from all methods to estimate detection probabilities of individual methods. Estimating probability of occupancy at the local scale (i.e., the scale of the sampling location within the lake, θ) allows for the relaxation of the closure assumption and provides information on how available species are to spatial replicate sampling within the lake (Nichols et al. 2008; Pavlacky et al. 2012). When θ is high and varies little, species are distributed throughout the lake and available to spatial replicates. When θ is low or has high variation, species may be patchily distributed within the lake and will not be available to all spatial replicates which can induce estimation bias (Kendall and White 2009). We used a single season parameterization and included year as a covariate (see below) because we did not sample any sites in both years. We split the species data into two sets based on fish body size and analyzed each data set separately because not all gear types catch fish of both size classes (e.g., gill nets catch only large-bodied fish). No large-bodied species (including juveniles) were caught in gear that targeted small-bodied species. We only included fish species that had a naïve occupancy > 10% to ensure we had adequate data to estimate detection probability (MacKenzie et al. 2005). Although Arctic grayling had a naïve occupancy of 16%, we analyzed this species separately from other large-bodied species because sparse detection data required a simple detection model without site covariates.

We created a set of *a priori* models in the program PRESENCE (Version 4.4, Hines 2006). We modeled occupancy with a purposely simple structure because we were primarily interested in detection probability (occupancy will be investigated further elsewhere). We included two covariates for occupancy – one representing the propensity of a site to be colonized by a species (presence of stream connection) and the other representing the propensity for species to go locally extinct (area of the lake >2 m which represents the area with depths greater than the maximum winter ice depth; Grunblatt and Atwood 2014). These two factors have been important in determining fish distribution in Arctic lakes in the foothills of the Brooks Range (Hershey et al. 2006). We assumed that the probability a species is present at the immediate sample location given the lake is occupied (θ) was constant because we did not see a compelling biological basis for variation in θ among survey locations within a lake and we did not have *a* *priori* information on how θ might vary by species or covariates. Because our primary goal was estimation of gear- and species-specific detection probabilities, these variables were included in every model. We also examined the influence of four covariates likely to influence detection probability, including: lake area, percent of the lake deeper than 2 m (Grunblatt and Atwood 2014), day from the beginning of sampling for each season (4-Jul in 2009 and 23-Jun in 2010) which may be related to seasonal changes in fish abundances, and year (2009 or 2010). We standardized all continuous covariates by calculating z-scores (Donovan and Hines 2006) and limited interactions to 2-way for interpretation and parsimony. Finally, we examined gear-specific covariates for gear types that had sample specific covariates that may affect detection probability. We first considered whether detection probabilities differed between the pelagic and benthic gill nets for large-bodied species or between the shore and deep minnow traps for small-bodied species. Because sample covariates were method-specific and contained missing data for sample covariates, we tested whether sample covariates were important for fyke net (N = 83) and deep minnow traps (N = 61) in separate analyses. We investigated two site covariates specific to the fyke net: whether or not it was set next to a stream connection ("stream") and the time of the set (morning - evening, or evening - morning). For the deep minnow trap, we assessed whether detection probability was affected by the water depth of the trap.

For all analyses described above, we examined the candidate model sets using an information-theoretical approach (Burnham and Anderson 2002). We ranked models using Akaike's Information Criterion, corrected for sample size (AIC_c, Burnham and Anderson 2002). We ranked models from lowest to highest AIC_c values and calculated ΔAIC_c as the difference in AIC_c relative to the model with the lowest AIC_c value (Burnham and Anderson 2002). Determining sample size for occupancy models is still a topic of debate (i.e., whether the sample size is the number of sites or the number of surveys; MacKenzie et al. 2006), thus we used the mean value between the number of sites and the number of surveys to adjust the sample size (MacKenzie et al. 2012). To check for overdispersion (i.e., inadequate variance structure in the model; Mackenzie et al. 2006), we ran goodness-of-fit tests (MacKenzie and Bailey 2004) on single season models for each set of repeat samples (i.e., the first sample for each gear type) using our most complex model. With evidence for overdispersion (the dispersion parameter, $\hat{c}$, is greater than one), we adjusted the selection criteria ($QAIC_c$) and sample variances (Burnham and Anderson 2002). Because our objectives were to resolve sampling issues, detection probabilities are the main focus. We are exploring occupancy probabilities in more detail in a separate effort (Haynes, unpublished data) that focuses on habitat use, and thus, occupancy probabilities are not presented here. Parameter estimates and covariate beta coefficients (β) are presented ± standard error unless otherwise specified.

Results

Multi-method Analysis

Goodness-of-fit tests on the multi-method datasets suggested that there was no lack of fit for either small- (mean $\hat{c}$ ± SD = 1.045 ± 0.213) or large-bodied fish analyses (mean $\hat{c}$ ± SD = 0.592 ± 0.248); we therefore did not adjust for overdispersion. The most complex models received the highest support based on the AIC scores for both the small and large-bodied fishes (Tables 2.1 and 2.2). For small-bodied species, the detection probabilities of deep and shore minnow traps differed ($\Delta AIC_c = 270.64$). For large-bodied species (broad whitefish and least cisco), the best fitting model ascribed equal detection probabilities to pelagic and benthic gill nets.

For both small and large-bodied species, detection probabilities varied drastically among methods and species (Tables 2.3 and 2.4). Deep minnow traps had the highest detection probability of any method for Alaska blackfish (0.25 ± 0.03), while shore minnow traps were better for sampling ninespine stickleback (0.60 ± 0.03) and slimy sculpin (0.02 ± 0.01). Fyke nets generally had high detection probabilities for each species and were the best method for detecting least cisco (0.82 ± 0.05), Arctic grayling (0.16 ± 0.06), and ninespine stickleback (0.77 ± 0.04). Beach seining generally had low detection probabilities for all species, with the exception of slimy sculpin, for which it was the method with the highest detection probability (0.13 ± 0.05). Gill nets had high detection probabilities for broad whitefish (highest, 0.39 ± 0.07) and least cisco (0.56 ± 0.06), but not for Arctic grayling (0.02 ± 0.01). Estimates of small scale occupancy (local occupancy at a sample location within a lake θ) were high for both small (0.959 ± 0.020) and large-bodied species (0.885 ± 0.038).

The effects of site covariates on detection varied in magnitude and direction depending on the sampling method and species group (small or large-bodied, Table 2.5). Lake depth generally had a positive influence on detection, except in the case of sampling large-bodied species with the fyke net (logit β = -0.65 ± 0.18). Lake area generally had a negative effect on detection, but most effects were weak with the exception of fyke net (small-bodied, logit β = -0.44 ± 0.13), shore minnow traps (logit β = -0.23 ± 0.08) and gill net, for which there was a positive effect (logit β = 0.43 ± 0.20). Day and Year effects were highly variable among methods. There was a notably strong positive effect of day on fyke net detection probability for large-bodied (logit β = 0.93 ± 0.24), and a positive but weaker effect for small-bodied species (logit β = 0.15 ± 0.11).

Single Method - Sample Covariates

We found overdispersion in the data used to examine sample covariates for fyke nets ($\hat{c}$ = 2.62) and deep minnow traps ($\hat{c}$ = 1.40) and thus adjusted for overdispersion. Further, we ran the deep minnow trap analysis without slimy sculpin because they were found in only 3 deep minnow traps total. Top models for both the fyke net and deep minnow trap analysis included only species-effects, and model ranking suggested only limited support for sample covariates in both cases (Tables 2.6 and 2.7). Setting a fyke net near a stream connection had little effect on detection probability (logit β = -0.05 ± 0.19, Model 3, Table 2.6). When we examined the Catch-Per-Unit-Effort (CPUE) of the two most abundant species (least cisco and ninespine stickleback), we found no notable difference in CPUE between fyke nets set either adjacent to (ninespine stickleback = 520 ± 355; least cisco = 57 ± 24) or apart from a connection (ninespine stickleback = 693 ± 532; least cisco = 45 ± 16). Checking the fyke net in the morning as opposed to the evening had a weak negative effect on detection probability (logit β = -0.11 ± 0.17, Model 2, Table 2.6) suggesting that fish may be more likely captured during the day compared with overnight sets. Support for an interaction effect with species and the sample covariates was weak (Time*Species model $\Delta QAIC_c$ =11.11, Stream*Species model $\Delta QAIC_c$ = 11.92). Depth of the deep minnow traps had some support from the data as a positive influence on detection probability; however, this effect size was also relatively weak and poorly estimated (logit β = 0.13 ± 0.09, Model 2, Table 2.7).

Discussion

Detection probability varied considerably by species, method, and habitat conditions. This highlights the importance of considering not only the actual values of detection, but also incorporating both species- and habitat-covariates when designing studies intended to understand fish distribution across North Slope lakes. Although the most widespread and common species, such as least cisco and ninespine stickleback, had high detection probabilities for most methods, no method provided detection probabilities greater than 0.9 for a single sampling event. Conversely, species such as slimy sculpin and Arctic grayling had relatively low detection probabilities for all methods, and are thus difficult to sample regardless of method. Finally, other species, such as broad whitefish in gill nets, had a specific method that provided much higher detection probability.

High estimated values of θ suggest that, if fish species are present at the scale of the lake, they are likely available to spatial replicates within the lake itself. Thus, data support that spatial replication can be used in addition to or in lieu of temporal replication in North Slope lakes (Kendall and White 2009; Pavlacky et al. 2012). Because our values of θ were high with low standard errors, we suggest using data from spatially replicated surveys to sample occupancy of North Slope fishes in lakes is a robust approach because fish generally occupy a large proportion of the lake. This is an important consideration when sampling remote lakes that are difficult and costly to access because using spatial replicates can potentially decrease the time spent at the lake and reduce or eliminate the need for repeated visits to the lake. However, although we kept θ constant, θ is less likely to be constant for rare or patchily distributed species and this should be considered in further analyses.

Our results indicate a sample design to assess the entire fish community of a lake may be most effective if it includes multiple sampling methods. In addition to providing high detection probabilities across species, a multi-method approach may provide the highest sampling efficiency, as multiple gears can be deployed simultaneously, and active sampling (e.g., beach seining or dip netting) can occur while passive sampling gears are in place. However, investigators must weigh the detection probabilities of individual or combined gear with the cost of transport, deployment, and sampling. Adding multiple methods and replicates generally will increase detection probability, but the cost and time investment will trade off with these increases (Mattfeldt and Grant 2007).

Until now, detection probabilities of different gear types for Arctic fish species were lacking. Results from this study will prove useful in designing future sampling protocols for lakes on the North Slope. Because other areas of the circumpolar Arctic are replete with large thermokarst lakes (Smith et al. 2007), our results may be useful in designing surveys in other regions as well. Investigators must choose between allocating sufficient sampling efforts at a given site to ensure target species are detected if present, with efforts to sample multiple sites (MacKenzie et al. 2005). Computer programs that can guide the design of occupancy studies (monitoring or research), such as GENPRES (Bailey et al. 2007) or SODA (Guillera-Arroita et al. 2010), require values for detection probabilities and results presented here can provide those initial estimates. Investigators can also use the detection probabilities presented here to determine the number of surveys necessary given a goal of detecting a species with a desired level of certainty. For example, an investigator may plot a cumulative detection probability (i.e., the detection probability of >1 survey) and determine how many replications are necessary to detect the species with 85% certainty (Figure 2.2). In this example, each species was sampled with the method with the highest detection probability, resulting in a variable number of samples that are required to achieve a cumulative detection probability > 0.85, depending on the species considered. For instance, least cisco would require only two repeated samples with fyke nets while slimy sculpin, which has the lowest detection probability, would require 14 repeated samples with a beach seine to achieve the same cumulative detection probability. When targeting multiple species or the whole fish community, investigators can add detection probabilities of different gear types to determine the cumulative detection probability for each species given a sampling protocol. Further, investigators can optimize the sample design by balancing the time, cost, and desired cumulative detection probability (e.g., Mackenzie and Royle 2005, Bailey et al. 2007). Similarly, if the goal is to detect a change in occupancy over time, investigators may consider design trade-offs in the context of a power analysis (Guillera-Arroita and Lahoz-Monfort 2012). If investigators wish to reduce mortality, they could choose methods that provide similar detection methods to those that have higher mortality levels (e.g., gill nets). Further, the level of sampling required to achieve a particular cumulative detection probability could be more precise, thus allowing for more streamline sampling which often leads to less mortality. Regardless of species or method, our results suggest that multiple samples are required to detect species with the high degree of confidence necessary to avoid bias (i.e., detection probability ≥ 0.9, McKann et al. 2012).

Site covariates showed high variability in magnitude and direction depending on the species group and the sampling method. Standard sampling methods for fishes generally recommend more survey effort for larger lakes (e.g., Bonar et al. 2009, p. 92), and we found a general negative effect of lake size on detection probability that supports this recommendation. However, we noted some exceptions, including gill net and dip net detection probabilities, which had a positive relationship with lake area. Detection probabilities were generally higher with increasing lake depth (i.e., % area >2m in depth), suggesting that most gear types are more effective at capturing target species in lakes that have a higher percentage of their area >2m in depth. Interestingly, this included gear types such as dip nets and minnow traps deployed on the shoreline. Effects of this variable may be related to the productivity of deeper lakes leading to higher abundances of fish, which in turn, could positively affect detection probability (Royle and Nichols 2003). Day and year covariates indicate temporal variation by method and species group. These temporal effects may be both biological (e.g., changing abundances through the season or between seasons) or related to sampling (e.g., crews becoming more experienced through time). Regardless of whether these temporal effects are biological or sampling induced, inclusion of temporal effects in the analysis minimizes bias in estimates of lake occupancy.

A likely source of heterogeneity in site-specific detection is differences in fish abundance among sites. Detectability is not only a function of gear type, habitat, and species, but also the number of individuals in the site that will be vulnerable to the gear in question (Royle and Nichols 2003). By incorporating habitat features important for these fishes (e.g., lake size) in our detectability models, we likely indirectly accounted for some of this heterogeneity. Further, underlying heterogeneity does not preclude the use of these results in areas where similar environmental conditions and abundances of fish are expected.

Sample covariates that did not appear in our top models may still merit consideration for further study. For example, the depth of the deep minnow traps did not greatly influence the detection probability of Alaska blackfish or ninespine stickleback, potentially due to the low amount of variation in the depths we examined (all lakes were relatively shallow and we always targeted the deepest portions). For fyke nets, we were surprised that time of set or location of set relative to stream connections did not greatly affect the detectability of fish species, considering that there are strong reasons to believe that both these covariates are likely related to diel patterns (night versus day sets) and migration patterns (adjacent to or away from a connection) of fish movement, which in turn, would affect the probability of detection. The lack of difference between location of sets (at or away from a connection) suggests that, generally, movement along the shoreline of a lake may be similar to movement in and out of a connection. Similarly, because of known relationships between fish movement and the diel cycle (e.g., Bohl 1979; Levy 1990; Natsumeda 1998), we expected differences in detection probabilities for sets checked after a 12 h night set versus a 12 h day set. Lack of a strong relationship between check time and detection probability may be due to the lack of a strong diel cycle in the Arctic in the summer, during which there is 24 h sunlight (Kahilainen et al. 2004).

We chose gear types that represented commonly used techniques in fisheries sampling. Gear types used in other studies may differ in certain aspects such as mesh size and net material and length. These differences could lead to differences in detection probability. However, gear types such as minnow traps, variable mesh gill nets, and dip nets are standardly used in many sampling protocols (e.g., Nielsen and Johnson 1983; Bonar et al. 2009). Other gear we used which may vary more in size and shape from study to study, such as the fyke nets and beach seines, were designed specifically for sampling lakes on the North Slope, and thus, we would recommend studies use similar gear when sampling in this area. If similar gear is used, detection probabilities provided here should provide good values for preliminary planning. If gear differs from what we used, these detection probabilities can provide a starting point for investigators, who may adjust probabilities according to perceived differences in catch efficiencies of the differing gear.

The occupancy modeling framework used here allowed for direct estimation of detection probabilities from data containing repeated surveys and direct comparisons among methods. Valid inferences of population level parameters such as occupancy require an adequate sample design that considers detection probability (Pavlacky et al. 2012). Our results suggest that failure to incorporate detection probabilities will bias occupancy estimates and the description of the species-environment relationship. Further, this bias can influence validation of predictive models (Long et al. 2011). Results from this study provide investigators critical information about the sampling efficiencies of different gear types for common species on the North Slope and will be instrumental in designing research or monitoring programs in the future. Given that the North Slope is relatively poorly sampled for fish and is liable to face impacts from climate change and resource development (e.g., water withdrawal for ice roads), results from this study should be useful for planning sampling frameworks for future inventory and monitoring efforts. Further, these results can be used to address similar environmental and resource management issues facing Arctic areas of Canada and Eurasia, allowing for a more informed design of sampling protocols aimed at sampling fish populations in Arctic lakes.

Ongoing climate change is given to have the strongest impact in Arctic regions (Martin et al. 2009b), and there is anticipated to major changes in the function of freshwater ecosystems in the North Slope (Reist et al. 2006; Wrona et al. 2006). Given the complexity of aquatic systems, the potential for indirect effects, and confounding factors such as anthropogenic development and oil exploration (Reist et al. 2006), reliable baseline data and monitoring programs are crucial to understand changes to aquatic ecosystems of the far north. Beyond a regional understanding, Arctic systems are also excellent model ecosystems for studying the impacts of climate change because impacts are likely to be more pronounced in the far north. Our methods provide a means by which researchers and managers can acquire data to investigate these sorts of questions with maximum flexibility of circumstances and gear (required in a place as difficult to sample as the North Slope), but with less concern for the bias that multiple gear types and changing circumstances can bring.

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Table 2.1: Model ranking for the multi-method analysis for small-bodied fish species based on Akaike's Information Criterion adjusted for sample size (AIC_c), differences in AIC_c (ΔAIC_c), model weight, model likelihood, and number of parameters (K). Fish were sampled in lakes on the Arctic Coastal Plain, Alaska.

Model[a]	AIC_c	ΔAIC_c	AIC wgt	Likelihood	K
p(LakeDepth + LakeArea + Day + Year + Species*Method)	4613.90	0.00	1.00	1.00	41
p(LakeDepth + LakeArea + Species*Method)	4665.46	51.56	0.00	0.00	31
p(Day + Year + Species*Method)	4666.21	52.31	0.00	0.00	31
p(LakeDepth + LakeArea + Day + Year + Species*Method), No Method*Covar	4691.17	77.27	0.00	0.00	25
p(Species*Method,)	4727.76	113.86	0.00	0.00	21
p(LakeDepth + LakeArea + Day + Year + Species*Method), DMT = SMT	4884.54	270.64	0.00	0.00	34
p(LakeDepth + LakeArea + Day + Year + Species + Method)	4969.04	355.14	0.00	0.00	31

[a] All models included area of lake below 2 m and presence of stream connection as covariates for occupancy probability (ψ) while local occupancy (θ) was kept constant among surveys. Interaction between method and habitat and temporal covariates were included unless indicated (No Method*Covar). Detection probabilities of deep (DMT) and shore minnow traps (SMT) were estimated separately unless otherwise indicated (DMT = SMT).

Table 2.2: Model ranking for the multi-method analysis for large-bodied fish species (least cisco and broad whitefish) based on Akaike's Information Criterion adjusted for sample size (AIC_c), differences in AIC_c (ΔAIC_c), model weight, model likelihood, and number of parameters (K). Fish were sampled in lakes on the Arctic Coastal Plain, Alaska.

Model[a]	AIC_c	ΔAIC_c	AIC wgt	Likelihood	K
p(Species*Method + LakeArea + LakeDepth + Year + Day)	1081.27	0.00	0.97	1.00	23
p(Species*Method + LakeArea + LakeDepth)	1089.39	8.12	0.02	0.02	17
p(Species*Method + LakeArea + LakeDepth + Year + Day), No Method*Covar	1091.15	9.88	0.01	0.01	15
p(Species*Method + Year + Day)	1092.08	10.81	0.00	0.00	17
p(Species*Method)	1092.46	11.19	0.00	0.00	11
p(Species*Method + LakeArea + LakeDepth + Year + Day), BGN ≠ PGN	1092.98	11.71	0.00	0.00	29
p(LakeArea + LakeDepth + Year + Day)	1119.13	37.86	0.00	0.00	20

[a] All models included area of lake below 2 m and presence of stream connection as covariates for occupancy probability (ψ) while local occupancy (θ) was kept constant among surveys. Interaction between method and habitat and temporal covariates were included unless indicated (No Method*Covar). Detection probabilities of benthic (BGN) and pelagic gill nets (PGN) were estimated as equal unless indicated otherwise (BGN ≠ PGN).

Table 2.3: Detection probability estimates with standard errors of small-bodied fish species for each gear type. Models included day of sampling, year, lake depth, and lake area as covariates for detection and a species-method interaction. Detection estimates are for average values of the covariates in 2009. Fish were sampled in lakes on the Arctic Coastal Plain, Alaska.

Species	Fyke Net	Beach Seine	Deep Minnow Trap	Shore Minnow Trap	Dip net
Ninespine stickleback	0.766 (0.035)	0.665 (0.059)	0.117 (0.017)	0.598 (0.033)	0.370 (0.032)
Alaska blackfish	0.128 (0.025)	0.069 (0.027)	0.251 (0.029)	0.115 (0.018)	0.083 (0.016)
Slimy sculpin	0.038 (0.012)	0.129 (0.045)	0.005 (0.003)	0.017 (0.007)	0.027 (0.010)

Table 2.4: Detection probability estimates and standard errors of large-bodied fish species for each gear type. Models for broad whitefish and least cisco included day of sampling, year, lake depth, and lake area as covariates for detection and a species-method interaction. Detection estimates for these species are for average values of the covariates in 2009. The detection probability model for Arctic grayling included only the species-method interaction. Fish were sampled in lakes on the Arctic Coastal Plain, Alaska.

Species	Fyke Net	Beach Seine	Gill net
Least cisco	0.815 (0.049)	0.231 (0.089)	0.556 (0.055)
Arctic grayling	0.163 (0.060)	0.071 (0.045)	0.015 (0.011)
Broad whitefish	0.104 (0.033)	0 (0)	0.378 (0.067)

Table 2.5: Logit-scale regression coefficients of site covariates for the top models for small and large-bodied fish species. Fish were sampled in lakes on the Arctic Coastal Plain, Alaska.

		Large-bodied		Small-bodied	
Covariate	Method	Estimate	SE	Estimate	SE
Day[1]	fyke net	0.925	0.242	0.145	0.112
	beach seine	0.196	0.394	-0.304	0.158
	deep minnow trap			-0.005	0.084
	shore minnow trap			-0.327	0.081
	dip net			0.042	0.088
	gill net	0.110	0.173		
Year	fyke net	-0.806	0.372	0.841	0.221
	beach seine	-0.433	0.603	-0.591	0.304
	deep minnow trap			0.367	0.168
	shore minnow trap			-0.532	0.155
	dip net			-0.579	0.167
	gill net	0.140	0.259		
Lake Area[2]	fyke net	0.053	0.183	-0.442	0.137
	beach seine	-0.160	0.341	-0.087	0.147
	deep minnow trap			-0.082	0.090
	shore minnow trap			-0.231	0.081
	dip net			0.117	0.073
	gill net	0.427	0.197		
Lake Depth[3]	fyke net	-0.645	0.180	0.531	0.116
	beach seine	0.482	0.386	0.547	0.174
	deep minnow trap			0.133	0.102
	shore minnow trap			0.283	0.082
	dip net			0.221	0.092
	gill net	0.008	0.117		

[1] Measured as day from beginning of the sampling season with the first day = 0

[2] Mean ± SD = 146.3 ± 192.8 ha, Range = 15.0-1489.3 ha

[3] Mean ± SD = 92.8 ± 141.7 ha, Range = 0-1109.2 ha

Table 2.6: Model ranking based on Akaike's Information Criterion adjusted for sample size and overdispersion ($QAIC_c$), differences in $QAIC_c$ ($\Delta QAIC_c$), model weight, model likelihood, and number of parameters (K) for the single-season model of fyke net detection probability for all fish species. Fish were sampled in lakes on the Arctic Coastal Plain, Alaska.

Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ wgt	Likelihood	K
p(Species)	549.73	0.00	0.55	1.00	9
p(Species + Time)	551.77	2.04	0.20	0.36	10
p(Species + Stream)	551.92	2.19	0.18	0.33	10
p(Species + Stream + Time)	553.98	4.25	0.07	0.12	11
p(Species + Time + Time*Species)	560.84	11.11	0.00	0.00	15
p(Species + Stream + Stream*Species)	561.65	11.92	0.00	0.00	15
p(.)	568.77	19.04	0.00	0.00	4

Note: p(.) represents the null model (no covariates) for detection. The model set included models with sample covariates time (whether fyke net sets sampled morning - evening, or evening - morning) and stream (whether the fyke net was set at or away from a stream connection). All models included area of lake below 2 m and presence of stream connection as covariates for occupancy (ψ), while local occupancy (θ) was held constant among surveys.

Table 2.7: Model ranking based on Akaike's Information Criterion adjusted for sample size and overdispersion ($QAIC_c$), differences in $QAIC_c$ ($\Delta QAIC_c$), model weight, model likelihood, and number of parameters (K) for the single-season model of sinking minnow trap detection probability analysis for small-bodied fish species. Fish were sampled in lakes on the Arctic Coastal Plain, Alaska.

Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ wgt	Likelihood	K
p(species)	486.24	0.00	0.34	1.00	5
p(species+MTDepth)	486.89	0.65	0.25	0.72	6
p(species+MTDepth+species*MTdepth)	486.90	0.66	0.25	0.72	7
p(.)	488.89	2.65	0.09	0.27	4
p(MTDepth)	489.35	3.11	0.07	0.21	5

Note: p(.) represents the null model (no covariates) for detection. Model set included models with the depth of the sinking minnow trap (MTDepth) as a covariate. All models included area of lake below 2 m and presence of stream connection as covariates for occupancy (ψ), while local occupancy (θ) was held constant among surveys.

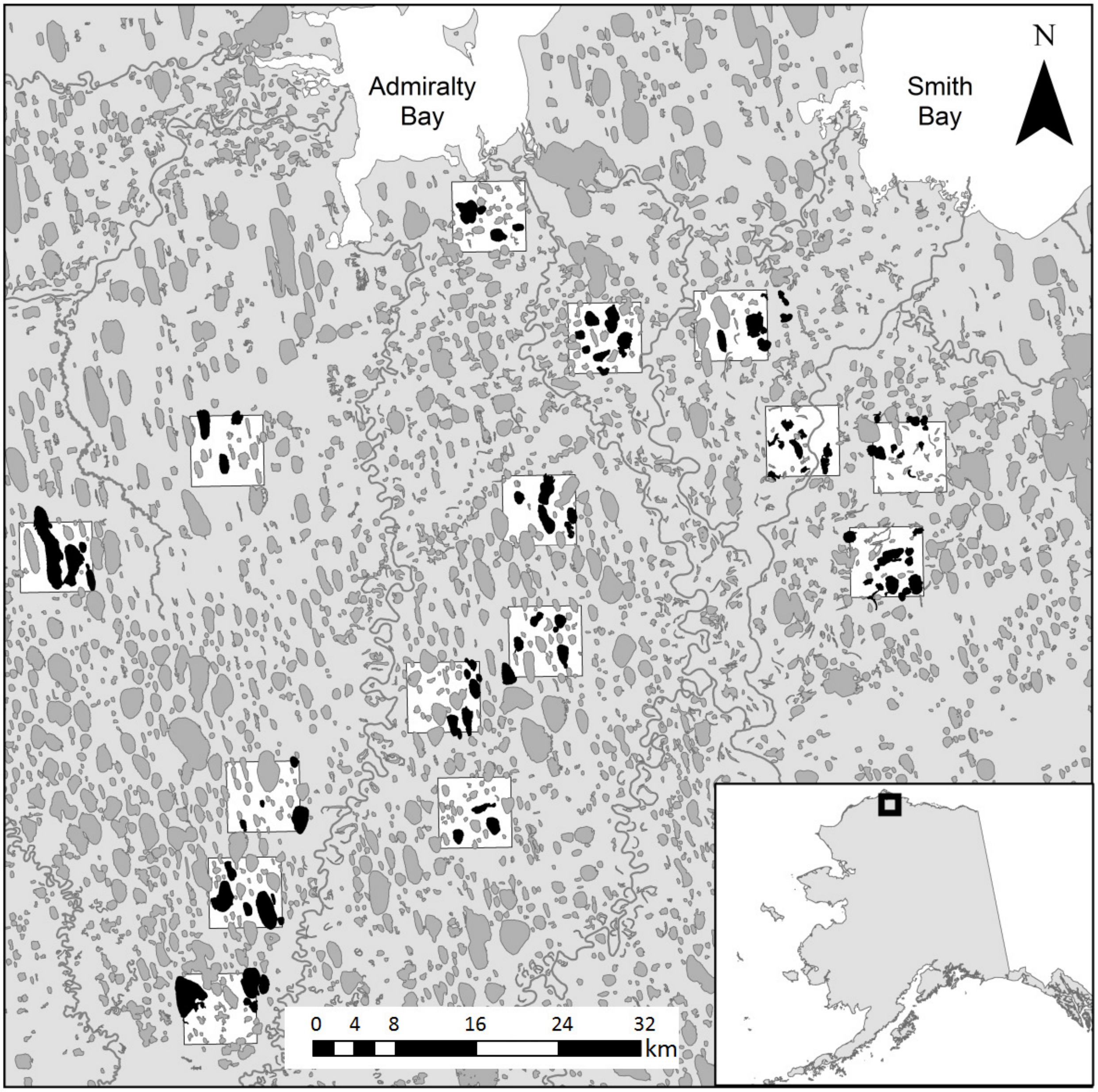

Figure 2.1: Study area on the North Slope of Alaska. Sample plots are shown as white boxes and sampled lakes are shaded in black.

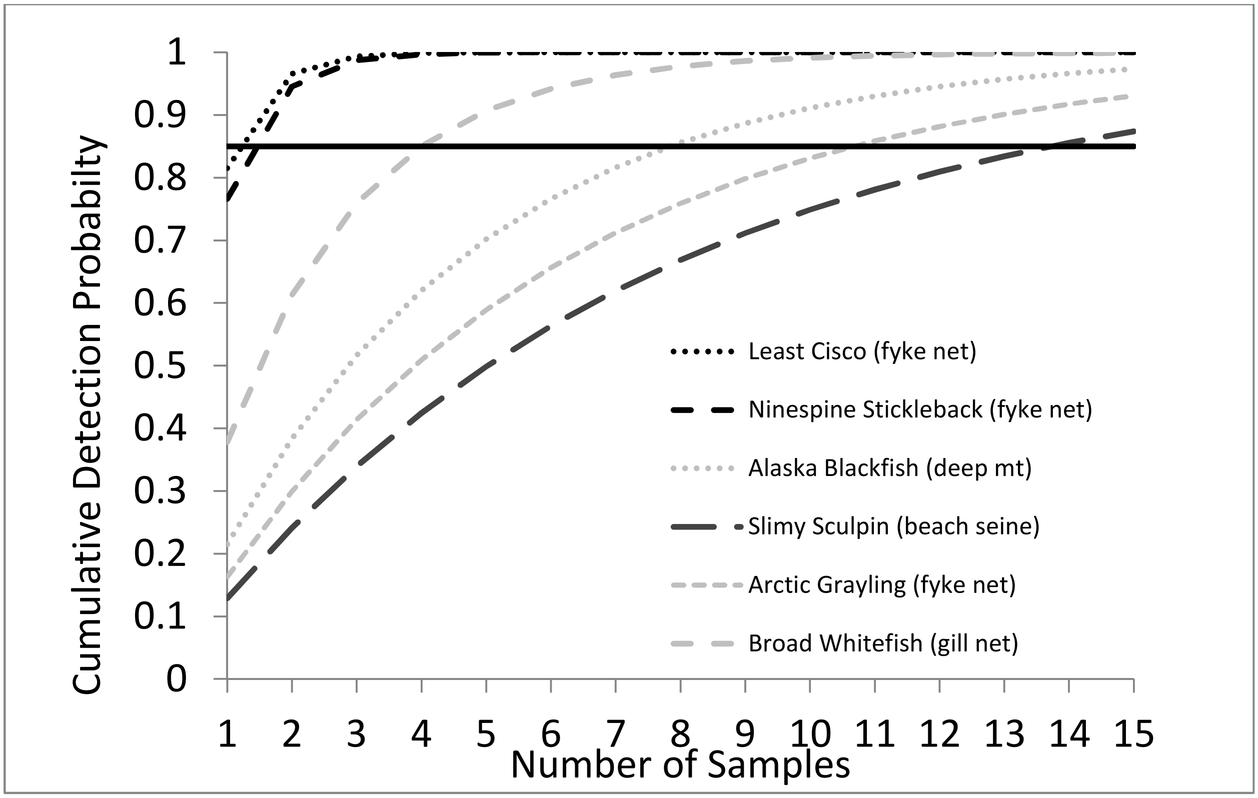

Figure 2.2: Example of the number of repeated samples required to achieve a cumulative detection probability of 0.85 (solid black line) using the gear type with the highest detection probability for each respective species. Detection estimates are for average values of the covariates in 2009.

Chapter 3: Patterns of lake occupancy by fish indicate different adaptations to life in a harsh Arctic environment[1]

Abstract

For six fish species sampled from 86 lakes on the Arctic Coastal Plain, Alaska, we examined whether lake occupancy was related to variables representing lake size, colonization potential, and/or the presence of overwintering habitat. We found the relative importance of each factor for a given species could be related to its ecology and adult size. The three large-bodied migratory species, least cisco (*Coregonus sardinella*), broad whitefish (*Coregonus nasus*), and arctic grayling (*Thymallus arcticus*), were influenced by factors associated with the likelihood of fish recolonizing lakes, including whether the lakes had a stream connection. Of the large-bodied species, least cisco had the highest likelihood of occupancy (estimate ± SE = 0.52 ± 0.05) and models provided evidence that least cisco exhibit both migratory and resident forms. Models for small-bodied fish differed among species, indicating different niches. Ninespine stickleback (*Pungitius pungitius*) were the most widespread and ubiquitous of the species captured (occupancy probability = 0.97 ± 0.01); they were captured in lakes that freeze to the bottom, suggesting they disperse widely and rapidly after spring freshet, including colonization of sink habitats. Alaska blackfish (*Dallia pectoralis*) had a lower occupancy (occupancy probability = 0.76 ± 0.05) with a distribution that reflected tolerance to harsh conditions. Slimy sculpin (*Cottus cognatus*) had an occupancy probability of 0.23 ± 0.06, with a distribution indicating its marine origin. Based on these patterns, we propose an overall model of primary controls on the distribution of fishes on the Arctic Coastal Plain of Alaska. Harsh conditions, including lake freezing, limit occupancy in winter through extinction events while lake occupancy in spring and summer is driven by directional migration (large-bodied species) and undirected dispersal (small-bodied species).

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[1] Haynes T.B., A.E. Rosenberger, M.S. Lindberg, M. Whitman, J.A. Schmutz. 2014. Patterns of lake occupancy by fish indicate different adaptations to life in a harsh Arctic environment. Freshwater Biology. 59: 1884-1896.

Introduction

Patterns of habitat occupancy are a consequence of the relationship between species traits and the habitat features that limit their distribution (Poff, 1997). The distribution of fish may be affected by historical constraints (e.g. glaciation; Oswood *et al.*, 2000), barriers to local colonization (Spens *et al.*, 2007), or factors that promote recruitment and overall population persistence (Salonen *et al.*, 2009). At regional scales, the distribution of fish is shaped by climate, large scale barriers to dispersal and historical biogeographical influences (Tonn *et al.*, 1990). At finer spatial scales, distribution is influenced by the extent, shape and abiotic features of the habitat, the structure of the surrounding landscape, and biological factors (e.g. competition and predation; Jackson *et al.*, 2001). Controls on fish distribution are complex and act on a number of scales. However, this complexity can be alleviated in situations where the system is well-studied or has a single dominant factor (e.g. hypoxia, severe cold) that simplifies the number of filters determining assemblage composition.

Arctic lakes provide an excellent opportunity to examine how environmental features affect the distribution of fish and how species are adapted to a harsh and dynamic environment. Compared with other aquatic systems, lakes are isolated (Magnuson, 1976), and can be examined as discrete patches with a limited number of environmental influences. Biologically, Arctic lakes are relatively simple because of low species diversity and productivity, and because species have physiologically and geographically constrained distributions (Hershey *et al.*, 1999). Further, these systems are less affected by anthropogenic influences that complicate ecological study, including heavy fishing pressure, pollution, introduction of non-native species, transfer and stocking of native species, and alterations of waterways.

Fish assemblages on the Arctic Coastal Plain (ACP) are largely recruited from the fauna of the Beringian refugia, but also include species that took advantage of Pacific Coast or Mississippi Pleistocene refugia (Oswood *et al.*, 2000). At finer spatial scales, species-specific responses to landscape controls, like colonization potential and the presence of local refugia, are likely to be reflected in differences in distribution patterns among species (Jackson *et al.*, 2001). Fishes on the ACP have diverse morphologies and ecologies, including major life history traits such as reproductive timing and investment, migratory patterns, and trophic position (Reynolds, 1997; Hershey *et al.*, 1999). Species also differ in their ability to persist in lakes and to colonize new lakes. These differences among species traits probably drive the variation in occupancy among fishes on the ACP.

There are relatively few descriptions of the distributions of fish on the ACP and elsewhere in the Arctic. Two notable studies include Hershey *et al.* (1999), who suggested a geomorphic-trophic conceptual model of the distribution of Arctic fish, and Hershey *et al.* (2006), who provides empirical models of fish distributions in lakes in relationship to landscape features. Both these studies were restricted to an area (18,000 km^2) in the foothills of the Brooks Range Mountains, which differs from most of the ACP, in terms of fish species composition and abundance, landscape features and topography, geomorphic constraints, and glaciation history (Oswood *et al.*, 2000). Catalogues of fish inventories that are used to manage fish populations, such as the Anadromous Waters Catalogue (Alaska Department of Fish & Game) also have very coarse and limited data for the ACP. To improve our understanding of the distribution of lacustrine fish in the Arctic, we investigated the occupancy of six species across a broad northerly area of the ACP. We examined three large-bodied species, least cisco (*Coregonus sardinella*), broad whitefish (*Coregonus nasus*) and arctic grayling (*Thymallus arcticus*), and three small-bodied species, ninespine stickleback (*Pungitius pungitius*), Alaska blackfish (*Dallia pectoralis*) and slimy sculpin (*Cottus cognatus*). These species vary in their ecological attributes and life histories, which can lead to species-specific responses to spatial and temporal variation in environmental conditions (Winemiller & Rose, 1992) and, ultimately, variation in lake occupancy (Miyazono *et al.*, 2010). We expected that local and regional features relating to local persistence and colonization potential in lakes would determine fish occupancy; however, the scale and strength of the effects would depend on the biology of the individual species, including their dispersal and migratory capabilities and tolerance to winter conditions. Our overall goal was to provide a conceptual model of primary controls on the distribution of fish in Arctic lakes, contrasting the effects of landscape connectivity and overwintering refugia on fish species that vary in body size, tolerance to winter conditions and ecology.

Methods

We sampled 86 lakes for fish over a large area (~ 8500 km^2) of the ACP located within the National Petroleum Reserve – Alaska. To our knowledge, no sampling had been conducted on these waterbodies previously. We focused on lakes in 16 plots, each 7 x 7 km in dimension, randomly distributed across the study area (Figure 3.1). Within a plot, we selected a lakes with a surface area > 7 ha, at random except that half were occupied by piscivorous yellow-billed loons (*Gavia adamsii*) and half not.

We began sampling on 4 July in 2009 and 23 June in 2010, shortly after spring freshet (when snow and ice had melted rapidly and caused widespread flooding) and continued until mid-August, encompassing the growing season for fish. Three sampling crews (two-four people in each) worked independently on separate lakes throughout the season. Crews sampled each lake during a single visit of 48-72 h before moving to the next lake. We used five methods to sample the fish, including: gillnets (two nets, three replicates net^{-1}), minnow traps (eight traps, two replicates trap^{-1}), fyke nets (two nets, two replicates net^{-1}), dip nets (one net, 30 replicates net^{-1}) and beach seines (one net, two replicates net^{-1}). Samples were replicated spatially (several sets of the same gear sampling at the same time) and temporally (a single set of gear used a number of times). For example, we used two fyke nets (two spatial replicates), each checked twice (two temporal replicates) for a total of four replicates per lake. Because our temporal replication took place over a short period (i.e. < 72h), it is unlikely that we violated the site-closure assumption for occupancy modelling (MacKenzie *et al.,* 2006). We generally deployed fyke nets and minnow traps before midday and conducted beach seine, dip net and gill net sampling throughout the afternoon. Although there was some variation in the timing of gear deployment, our previous work suggested that there were no strong diurnal effects on gear sampling efficiency (Haynes *et al.*, 2013). Methods used for each gear type are described below and in greater detail in Haynes *et al.* (2013).

Gill nets – We used two variable-mesh gill nets measuring 38 m x 1.8 m with five panels ranging in mesh size from 1.3 to 6.5 cm. We checked gill nets every two to three hours, then removed the nets after the third check.

Minnow Traps – We baited eight Gee-style galvanized steel minnow traps (2.5 cm opening with 6 mm mesh) with preserved salmon eggs and generally deployed traps before midday. We deployed four traps individually in shallow water along the shoreline ("shore minnow traps") and sunk four traps in deepest zone of the lake ("benthic minnow traps"). Shore and benthic minnow traps had different probabilities of catching fish and were therefore considered as two separate methods (Haynes *et al.*, 2013). We checked traps after 12 h, re-baited and replaced them, and checked and pulled them after 24 h.

Fyke nets – We sampled shorelines with two fyke nets, each with 15.2 x 1.2 m wings and a 30.5 x 1.2 m centreline with 0.6 cm sized stretched mesh. Wings and centreline had float lines and weighted lead lines. The hoop net was constructed of 0.3 cm sized stretched mesh and had a frame opening of 1.1 x 1.1 m, followed by five sequential hoop frames spaced 0.8 m apart and measuring 0.6 x 0.6 m in size. The hoop net had three net throats within the frame measuring 15 x 23 cm at the middle of each throat. We checked nets twice for fish, once after about 12 h and again after 24 h when we removed the nets.

Dip nets – We swept dip nets (3 mm mesh; two opening sizes 28 x 38 x 20 and 41 x 41 cm) along the lake bottom adjacent to the shore for three eight-minute intervals and identified and counted fish for each interval.

Beach seine – We employed a 3 mm mesh beach seine measuring 15 m in length that tapered in width from 3 m at the middle to 1.2 m at the wings. We conducted two beach seine replicates, covering approximately 10-15 m in length. The second replicate was offset from the first by at least 5 m parallel along the shore.

Environmental Variables

For hypothesis testing and model development, we categorized environmental variables (Table 3.1) based on proposed ecological mechanisms determining the distribution of fish, including patch size (one variable), directional migration (five variables), undirected dispersal (four variables) and persistence (two variables). Variables were evaluated and quantified for two spatial scales: local (the scale of the sample lake) and regional (the mean value of the variables from lakes within the boundaries of a set of 7 x 7 km plots gridded across the study area). Although we measured water quality variables (dissolved oxygen, temperature, pH, specific conductivity) on most lakes, we did not consider these variables in analyses because lakes varied little in water chemistry (also noted by Hershey *et al.*, 2006).

Patch size can represent the amount and diversity of habitat available to a species. Small lakes, like small islands (MacArthur & Wilson, 1967), may have lower colonization rates simply due to their size. We expected patch size to be important for all species, especially resident species. We calculated the patch size as the lake surface area (“L_LakeArea”).

Swimming aquatic organisms require hydrological connections between lakes to disperse (De Bie *et al.*, 2012). For lakes, colonization potential can be influenced by environmental features that promote directional migration (i.e. movement to a specific location) or undirected dispersal (i.e. movement with no specific destination). The importance of directional migration versus undirected dispersal for fish depends on species. We predicted that the ‘occupancy probability’ (the probability of a species being present in a lake) for large-bodied species would be influenced by directional migration over relatively long distances along migratory pathways from overwintering habitats (river systems and estuaries) into lakes in the summer for breeding. We considered the following variables as likely influences on colonization potential along migratory pathways: hydrologic connectivity (both local and regional), regional lake area and regional measures of the distance to the coast and to the nearest river. We defined local hydrologic connectivity (“L_Connect”) as the existence of a surface waterway (generally a stream) connecting a focal (surveyed) lake to another water body (stream, river, lake, pond or wetland). We determined whether a lake had a connection during the summer by a combination of observations of a digital map (i.e. National Hydrography Dataset), aerial photographs and ground-observation (truthing). Regional connectivity (“R_Connect”) is a measurement of the total linear distance (km) of streams and rivers at the regional scale (i.e. within a 7 x 7 km grid). Lakes may provide stepping-stones for fish migration, and we calculated regional lake area (“R_LakeArea”) as the mean L_LakeArea at the regional scale. We measured the distance to the nearest river (“R_DistRiver”) or to the north coast (“R_DistCoast”) as the shortest linear distance to the feature from the centroid of the 7 x 7 km grid cell.

We predicted that lake occupancy by resident, small-bodied species would be influenced by variables related to undirected dispersal (i.e. variables that may promote general dispersal, with no specific destination). Variables we considered to be related to undirected dispersal included regional and local measures of altitudinal gradient and distance among lakes. These variables may affect dispersal ability during the spring freshet, when low lying flood waters can create temporary pathways for dispersal. As a measure of local altitudinal gradient (“L_Grad”), we used the mean value of the lake altitude relative to the minimum value within a set of ‘buffer zones’ (5-10 m, 10-25 m, 25-100 m) around the lake perimeter (Gross *et al.*, 2013). The regional altitudinal gradient ("R_Grad") was calculated as the mean L_Grad at the regional scale. We measured local distance between lakes ("L_DistLake") as the distance of the sample lake to the next closest lake > 7 ha in surface area. We calculated the regional distance between lakes ("R_DistLake") as the mean value of L_DistLake at the regional scale.

Lake depth can be an important driver of fish distributions on the ACP through its influence on the persistence over winter of resident fish. The ACP has extremely cold winters during which much of the water becomes frozen. When stream and river connections freeze, it restricts fish movements and isolates fish populations within the lakes. Lakes may partially or completely freeze, depending on the water depth (generally depths < 1.6-2.2 m freeze to the bottom; Jeffries *et al.*, 1996; Grunblatt and Atwood, 2014). When shallower lakes freeze partially to the bottom, fish habitat within that lake becomes restricted, and this can reduce or eliminate local populations due to anoxia in liquid water under the ice. If the entire lake freezes, local extinction occurs. Synthetic Aperture Radar (SAR) satellite imagery shows strong differences in signal between ice extending to the lake bed and ice with liquid water beneath (Jeffries *et al.*, 1996). We used SAR modelled data of the proportion of the lake (by surface area) that does not freeze to the bottom (Grunblatt and Atwood, 2014) to represent the amount of deep, unfrozen water available to fish within a lake. Deep-water refugia can promote survival through extreme winter or summer temperatures. We predicted that non-migratory (resident) species would have higher occupancy probabilities in lakes with more refugia. The availability of winter refugia (L_RefArea) was calculated as the percentage of the lake surface area that did not freeze to the bottom during winter, as inferred from SAR imagery collected in late winter (April 2009; Grunblatt and Atwood, 2014). Regional availability of winter refugia (R_RefArea) was calculated as the sum of the lake surface area that does not freeze to the bottom during winter from all lakes within each 7 x 7 km grid cell.

Data Analysis

We used occupancy modelling and an information theoretic approach to model selection to estimate occupancy probability and to examine whether specific environmental covariates affected it. For each pair of variables showing a high degree of colinearity (correlations ≥ 0.70; Berry & Felman, 1985), we removed the variable that showed the highest correlation with others in the set. This excluded R_LakeArea (correlated with R_RefArea) and R_Connect (correlated with R_DistCoast) from further analysis. We created a set of *a priori* models in the program PRESENCE (Version 5.7; Hines, 2006) using the single season, multi-method occupancy modeling parameterization (Nichols *et al.*, 2008). Although we had two years of data, we did not sample any site in both years so we could not use a multi-season approach. Haynes *et al.* (2013) explicitly examined detection for these data and found cumulative detection probability to be high and to vary by sampling method, lake area, relative lake depth (inferred by SAR imagery), day and year. We used the detection probability structure from Haynes *et al.* (2013) to examine occupancy by allowing detection probability to vary by sampling method and four site covariates: L_LakeArea, L_RefArea, Day and Year, where Day was the number of days from the beginning of sampling and Year was binary (representing 2009 or 2010).

We constructed separate candidate model sets for each species to determine its occupancy was associated with variables categorized by their spatial scale (local or regional scales) and perceived ecological relevance, including: patch (lake) size, directional migration or undirected dispersal (affecting colonization potential), or overwinter habitat variables (affecting population persistence). We used a two-step approach to reduce the number of candidate models in the model set. First, for each variable category (4), we ran combinations of variables based on scale (local *versus* regional *versus* local plus regional variables) and ranked these in the overall model set, including a saturated and a null model (18 models). Using the highest ranked variable combination for each category determined from the previous step, we ran combinations of variables, grouped by category (e.g. directional migration *and* overwinter habitat), for all category combinations that remained (11 models). For example, based on the competing model set within each category, a species may be found in the first step to be influenced by L_LakeArea for patch size; L_Connect for directional migration; L_Grad, R_Grad and R_LakeDist for undirected dispersal; and L_RefArea for overwintering habitat. In the second step, all combinations of models from the four categories competed against each other (if more than one variable was important for a category, then those variables were entered together). The hypothetical species in the example above may have the top model in the second step include variables representing patch size and undirected dispersal, giving a top mode with the following covariates for occupancy: L_LakeArea, L_Grad, R_Grad, R_LakeDist.

For each species, we evaluated all models from both steps in the same model set by ranking models using Akaike's Information Criterion, corrected for sample size (AIC_c; Burnham & Anderson, 2002). Determining sample size for occupancy models is still a topic of debate (MacKenzie *et al.*, 2006) and thus we used the mean value between the number of sites and the number of surveys (least cisco and arctic grayling N = 683, broad whitefish N = 463, small-bodied species N = 1284) to adjust the sample size (MacKenzie *et al.*, 2012). To check for overdispersion, we ran a goodness-of-fit test for each species using the most complex model (MacKenzie & Bailey, 2004). When we found evidence for overdispersion, we adjusted the selection criteria ($QAIC_c$) and sample variances (Burnham & Anderson, 2002). We standardized all continuous covariates by calculating z-scores and did not consider interaction effects for ease of interpretation and parsimony. We eliminated models from the candidate set that did not converge. To adjust for model selection uncertainty, we used model averaging for all models with an AIC weight ≥ 0.01 to produce parameter estimates and standard errors for beta parameters (Burnham & Anderson, 2002). For each fish species, we examined parameter estimates and standard errors from model averaged results to determine a covariate's influence on occupancy. We considered variables to be biologically important if they had relatively large effect sizes and precise estimates.

Results

For all species, model estimates of occupancy were very similar to occupancy evident from the raw data ('observed occupancy'), because we conducted a large number of repeated surveys, which produced high cumulative detection probabilities (Haynes *et al.*, 2013). Model selection tables for each species are presented in Supporting Information (Tables A3.1-A3.5). Besides the six species we were investigating, we caught eight other fish species with observed occupancies too low to allow for occupancy modelling: Arctic char (*Salvelinus alpinus*; 3/86 lakes), northern pike (*Esox lucius*; 3/86 lakes), rainbow smelt (*Osmerus mordax*; 3/86 lakes), humpback whitefish (*Coregonus pidschian*; 2/86 lakes), three-spined stickleback (*Gasterosteus aculeatus*, 2/86 lakes), Arctic flounder (*Liopsetta glacialis*, 1/86 lakes), fourhorn sculpin (*Myoxocephalus quadricornis*, 1/86 lakes) and burbot (*Lota lota*; 1/86 lakes). Two fishless lakes were sampled during the beginning of the season (Day 0 and Day 5); these were unconnected and relatively isolated (large local distance between lakes; one lake had a high local altitudinal gradient [L_Grad] value).

The occupancy of least cisco was influenced by variables related to directional migration (L_Connect, R_DistCoast) and suitable habitat within the lake (L_RefArea, L_LakeArea; Figure. 3.2a,b). Least cisco were more likely to be in lakes connected to streams (logit $\beta_{L\_Connect}$= 1.51 ± 0.62) and closer to the coast (logit $\beta_{R\_DistCoast}$= -1.26 ± 0.37). Least cisco occupancy probability increased as a greater percentage of the lake remained unfrozen during winter (i.e. deeper lakes; logit $\beta_{L\_RefArea}$= 0.54 ± 0.34) and for larger lakes (logit $\beta_{L\_LakeArea}$ = 0.99 ± 0.53). Least cisco had an observed occupancy of 0.51 and an estimated occupancy from the null model of 0.52 ± 0.05.

The occupancy probability of broad whitefish was positively related to directional migration variables (L_Connect, R_DistCoast) and negatively related to the distance between lakes (L_DistLake; Figure 3.2c,d). Broad whitefish were more likely to occupy lakes that were connected to streams (logit $\beta_{L\_Connect}$= 2.69 ± 1.38; Table 3.2), closer to the coast (logit $\beta_{R\_DistCoast}$= -1.24 ± 0.69) and close to another lake (logit $\beta_{L\_ DistLake}$ = -0.803 ± 0.466). Broad whitefish had an observed occupancy of 0.27 and an estimated occupancy from the null model of 0.31 ± 0.06.

Four of the most complex models of arctic grayling occupancy (K = 11-19) failed to converge and were removed from model rankings. Arctic grayling were more likely to be found in lakes that were locally connected (logit $\beta_{L\_Connect}$= 2.77 ± 1.26; Table 3.2). Grayling were found at 14 of the 86 lakes (observed occupancy = 0.16) and had an occupancy estimate of 0.27 ± 0.09 from the null model.

Ninespine stickleback were found at 83 of the 86 sample sites (observed occupancy = 94 %). Because they were found at almost every lake, it was not possible to investigate how covariates influenced occupancy. Based on the null occupancy model (i.e. no covariates for occupancy), occupancy for ninespine stickleback was estimated to be 0.97 ± 0.01.

We used criteria adjusted for overdispersion ($QAIC_c$) for model selection for Alaska blackfish. Based on the model-averaged results, occupancy of Alaska blackfish was influenced by regional distance among lakes and availability of winter refugia within the lake (Table 3.2). The probability of occupancy decreased as lakes became less densely distributed at the regional level (logit $\beta_{R\_DistLake} = -0.93 \pm 0.35$) and increased as a greater percentage of the lake remained unfrozen during winter (logit $\beta_{L\_RefArea} = 0.72 \pm 0.32$). Alaska blackfish had an observed occupancy of 0.74 and an estimated occupancy from the null model of 0.76 ± 0.05.

The distance of the plot to the coastline influenced occupancy of slimy sculpin, with probability of occupancy decreasing as distance from the coast increased (logit $\beta_{R\_DistCoast} = -0.86 \pm 0.68$; Table 3.2). Slimy sculpin were also more likely to occupy lakes that had a stream connection (logit $\beta_{L\_Connect} = 1.04 \pm 1.29$). However, neither R_DistCoast nor L_Connect were estimated with a high level of precision. Observed occupancy was 0.13 and estimated occupancy from the null model was 0.23 ± 0.06.

Discussion

Lake occupancy by fish was associated with colonization potential (i.e. variables related to directional migration or undirected dispersal) while other habitat features, such as lake size and the availability of deep water refugia, were also important for certain species. Broad scale assemblage patterns may depend on whether dispersal rates exceed extinction rates (Shurin *et al.*, 2009), especially when local habitat characteristics vary little (Spens *et al.*, 2007) as they do for ACP lakes. Given that patch connectivity is increasingly recognized as important in structuring aquatic communities (Fullerton *et al.*, 2010), it is not surprising that colonization plays a key role in shaping the Arctic fish communities. In the Arctic, hydrological connectivity plays a primary role in affecting colonization potential and strongly corresponds to the spatial patterns of resources and organisms (Lesack & Marsh, 2010) including fish (Hershey *et al.*, 1999, 2006). The role of colonization was evident from the importance of local connectivity, whereas the availability of winter refugia (a proxy for persistence potential) was less important than we predicted. However, the relative importance of colonization and local extinction probably varies seasonally. Because we were examining occupancy after the spring freshet, when fish have already dispersed and colonized new habitats, we found colonization to be a stronger driver of fish occupancy than factors associated with overwinter survival (persistence).

Based on our findings, we propose a conceptual model of the primary drivers of fish distribution and occupancy on the Arctic Coastal Plain (Figure 3.3). At the ecoregional (or hydroregional) scale, distribution and species composition of fish in the Arctic has been shaped by the Pleistocene glaciations (Oswood *et al.*, 2000). At finer scales, the functional relationships between the ecology and life history of individual species and the dynamics of the harsh Arctic environment are the likely determinants of current habitat occupancy. These traits include dispersal capabilities when faced with a seasonally dynamic hydrology (Shurin *et al.*, 2009) and the ability to persist through harsh winters (Jackson *et al.*, 2001). Given that species vary ecologically, we can expect that in the face of the dynamic Arctic environment, the influence of environmental characteristics on species occupancy is likely to vary temporally and among species. During the winter, when lakes are covered with ice, deep water refugia are likely the primary driver of fish distribution, with a lack of refugia resulting in local extinctions (Figure 3.3). This is particularly important for resident species that do not migrate out of lakes in the autumn. In this region, Alaska blackfish were widely distributed and ninespine stickleback were nearly ubiquitous, suggesting that both these species can tolerate winter conditions. Shallow lakes that freeze to the bottom are likely to lose their fish. However, even in lakes with deep water refugia, conditions can be harsh enough to cause local population loss (e.g. Danylchuk & Tonn, 2003). As the winter proceeds and surface ice increases in thickness, the remaining water can be hypoxic, saline (due to the concentration of solutes; Salonen *et al.*, 2009) and very cold. In general, small-bodied species require less oxygen and both ninespine stickleback and Alaska blackfish can tolerate low oxygen concentration (Lewis *et al.*, 1972; Crawford, 1974). Ninespine stickleback also tolerate high salinity (Nelson, 1968). These adaptations allow sticklebacks and blackfish to overwinter in lakes where other species cannot. This is especially the case for the Alaska Blackfish, which may be more tolerant due to its air-breathing capabilities and resistance to extreme cold (Scholander *et al.*, 1953). The occupancy models showed that Alaska blackfish were more likely to be found in lakes with more deep water refugia, likely because they overwinter in these lakes. Conversely, slimy sculpin may be less tolerant of winter conditions than sticklebacks and blackfish. This disparity in tolerance may restrict slimy sculpin to areas with large amounts overwintering habitat (Hershey *et al.*, 2006), which is reflected in their restricted distribution and low occupancy rates. If these refugia also harbor overwintering piscivores, this may further affect slimy sculpin through predation (Hanson *et al.*, 1992).

As ice melts during spring, fish occupancy becomes less dependent on deep water refugia (Figure 3.3). Rapid thawing is accompanied by a spring freshet, causing an increase in water level, widespread flooding and an overall increase in landscape connectivity. Lakes become connected temporarily, at which point undirected dispersal is an important driver of fish occupancy for small-bodied species, particularly those capable of rapid recolonization of depopulated lakes. Although movement capabilities and body size are generally positively related (De Bie *et al.*, 2012), the small size of Alaska blackfish and ninespine stickleback may aid dispersal through ephemeral pathways in early spring. Many of these connections are temporary and shallow, do not have directional flow, and are potentially difficult to navigate for larger-bodied species. The number of ephemeral connections peaks in the spring and declines thereafter (Figure 3.3). However, ephemeral connections may continue to act as dispersal conduits for small-bodied species through the summer; young or adults may disperse opportunistically at times of high water. This may be particularly true in landscapes where lakes are close together and may occasionally become connected. Perhaps for this reason, Alaska blackfish were more likely to be found in areas where lakes were close together.

Alaska blackfish are physiologically tolerant of winter conditions, possessing an air-breathing organ that allows them to breathe air (Crawford, 1974), including that trapped under the ice of frozen lakes (Campbell *et al.* 2014). Such specialist adaptations and limited dispersal capabilities suggest that tolerance explains their persistence. Ninespine sticklebacks, in contrast, may be less tolerant than blackfish but appear to have a dispersal and recolonization capabilities characteristic of an opportunistic life history (Winemiller & Rose, 1992). It seems possible that sticklebacks are widely distributed in the Arctic largely due to their ability rapidly to recolonize depopulated lakes via shallow and ephemeral connecting water bodies, indicating that stickleback are resilient rather than tolerant. The ninespine stickleback has a short generation time, grows quickly and can reaches high population density quite rapidly (Cameron *et al.*, 1973). They were often caught in large numbers; in some lakes, a 12 h fyke net set would catch more than 10,000 individuals (100 fold greater than the maximum Alaska blackfish catch-per-unit-effort). Such high density may make dispersal more likely and perhaps density dependent. Although stickleback dispersal has not been studied directly in this region, Cameron *et al.* (1973) noted major population movements at the beginning of the growing season at a single lake, supporting our speculation that sticklebacks use the spring freshet for dispersal and recolonzation.

The spring freshet is also an important time for large-bodied migratory species. Formerly frozen rivers and streams begin to flow and connect overwintering and summer foraging habitats

(Figure 3.3). Large-bodied species demonstrate characteristics of a ‘periodic’ life history (Winemiller & Rose, 1992; Miyazono, *et al.* 2010); in summer, they migrate from overwintering habitats into connected systems. This may have been reflected in the occupancy patterns of large bodied species, which were associated with local lake connectivity. Least cisco, broad whitefish and arctic grayling have a strong ability to colonize lakes with connections that remain wet through the growing season, but not lakes with only ephemeral connections. The spatial arrangement and composition of landscape features are also important, which can affect colonization potential beyond direct measures of connectivity alone (Dunning *et al.*, 1992). We found that the broad whitefish was more likely to occur in regions where lakes were spaced closer together. Although we initially categorized the L_DistLake variable as related to undirected dispersal, it may also be important for migratory species, which can use lakes as migratory stepping-stones. Least cisco and broad whitefish were more likely to be found in lakes closer to the north coast, which allows better access to the marine feeding and overwintering habitat (Reist & Bond, 1988).

The probability of occupancy for least cisco was also positively related to local habitat features, including lake size and availability of overwintering refugia. These features may be more important for least cisco, than for other large-bodied species, because least cisco may have a resident form. Least cisco can have riverine, anadromous and lacustrine forms (Reist & Bond, 1988), and thus, certain populations of least cisco may overwinter in large lakes with deep-water refugia. If least cisco are permanent residents in some lakes on the ACP, it would explain the importance of deep water refugia and lake size for them but not other large-bodied species. It might be that all three large-bodied species move into lakes during the summer to feed and then leave for winter refugia in streams and rivers, which can be widespread on the ACP (Huryn *et al.*, 2005), or in the sea. However, if a connected lake becomes isolated due to changes in the stream network, migratory fish may become trapped in a lake (Hershey *et al.*, 2006). If this occurs, least cisco may survive if suitable overwintering habitat is present. In support of this, we found least cisco was the most widely distributed of the large-bodied species in our study, and occurred in the widest range of habitats, including nine lakes without obvious connections (in seven of which we captured young-of-the-year least cisco).

During summer, ephemeral connections dry up, and thus we hypothesize a decline in the importance of undirected dispersal for lake occupancy (Figure 3.3). As summer progresses and lakes warm, deep water refugia may again increase in importance by providing cool water for cold stenotherms, such as whitefish (e.g., Jacobson *et al.*, 2011). The increase in importance of deep water refugia continues into late summer/early autumn as fish face an increasing risk of isolation in unsuitable overwintering habitat before freeze-up. During early autumn, there is presumably a pulse of fish movement as migratory species move to the rivers or marine overwintering habitat. Because some ephemeral connections are reestablished by autumn rain, there is also a brief opportunity for undirected dispersal, especially for ninespine sticklebacks. By late autumn lakes, streams and rivers begin to freeze again, restricting fish movement and, increasing once more the importance of deep water refugia for overwintering fish.

Because winter conditions cause local extinction in many lakes, fish occupancy on the ACP in the winter may be similar to other systems where extinction or niche partitioning is more important than colonization in shaping distributions (e.g. Magnuson *et al.*, 1998, Warfe *et al.*, 2013). Many lakes may be suitable during the summer but cannot sustain fish populations over the winter. Migratory species move out of these habitats before winter and other species which dispersed into these habitats and establish populations in the summer are unlikely to survive. For example, ninespine sticklebacks were found in four lakes without overwintering habitat (i.e. 0 % of the lake area is over 2 m in depth). These shallow lakes are probably population sinks for rapid dispersers such as ninespine stickleback (Olden *et al.*, 2001). However, if these shallow lakes are connected, they may be temporary habitat for migratory species (e.g. least cisco were also found in two of these four shallow lakes that had connections). If we were to examine lake occupancy during the winter, we would undoubtedly find a more restricted distribution for all species. Further, because winter conditions are likely to affect species differently, species relative occupancy rates would change. For example, because blackfish have more physiological adaptations for winter conditions, they may be more widespread during winter compared with ninespine stickleback. Thus, we hypothesize that the importance of local persistence alternates with that of colonization potential, the magnitude of that change depending on species.

We used a knowledge of fish distribution patterns to provide insight into how fish species are able to persist in the harsh and dynamic environment of the Arctic Coastal Plain. Given that this is a large region, encompassing tens of thousands of lakes, ponds and wetlands, future work should aim to expand and test these hypotheses by using both species distribution and life history studies. Additionally, examination of fish distributions at the assemblage level is needed to determine which of the factors we have identified (or may have missed) are driving patterns in species richness. Given the strong effects of variables such as connectivity (during the growing season) and deep water refugia (during winter), species richness may be primarily shaped by these factors (e.g. Olden *et al.* 2001) which could result in two or three distinct fish assemblages (e.g. Mehner *et al.*, 2005). Lastly, the environmental variables identified here as organizing factors of fish distribution can serve as hypotheses to be tested by molecular markers. Have widespread lake connectivity and frequent dispersal led to homogenous patterns of genetic variation across the ACP for some species? Genetic assessments would also permit inference of how past populations of Arctic fish have responded to historical climate perturbations, thus yielding insights into how their distributions may respond to future change (e.g. Hope *et al.*, 2013).

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Table 3.1: Description of environmental covariates considered in the analysis of occupancy probabilities for fish species on the Arctic Coastal Plain, Alaska.

Covariate	Scale	Abbreviation	Ecological Relevance[a]	Range[b]
Lake Area	Local	L_LakeArea	Local Patch Size	0.2-14.9 km^2
	Regional	R_LakeArea	Directional migration	5.0-27.9 km^2
Hydrologic Connectivity	Local	L_Connect	Directional migration	0-1 (binary)
	Regional	R_Connect	Directional migration	2.9-66.1 km
Distance to River	Regional	R_DistRiver	Directional migration	0.3-13.0 km
Distance to Coast	Regional	R_DistCoast	Directional migration	5.5 - 83.0 km
Altitudinal Gradient	Local	L_Grad	Undirected dispersal	-0.4-1.7 m
	Regional	R_Grad	Undirected dispersal	0.3-1.3 m
Lake Distance	Local	L_DistLake	Undirected dispersal	16-657 m
	Regional	R_ DistLake	Undirected dispersal	47-263 m
Winter Refugia	Local	L_RefArea	Persistence	0-96 %
	Regional	R_RefArea	Persistence	0-61,623 km^2

[a] Ecological Relevance - the perceived ecological influence of covariates on fish occupancy.

[b] We standardized all continuous variables into z-scores (mean = 0, SD = 1) before analysis.

Table 3.2: Model averaged estimates of the untransformed β parameters (± SE) for occupancy models of five fish species occurring in lakes on the Arctic Coastal Plain, Alaska. The ninespine stickleback was omitted because its high occupancy across the study area precluded investigation of relationships between occupancy and covariates.

	Small-bodied species		Large-bodied species		
	Alaska blackfish	Slimy sculpin	Least cisco	Broad whitefish	Arctic grayling
Variable	logit β	logit β	logit β	logit β	logit β
R_ DistLake	-0.93 ± 0.35	-0.26 ± 0.42	-0.81 ± 0.81	-1.30 ± 1.50	0.32 ± 0.51
L_RefArea	0.72 ± 0.32	0.60 ± 0.97	0.54 ± 0.34	0.23 ± 0.70	0.26 ± 0.45
L_Connect	0.94 ± 0.86	1.04 ± 1.29	1.51 ± 0.62	2.69 ± 1.38	2.77 ± 1.26
L_LakeArea	0.19 ± 0.37	0.95 ± 1.13	0.99 ± 0.53	-0.91 ± 1.47	0.10 ± 0.38
R_Grad	-0.41 ± 0.50	0.21 ± 0.47	0.39 ± 0.39	-0.27 ± 0.81	-1.18 ± 1.05
L_Grad	-0.33 ± 0.45	0.06 ± 0.37	-0.17 ± 0.36	-0.94 ± 1.16	NA
R_RefArea	0.47 ± 0.57	0.35 ± 0.59	-0.83 ± 0.88	-0.93 ± 0.95	NA
L_ DistLake	-0.30 ± 0.40	0.17 ± 0.35	-0.81 ± 0.81	-0.78 ± 0.57	NA
R_DistCoast	NA	-0.86 ± 0.68	-1.26 ± 0.37	-1.24 ± 0.69	-0.12 ± 0.44
R_DistRiver	NA	-0.38 ± 0.50	-0.05 ± 0.29	-0.01 ± 0.40	0.07 ± 0.44

Note: Models included in the model averaging procedure had an AIC_c weight of 0.01 or greater. "NA" represents variables that were not included in the models used for averaging.

Figures:

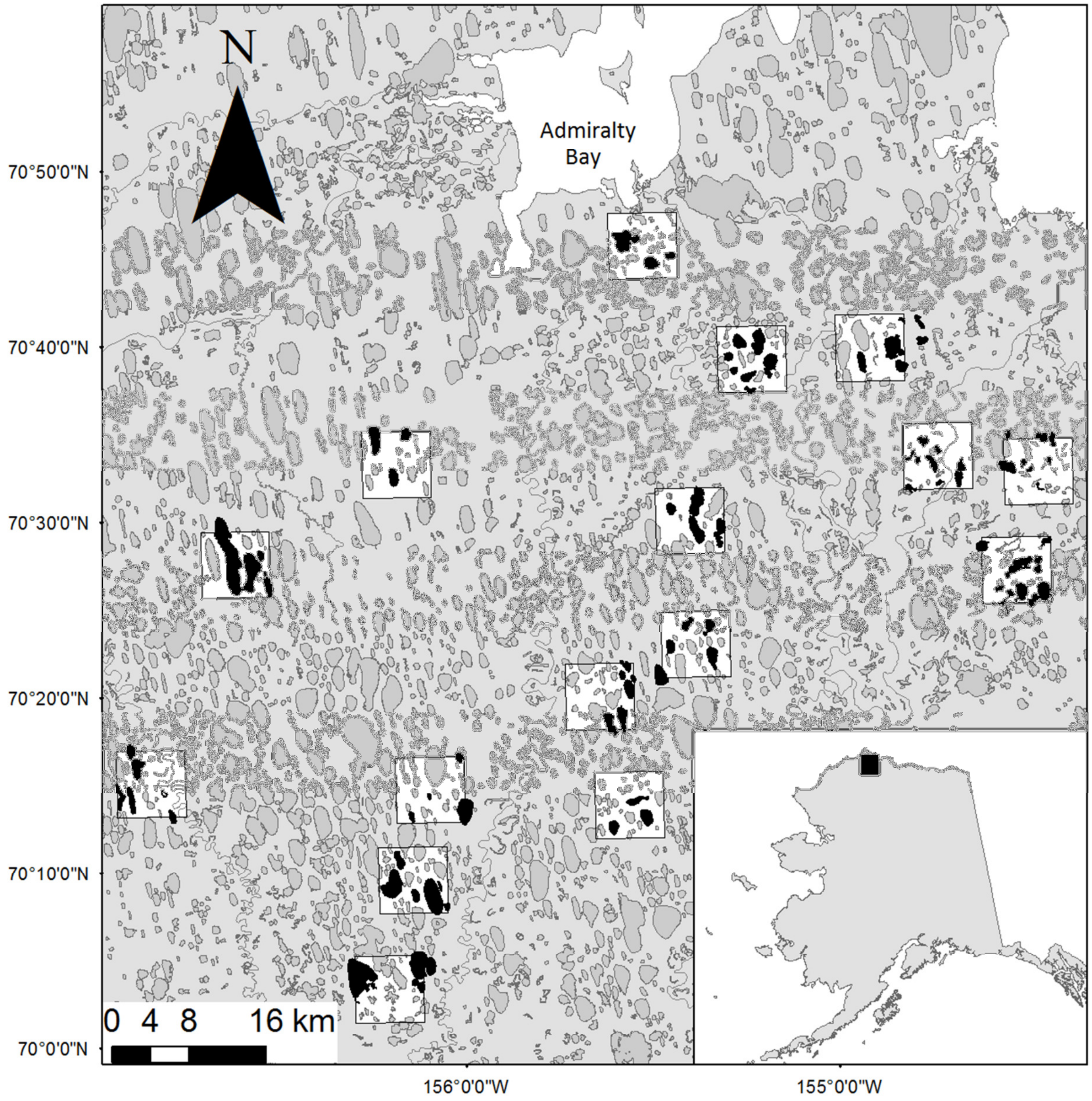
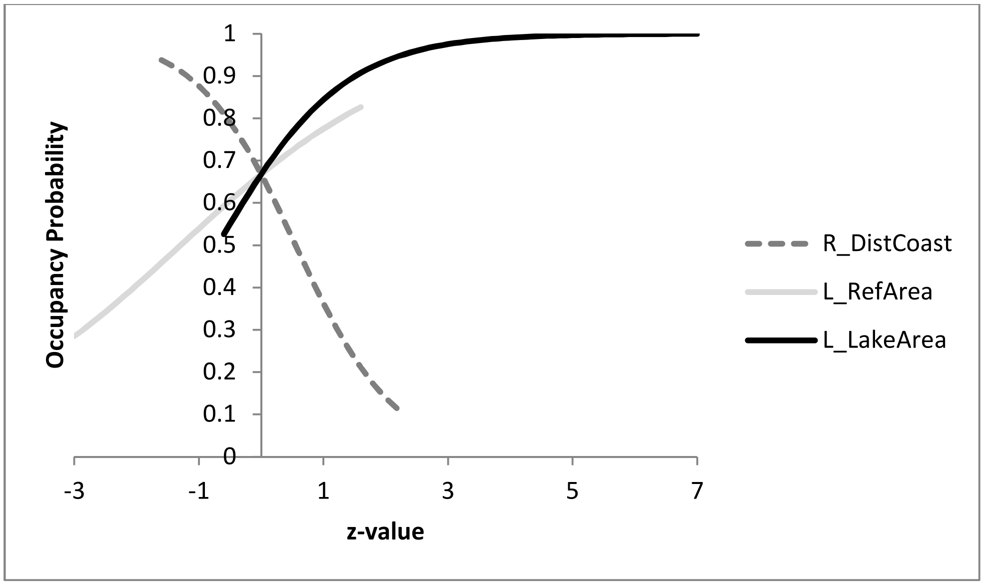


Figure 3.1: Study area on the Arctic Coastal Plain, with inset map of Alaska showing the study region (black box). White squares represent 7 x 7 km sample plots, and study lakes are shown in black.

A


Occupancy Probability
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0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
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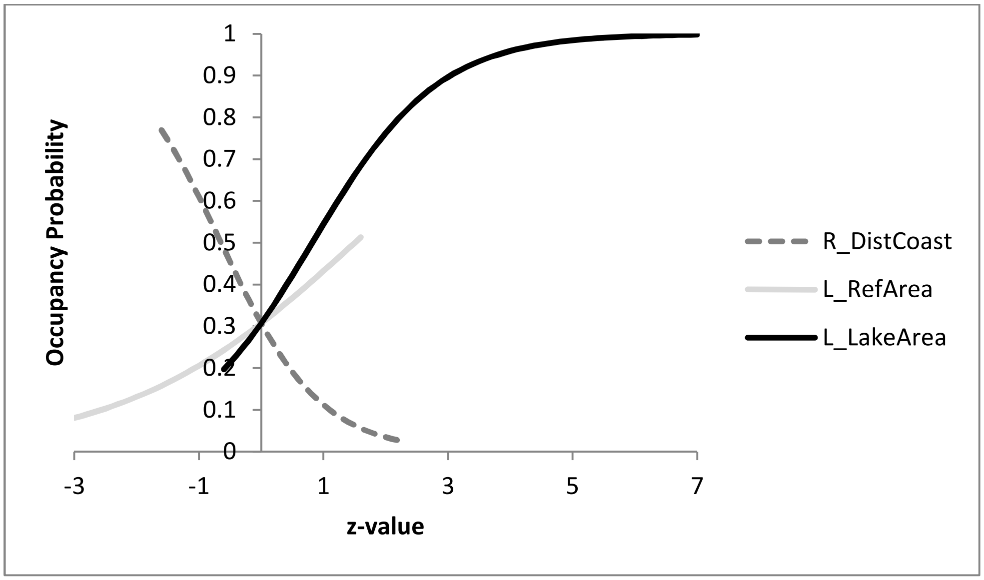
-3
-1
1
3
5
7
z-value
R_DistCoast
L_RefArea
L_LakeArea

B


Occupancy Probability
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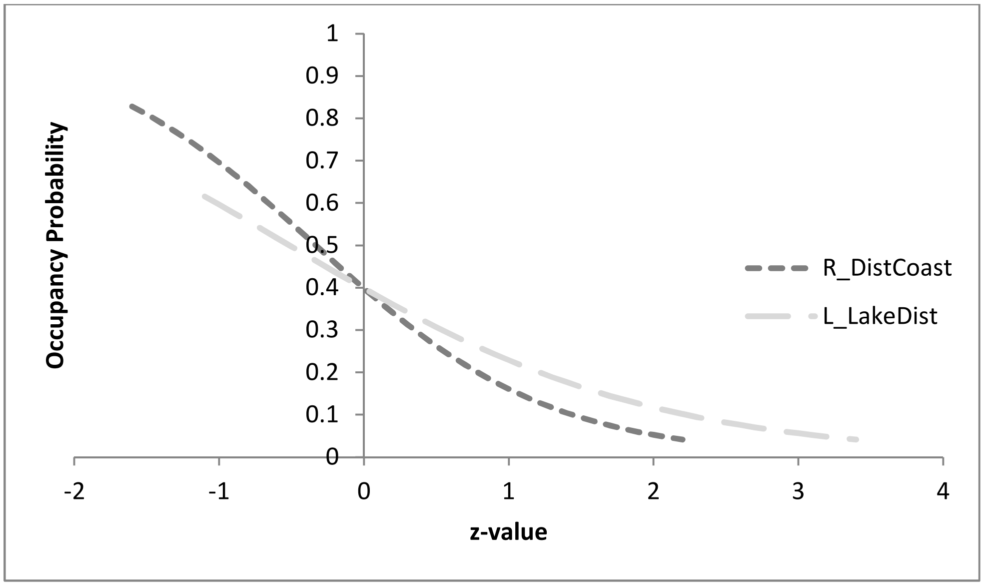
R_DistCoast
L_RefArea
L_LakeArea

C



D

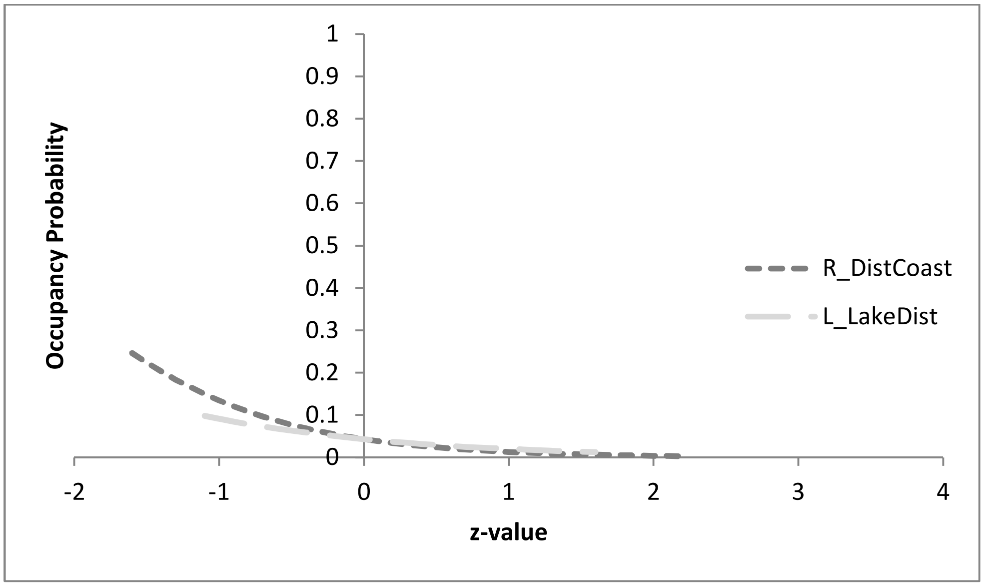


Figure 3.2: An example of how lake occupancy probability of two fish species [least cisco, a) and b); broad whitefish, c) and d)] varied in relation to environmental covariates. Covariates important for one or both of these species included distance to the coast (R_DistCoast), percent of lake that remains unfrozen during winter (L_RefArea) and lake surface area (L_LakeArea), distance to next nearest lake (L_LakeDist) for lakes with (a, c) or without a stream connection (b,

d). Curves represent the occupancy probability over the standardized (z-value) of the covariates while holding the other covariates at their mean values. The y-axis intercept represents the occupancy probability for a site with a connection (a,c) or without a connection (b,d) for the mean values of all continuous covariates.

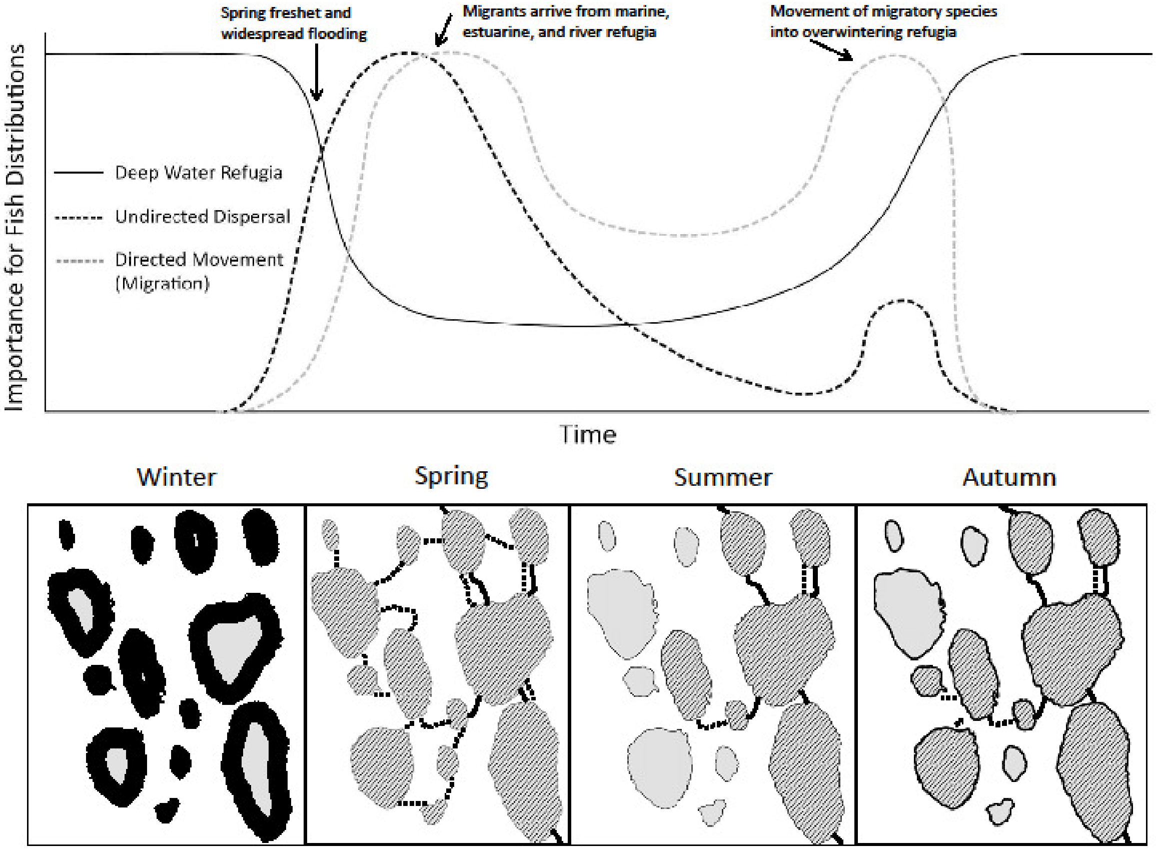


Figure 3.3: A conceptual model summarizing hypotheses on the environmental drivers of fish occupancy in lakes on the Arctic Coastal Plain, Alaska. During winter, deep water refugia (in grey) are the primary driver of fish distributions, with ice (black fill) preventing lake connectivity. In spring, rapid thawing increases flooding and lake connectivity (lakes with hashed fill) due to the presence of ephemeral connections (dashed connecting lines) - increasing the importance of undirected dispersal. Permanent connections (solid connecting lines) are important for both dispersal and directed migration, because migrants arrive after spring flooding has receded and ephemeral connections disappear. A pulse of fish movement during late summer/early autumn accompanies the migration of species to river or marine overwintering habitat. In early autumn, ephemeral connections have reformed due to precipitation, increasing the importance of undirected dispersal for lake occupancy prior to winter freeze-up.

Appendix

Table A3.1: Model ranking based on Akaike's information criterion adjusted for sample size and overdispersion (QAICc), differences in QAICc (ΔQAICc), model weight, model likelihood, and number of parameters (K) for the single-season model of occupancy for Alaska blackfish in lakes on the Arctic Coastal Plain, Alaska.

Model[a, b]	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight[c]	Model Likelihood	K	Likelihood
psi(R_ DistLake, L_RefArea)	981.27	0.00	0.28	1.00	13	1518.43
psi(L_Connect, R_ DistLake, L_RefArea)	981.76	0.49	0.22	0.78	14	1515.95
psi(R_ DistLake, L_RefArea, L_LakeArea)	983.04	1.77	0.12	0.41	14	1517.98
psi(L_Connect, R_ DistLake, L_RefArea, L_LakeArea)	983.62	2.35	0.09	0.31	15	1515.65
psi(R_ DistLake)	984.27	3.00	0.06	0.22	12	1526.44
psi(R_Grad, R_ DistLake)	985.80	4.53	0.03	0.10	13	1525.62
psi(L_RefArea)	985.91	4.64	0.03	0.10	12	1529.04
psi(R_ DistLake, L_LakeArea)	986.02	4.75	0.03	0.09	13	1525.97
psi(L_Connect, R_ DistLake, L_LakeArea)	986.33	5.06	0.02	0.08	14	1523.22
psi(L_RefArea, R_RefArea)	986.43	5.16	0.02	0.08	13	1526.63
psi(L_Connect, L_RefArea)	986.58	5.31	0.02	0.07	13	1526.86
psi(L_ DistLake, L_Grad, R_Grad, R_ DistLake)	987.37	6.10	0.01	0.05	15	1521.61
psi(L_RefArea, L_LakeArea)	987.82	6.55	0.01	0.04	13	1528.84

[a] See Table 1 for variable definitions.

[b] Detection probability varied by method and was modelled with four site covariates: L_LakeArea, L_RefArea, Day, and Year, where Day was the number of days from the beginning of sampling and Year was binary (representing 2009 or 2010).

[c] Models with weights < 0.01 are not shown.

Table A3.2: Model ranking based on Akaike's information criterion adjusted for sample size (AICc), differences in AICc (ΔAICc), model weight, model likelihood, and number of parameters (K) for the single-season model of occupancy for slimy sculpin in lakes on the Arctic Coastal Plain, Alaska.

Model[a, b]	AIC_c	ΔAIC_c	AIC_c weight[c]	Model Likelihood	K	Likelihood
psi(R_DistCoast)	272.24	0.00	0.13	1.00	12	247.99
psi(R_DistCoast, L_LakeArea)	273.25	1.01	0.08	0.60	13	246.96
psi(R_DistRiv, R_DistCoast)	273.42	1.18	0.07	0.55	13	247.13
psi(R_DistCoast, R_ DistLake)	273.81	1.57	0.06	0.46	13	247.52
psi(.)	273.91	1.67	0.06	0.43	11	251.70
psi(R_DistCoast, L_RefArea)	274.10	1.86	0.05	0.39	13	247.81
psi(L_Connect)	274.10	1.86	0.05	0.39	12	249.85
psi(L_Connect, R_DistRiv, R_DistCoast)	274.13	1.89	0.05	0.39	14	245.80
psi(L_LakeArea)	274.20	1.96	0.05	0.38	12	249.95
psi(R_DistRiv)	274.67	2.43	0.04	0.30	12	250.42
psi(L_RefArea)	274.78	2.54	0.04	0.28	12	250.53
psi(R_DistCoast, R_ DistLake, L_LakeArea)	274.86	2.62	0.04	0.27	14	246.53
psi(R_DistCoast, L_RefArea, L_LakeArea)	275.20	2.96	0.03	0.23	14	246.87
psi(R_RefArea)	275.38	3.14	0.03	0.21	12	251.13
psi(R_ DistLake)	275.43	3.19	0.03	0.20	12	251.18
psi(R_DistCoast, R_ DistLake, L_RefArea)	275.57	3.33	0.02	0.19	14	247.24
psi(L_RefArea, L_LakeArea)	275.58	3.34	0.02	0.19	13	249.29
psi(L_ DistLake)	275.65	3.41	0.02	0.18	12	251.40
psi(R_Grad)	275.67	3.43	0.02	0.18	12	251.42
psi(R_ DistLake, L_LakeArea)	275.74	3.50	0.02	0.17	13	249.45
psi(L_Grad)	275.92	3.68	0.02	0.16	12	251.67
psi(R_ DistLake, L_RefArea)	275.97	3.73	0.02	0.15	13	249.68
psi(L_RefArea, R_RefArea)	276.38	4.14	0.02	0.13	13	250.09

Table A3.2 Continued

psi(R_DistCoast, R_ DistLake, L_RefArea, L_LakeArea)	276.74	4.50	0.01	0.11	15	246.36
psi(R_ DistLake, L_RefArea, L_LakeArea)	276.84	4.60	0.01	0.10	14	248.51

[a] See Table 1 for variable definitions.

[b] Detection probability varied by method and was modelled with four site covariates: L_LakeArea, L_RefArea, Day, and Year, where Day was the number of days from the beginning of sampling and Year was binary (representing 2009 or 2010).

[c] Models with weights < 0.01 are not shown.

Table A3.3: Model ranking based on Akaike's information criterion adjusted for sample size (AICc), differences in AICc (ΔAICc), model weight, model likelihood, and number of parameters (K) for the single-season model of occupancy for least cisco in lakes on the Arctic Coastal Plain, Alaska.

Model[a, b]	AIC_c	ΔAIC_c	AIC_c weight[c]	Model Likelihood	K	Likelihood
psi(L_Connect, R_DistRiver, R_DistCoast, L_RefArea, L_LakeArea)	726.63	0.00	0.26	1.00	14	698.00
psi(L_Connect, R_DistRiver, R_DistCoast, R_Grad, L_RefArea, L_LakeArea)	726.85	0.22	0.23	0.90	15	696.13
psi(L_Connect, R_DistRiver, R_DistCoast, L_LakeArea)	727.8	1.17	0.14	0.56	13	701.26
psi(L_Connect, R_DistRiver, R_DistCoast, R_Grad, L_LakeArea)	728.38	1.75	0.11	0.42	14	699.75
psi(saturated)	728.46	1.83	0.10	0.40	19	689.31
psi(L_Connect, R_DistRiver, R_DistCoast, L_RefArea)	729.35	2.72	0.07	0.26	13	702.81
psi(L_Connect, R_DistRiv, R_DistCoast)	730.40	3.77	0.04	0.15	12	705.93
psi(L_Connect, R_DistRiver, R_DistCoast, R_Grad, L_RefArea)	730.94	4.31	0.03	0.12	14	702.31
psi(L_Connect, R_DistRiver, R_DistCoast, R_Grad)	732.10	5.47	0.02	0.06	13	705.56

[a] See Table 1 for variable definitions.

[b] Detection probability varied by method and was modelled with four site covariates: L_LakeArea, L_RefArea, Day, and Year, where Day was the number of days from the beginning of sampling and Year was binary (representing 2009 or 2010).

[c] Models with weights < 0.01 are not shown.

Table A3.4: Model ranking based on Akaike's information criterion adjusted for sample size (AICc), differences in AICc (ΔAICc), model weight, model likelihood, and number of parameters (K) for the single-season model of occupancy for broad whitefish in lakes on the Arctic Coastal Plain, Alaska.

Model[a, b]	AIC_c	ΔAIC_c	AIC_c weight[c]	Model Likelihood	K	Likelihood
psi(L_Connect, R_DistRiv, R_DistCoast, L_ DistLake, R_RefArea)	318.96	0.00	0.25	1.00	13	292.15
psi(L_Connect, R_DistRiv, R_DistCoast, L_ DistLake, R_RefArea, L_LakeArea)	320.04	1.08	0.14	0.58	14	291.10
psi(L_Connect, R_DistRiv, R_DistCoast, L_ DistLake	320.20	1.24	0.13	0.54	12	295.51
psi(L_Connect, R_DistRiv, R_DistCoast, L_ DistLake, L_LakeArea)	320.54	1.58	0.11	0.45	13	293.73
psi(L_Connect, R_DistRiv, R_DistCoast, R_RefArea)	320.68	1.72	0.10	0.42	12	295.99
psi(L_Connect, R_DistRiv, R_DistCoast)	321.10	2.14	0.08	0.34	11	298.51
psi(L_Connect, R_DistRiv, R_DistCoast, L_LakeArea)	321.82	2.86	0.06	0.24	12	297.13
psi(L_Connect, R_DistRiv, R_DistCoast, R_RefArea, L_LakeArea)	322.14	3.18	0.05	0.20	13	295.33
psi(Saturated)	322.47	3.51	0.04	0.17	18	284.93
psi(L_Connect)	324.65	5.69	0.01	0.06	9	306.25

[a] See Table 1 for variable definitions.

[b] Detection probability varied by method and was modelled with four site covariates: L_LakeArea, L_RefArea, Day, and Year, where Day was the number of days from the beginning of sampling and Year was binary (representing 2009 or 2010).

[c] Models with weights < 0.01 are not shown.

Table A3.5: Model ranking based on Akaike's information criterion adjusted for sample size (AICc), differences in AICc (ΔAICc), model weight, model likelihood, and number of parameters (K) for the single-season model of occupancy for arctic grayling in lakes on the Arctic Coastal Plain, Alaska.

Model[a, b]	AIC_c	ΔAIC_c	AIC_c weight[c]	Model Likelihood	K	Likelihood
psi(L_Connect, R_Grad, L_LakeArea)	177.25	0.00	0.30	1.00	12	152.78
psi(L_Connect)	177.59	0.34	0.25	0.84	10	157.26
psi(L_Connect, L_LakeArea)	179.00	1.75	0.13	0.42	11	156.61
psi(L_Connect, L_RefArea)	179.21	1.96	0.11	0.38	11	156.82
psi(L_Connect, L_RefArea, L_LakeArea)	180.67	3.42	0.05	0.18	12	156.20
psi(L_Connect, R_DistRiv, R_DistCoast)	181.64	4.39	0.03	0.11	12	157.17
psi(R_Grad)	181.90	4.65	0.03	0.10	10	161.57
psi(R_Grad, R_ DistLake)	183.27	6.02	0.01	0.05	11	160.88
psi(R_Grad, L_RefArea)	183.61	6.36	0.01	0.04	11	161.22
psi(R_Grad, L_LakeArea)	183.75	6.50	0.01	0.04	11	161.36

[a] See Table 1 for variable definitions.

[b] Detection probability varied by method and was modelled with four site covariates: L_LakeArea, L_RefArea, Day, and Year, where Day was the number of days from the beginning of sampling and Year was binary (representing 2009 or 2010).

[c] Models with weights < 0.01 are not shown.

Chapter 4: Diet of yellow-billed loons in Arctic lakes during the nesting season inferred from fatty acid analysis

Abstract

Understanding the dietary habits of yellow-billed loons (*Gavia adamsii*) can give important insights into their ecology, particularly for nesting birds. We investigate the diet of yellow-billed loons nesting on the Arctic Coastal Plain using quantitative fatty acid signature analysis (QFASA). Tissue analysis from 26 yellow-billed loons and eleven prey groups (nine fish species and two invertebrate groups) from Arctic lakes suggest that yellow-billed loons are eating high proportions of Alaska blackfish (*Dallia pectoralis*), broad whitefish (*Coregonus nasus*) and three-spined stickleback (*Gasterosteus aculeatus*) during late spring and early summer. The prominence of blackfish in diets highlights the importance of this species' tolerance to winter conditions that permits its widespread availability during the early stages of loon nesting soon after spring thaw. The high proportions of broad whitefish and three-spined stickleback may reflect a residual signal from the coastal staging period prior to establishing nesting territories on lakes, when loons are more likely to encounter these species. Our analyses were sensitive to the choice of calibration coefficient based on data from three different species, indicating the need for development of loon-specific coefficients for future study and confirmation of our results. Regardless, coastally distributed species and species that successfully overwinter in lakes are likely key food items for yellow-billed loons early in the nesting season, before lakes become ice-free and colonized by fish species dispersing from winter refugia outside of the nesting lake.

Introduction

The yellow-billed loon (*Gavia adamsii*) is a large waterbird that winters in the marine coastal waters of North America and Eurasia and nests on Arctic lakes in Alaska, Canada and Russia. Unlike other loon species, such as the common loon (*G. immer*), relatively little is known about the ecology of yellow-billed loons, including diet (North 1994). Food limitation can produce strong bottom-up effects on a population's distribution and abundance (White 1978), and is therefore key in understanding many aspects of a species' ecology including distribution, population dynamics and ecological niche (Wiens and Rottenberry 1979, Sih and Christensen 2001).

The limited information available on the diet of yellow-billed loons is based on a few anecdotal records of stomach contents collected from loons in marine waters. Based on these collections (summarized by North 1994), yellow-billed loons forage on marine fish and invertebrates. Stomach contents from birds collected off the Alaskan coast contained tomcod (*Microgadus proximus*), sculpin species (family Cottidae; Cottam and Knappen 1939), rockfish (likely *Sebastes* sp., Bailey 1922) and a small amount of invertebrate prey (amphipods, isopods, shrimp and crab; Cottam and Knappen 1939). Other diet items included Pacific sanddabs (*Citharichthys sordidus*) from birds near Baja, California (Jehl 1970), and sculpin from birds near Norway (Collett 1894). Stickleback and salmonids were found in a bird in Russia, but it was unclear whether this loon was captured in a marine or freshwater system (Uspenskii 1969, cited in North 1994).

To our knowledge, no published information documents the diet of yellow-billed loons during the nesting season. Yellow-billed loons that are either nesting or rearing chicks (hereafter, breeding loons) require adequate prey to fulfill their reproductive requirements, including defending a territory, brooding eggs, and feeding and caring for chicks. Loons migrate from marine wintering areas to the Chukchi and Beaufort Sea coasts of Alaska in late May/early June and stage in coastal waters until ice on inland freshwater lakes begin to break up. Loons move onto lakes and begin nesting soon after open water is available. During this season, yellow-billed loons forage primarily on their nesting lake (North 1994, North 2008, J.A. Schmutz unpublished data), therefore nesting pairs must select lakes that meet habitat requirements and contain adequate food resources for successful reproduction. The availability of suitable prey is likely a major constraint on the reproductive success for a predator like yellow-billed loons (White 1978), given that loons must meet the extra energetic demands of the breeding season (Barr 1996).

It is difficult to infer diet of yellow-billed loons based on our current understanding of other loon species. The common loon (*G. immer*) forages primarily on fishes and also on a variety of crustaceans and other aquatic animals (Barr 1996). However, common and yellow-billed loon distributions generally do not overlap during breeding season; each species inhabits environments with different available prey, limiting the parallels that can be drawn regarding diet. On the Arctic Coastal Plain, the distribution of yellow-billed loons is sympatric with red-throated (*G. stellata*) and Pacific (*G. pacifica*) loons; however, these two species are much smaller in body size and have different ecological niches. Although diet information for other loon species on the Arctic Coastal Plain is similarly lacking, limited evidence suggests that Pacific loons (which can occasionally nest on the same lakes as yellow-billed loons; Haynes et al. 2014b) may feed prominently on invertebrate prey (reviewed in Russell 2002).

Loons are visual pursuit divers that capture and, most often, consume prey underwater. This behavior makes direct observation of prey taken by adult yellow-billed loons logistically infeasible. Observation of parents feeding their young is also difficult because adults and chicks avoid human presence and are highly mobile on large lakes. Given these limitations, indirect methods provide the most tractable way to estimate loon diet given the infeasibility of collecting the entire animal. Recent advances in molecular methods have made it possible for researchers to investigate the diet of species for which direct observation of feeding or lethal collection of stomach contents is impractical (Barrett et al. 2007). Indirect molecular methods may require capture of individual predators and potential prey for collection of tissue samples, but are generally non-lethal (Dunshea 2009). Here, we estimate the diet of yellow-billed loons breeding on the Arctic Coastal Plain using quantitative fatty acid signature analysis (QFASA; Iverson et al. 2004). QFASA models estimate the proportion of potential prey items in an individual predator's diet using the fatty acid (FA) signatures from the predator and the potential prey tissues, while accounting for FA metabolism by the predator (e.g., Iverson et al. 2004, Beck et al. 2007, Wang et al. 2010, Bromaghin et al. 2013). By estimating the diet of yellow-billed loons, this study provides context for yellow-billed loon breeding ecology, including how the spatial distributions of nesting yellow-billed loons may be influenced by prey distribution on the landscape.

Methods

Prey Tissue Collection

We collected potential prey (fish and invertebrates) at 32 lakes over an area of the Arctic Coastal Plain covering 9,000 km^2 (Figure 4.1) over two summer seasons (2009-2010) using multiple sampling techniques, including fyke nets, minnow traps, gill nets, dip nets and beach seines (see Haynes et al. 2013 for details). We euthanized fish by placing them in about 2 L of lake water with sodium bicarbonate tablets for approximately 10 minutes, and then pithing individuals to ensure they would not revive (Institutional Animal Care and Use Committee permit 149807-2). We wrapped prey in aluminum foil, placed the samples in vacuum pump plastic bags (Ziploc® brand Vacuum Freezer System), and used the vacuum pump to reduce the air volume in the sample bag. We placed samples in a cooler and transported them from the remote field location to a -20 °C freezer (within 24 hr).

Loon tissue collection

We captured 26 loons from 23 lakes for tissue collection (Figure 1). Twenty-two loons were captured with a bow-net (Salyer 1962) while a loon incubated eggs. Four loons during the nesting period were captured with a lift-net (Kenow et al. 2009) set away from the nest. A decoy loon and broadcasted recordings of loon calls lured the loon to the lift-net area. For 19 of these captured loons, we used a local anesthetic, scalpel, and forceps to remove a subcutaneous fat sample near and lateral from the uropygial gland, a common approach for avian species (Owen et al. 2010). The other 7 samples were from loons that underwent a surgery to implant a satellite transmitter (Korschgen et al. 1996). For these 7 loons, a sample of subcutaneous fat was obtained from the abdominal area after the abdominal wall was cut open in preparation for implanting the transmitter. All fat samples were placed in vials containing chloroform, in accordance with Budge et al. (2006), transported to a laboratory, and stored at -80 °C until analysis.

Tissue Preparation

Prey were allowed to partially thaw and homogenized using a Kinematica GmbH tissue homogenizer (Brinkmann Instruments, Switzerland) for small fish (< 250 mm fork length) and a blender with a glass jar (Oster, Sunbeam Products, Boca Raton, FL, USA) for large fish (>250 mm). We did not remove stomach contents of individuals because we aimed to characterize their FA signatures as prey for loons (Budge et al. 2002), which eat fish whole. When an individual's mass was <1 g, prey of the same species from the same lake were homogenized together to form composite samples. We measured out ~1 g of homogenized prey tissue into a glass vial with 4.5 mL of chloroform and stored vials in a -80°C freezer.

FA Analysis

FA methyl esters were prepared using an acidic transesterication (Budge et al. 2006, Wang et al. 2010). Thin layer chromatography indicated the presence of fatty alcohols in diet items resulting from the transesterication of wax esters. Wax ester alcohols were converted to their respective FAs (Budge et al. 2006) to account for wax esters in diets (Budge and Iverson 2003). FA methyl esters were quantified using temperature-programmed gas liquid chromatography on a Varian Autosystem II Capillary FID gas chromatograph fitted with a 30 m £ 0.25 mm id column coated with 50% cyanopropyl-methylpolysiloxane (DB-23) and linked to a computerized integration system (Varian Galaxie software; Iverson et al. 2002). Each chromatogram was manually assessed for correct peak identification.

We analyzed the diet of yellow-billed loons based on fatty acids using a QFASA package in program R (Iverson et al. 2004). We used three sets of calibration coefficients determined from feeding trials of captive common murres (*Uria aalge*; Iverson et al. 2007), spectacled eiders (*Somateria fischeri*) and Steller's eiders (*Polysticta stelleri*; Wang et al. 2010) and used the extended dietary subset of fatty acids, which includes 33 fatty acids that must be acquired through diet and eight fatty acids that can be biosynthesize by predators, but whose levels in predator tissues are influenced by diet (Iverson et al. 2004). We used a prey-on-prey simulation to determine the degree to which each prey species can be identified based on their FA signature (Iverson et al. 2004). If a prey item has a similar FA signature to different prey item types (i.e., different species), then QFASA will incorrectly or unpredictably assign dietary proportions of those prey species in the predator's diet. The prey-on-prey analysis is an iterative process (in our case, performed 100 times; Wang et al. 2010), whereas the prey data are randomly split into two sets for each prey item type – a set that acts as the prey data and a set that is modeled as the predator data without calibration coefficients (Iverson et al. 2004). Because calibration coefficients are not used, the FA signature of the prey item subset used as the predator diet should most closely reflect the subset of the same prey item type. With overlap in the FA signatures of prey items, the prey-on-prey analysis can reveal the prey item types among which QFASA has difficulty discriminating. Because prey samples require splitting to run the simulation, we removed prey item types that had sample sizes that were too low (N < 3 samples) to create useful splits.

Results

We collected samples from eleven fish species: Alaska blackfish (*Dallia pectoralis*), arctic flounder (*Liopsetta glacialis*), arctic grayling (*Thymallus arcticus*), broad whitefish (*Coregonus nasus*), burbot (*Lota lota*), least cisco (*Coregonus sardinella*), ninespine stickleback (*Pungitius pungitius*), northern pike (*Esox lucius*), rainbow smelt (*Osmerus mordax*), slimy sculpin (*Cottus cognatus*), and three-spined stickleback (*Gasterosteus aculeatus*). We also collected samples from two invertebrate orders: amphipods (order Amphipoda) and fairy shrimp (order Anostraca; Table 4.1).

FA Analysis

We removed burbot ($N = 2$ samples) and northern pike ($N = 1$ sample) from the prey-on-prey simulations due to low sample size. Prey-on-prey simulation results suggested that the FA signatures of prey items could be reasonably well classified with QFASA (mean classification accuracy ± SD = 85 ± 17 %). However, classification accuracy was low for least cisco (mean ± SD = 61 ± 20%) and slimy sculpin (mean ± SD = 65 ± 9%; Table 4.2, Figure A4.1). The low classification accuracy for these two species suggests that the QFASA model had difficulty discriminating least cisco and slimy sculpin from other diet items with similar FA signatures.

Results differed substantially between models using the calibration coefficients from common murres as compared to either eider species, which were similar to each other (Meynier et al. 2010, Budge et al. 2012; Figure 4.2). Specifically, diet estimates that used the common murre calibration coefficients differed substantially from models using the eider species coefficients. Ideally, we would have used calibration coefficients specific to yellow-billed loons but loon-specific coefficients do not exist. Because species-specific coefficients require captive feeding studies to generate (Iverson et al. 2004, 2007), limited availability of species-specific calibration coefficients is common. Given this, we chose the common murre calibration coefficient model to interpret results because of evolutionary and ecological similarities - loons are more taxonomically related to murres than eiders and both yellow-billed loons and murres are piscivores.

The estimate of diet based on fatty acid analysis included 129 prey samples from the 13 prey types (mean ± SD = 9.9 ± 6.3 samples per type). The model that used the common murre calibration coefficients estimated that Alaska blackfish, broad whitefish and three-spined stickleback made up the majority of the yellow-billed loon diet (Figure 4.2), although analysis indicated variation among individuals (Table 4.3). Yellow-billed loons show high diversity in diet at a sample population level, but much less diversity at an individual level. The diet patterns of individual loons showed many individuals fed primarily on a single species such as Alaska blackfish or broad whitefish.

Discussion

Based on the FA model that used the common murre calibration coefficients, the most prominent prey items in yellow-billed loon diet were Alaska blackfish, three-spined stickleback, and broad whitefish. Alaska blackfish is one of the most common freshwater species on the Arctic Coastal Plain, occupying about 75% of lakes > 7 ha in surface area (Haynes et al. 2014a). Also, blackfish are tolerant to harsh overwintering conditions (Scholander et al. 1953) and persist over winter months (Haynes et al. 2014a). Thus, blackfish are likely available at the beginning of the season when other species are either still moving into summering lakes (e.g., least cisco) or recovering from winter die-offs (e.g., ninespine stickleback; Haynes et al. 2014a). Although blackfish are generally not locally abundant, their availability soon after breakup may make them an important food source during the early stages of breeding for yellow-billed loons, when other prey species are less available. The sensitivity of our analysis to calibration coefficients used indicates the need for loon-specific calibration coefficients for future study and confirmation of our results.

We initially found it surprising that broad whitefish and three-spined stickleback were dominant prey items given they are not very common in lakes on the Arctic Coastal Plain; broad whitefish have a relatively low occupancy probability in lakes (found in about a third of lakes large enough for breeding yellow-billed loons), and three-spined stickleback have a distribution restricted to brackish lakes and coastal waters, with an extremely low occupancy probability further inland (Craig 1984, Haynes et al. 2014a). However, because we collected tissues from yellow-billed loons two to four weeks after they first arrived on the breeding lakes, the dominance of broad whitefish and three-spined stickleback in the diet may reflect a residual signal in the loon tissue from marine or brackish waters before they moved inland to choose nest sites. During spring, before ice cover has melted and inland lakes are available for nesting, loons may feed along the Chukchi coast or on coastal brackish lakes and ponds. Both broad whitefish and three-spined stickleback inhabit coastal waters, are likely found in lakes closer to the coastline (Haynes at el. 2014a), and are likely present in estuarine or brackish pond habitat occupied by staging loons prior to breeding (Craig 1984, Reist and Bond 1988). When lakes have thawed to the point that they are accessible to loons (when a ring of unfrozen water forms around the lake perimeter; North 1994) loons will migrate from staging areas to breeding lakes, behaviorally establish ownership of a lake, and commence mating and nest-building. Because of the gradual turnover of tissues (Wang et al. 2010), the FA signature during this late staging period in coastal areas may persist in fat samples gathered a few weeks later during mid-incubation.

We were also surprised that ninespine stickleback and least cisco were not important prey items based on the FA diet estimates. Ninespine stickleback is the most widespread fish species in the region (94% lake occupancy rate, Haynes et al. 2014a) and yellow-billed loons have been noted to feed stickleback to their young (J.A. Schmutz, unpublished data). However, during spring freshet, shortly after breakup, ninespine stickleback may be less available to loons compared to later in the season. During early spring, ninespine stickleback may have restricted distributions due to winter die-off, be more dispersed because of increased movement into flooded waterways, and less abundant early in the season because the first cohort of young-of-the-year stickleback is not present (Haynes et al. 2014a).

Least cisco is the most widely distributed large-bodied fish species in the region (occupancy probability > 50% of lakes greater than 7 ha; Haynes et al. 2014a) and are abundant in various size classes. Despite its apparent suitability as a prey item, least cisco were only important for two individual loons (Table 4.3). Least cisco had the highest misclassification rate based on the prey-on-prey simulations, so it is possible that the proportion of least cisco in yellow-billed loon diet may be underestimated. Alternatively, a low prevalence in diet may again be explained by the timing of the loon sampling. Early in the season, least cisco are migrating from overwintering habitat to summer feeding lakes (Haynes et al. 2014a) and thus likely have not arrived en masse before we sampled the loon tissues. Because of their high energy content (Ball et al. 2007) and high occupancy probability and abundance in lakes after June, we expect that least cisco plays a more important role in diet of breeding loons later in the season.

Individual specialization in populations of generalists is common and is often related to the sex or age of the individual (e.g., Bolnick et al. 2003, Woo et al. 2008, Bromaghin et al. 2013). For yellow-billed loons, this apparent specialization may actually reflect prey occupancy or availability at the breeding or staging site. For example, if yellow-billed loons nest on a lake with only Alaska blackfish in high availability, these breeders would be required to specialize on blackfish. Loons in lakes with a diversity of prey items available may be less likely to specialize but there may also be some benefits of specialization such as an increase in foraging efficiency (e.g., Watanuki 1992).

We found that a strong understanding of the prey ecology is important when investigating the diet of a predator. Knowledge of seasonal and spatial variation in both loon (Schmutz et al. 2014) and fish distributions (Haynes et al. 2014b) was key for interpretation of diet estimates. This information allowed us not only to determine what species are important, but also why they are important. Alaska blackfish may not be as abundant or calorie rich as other fish prey throughout the season; however, its widespread distribution in spring is likely what makes it a main prey item for loons arriving on lakes. Broad whitefish and three-spined stickleback are geographically restricted and have a low occupancy; however, these species are likely targeted in coastal staging areas before lake territories are formed. This finding highlights that understanding diet not only requires dietary models, but also an understanding of prey ecology and distributional patterns.

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Table 4.1: Prey samples collected from lakes on the Arctic Coastal Plain for dietary study of yellow-billed loons.

Common Name	Scientific Name	Abbreviation	Sample Size
Alaska Blackfish	*Dallia pectoralis*	ALBL	20
Arctic Flounder	*Liopsetta glacialis*	ARFL	5
Arctic Grayling	*Thymallus arcticus*	ARGR	15
Broad Whitefish	*Coregonus nasus*	BRWH	5
Burbot	*Lota lota*	BURB	2
Least Cisco	*Coregonus sardinella*	LECI	17
Ninespine Stickleback	*Pungitius pungitius*	NIST	15
Northern Pike	*Esox lucius*	NOPI	1
Rainbow Smelt	*Osmerus mordax*	RASM	14
Slimy Sculpin	*Cottus cognatus*	SLSC	7
Three-spined Stickleback	*Gasterosteus aculeatus*	THST	3
Amphipods	Order Amphipoda	AMPH	20
Fairy Shrimp	Order Anostraca	FAIR	5

Table 4.2: Results from prey-on-prey simulations using Quantitative Fatty Acid Statistical Analysis methods. The prey-on-prey analysis is an iterative process (performed 100 times in our case), where the prey data are randomly split into two sets for each prey type – a set that acts as the prey data and a set that is modeled as the predator data without calibration coefficients (Iverson et al. 2004). The simulation output can be used to determine how well QFASA can distinguish among prey item types based on how well QFASA correctly classifies the FA signatures of each prey type. The diagonal of the table represent the probability of correctly classifying a species.

Species*	ALBL	AMPH	ARFL	ARGR	BRWH	FAIR	LECI	NIST	RASM	SLSC	THST
ALBL	85.7	0.1	0.7	1.8	3.4	2.1	1.6	1.4	2.7	0.3	0.2
AMPH	0.2	81.7	1.9	0.1	2.9	9.1	0.0	0.1	0.6	3.4	0.0
ARFL	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
ARGR	0.3	0.3	0.0	82.6	0.7	4.0	7.1	0.8	1.7	2.3	0.0
BRWH	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0
FAIR	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0
LECI	6.7	0.2	0.0	9.6	0.6	1.3	60.6	1.1	19.9	0.1	0.0
NIST	6.4	1.9	0.4	2.2	1.1	2.9	1.3	79.1	1.7	2.9	0.1
RASM	0.1	0.3	0.3	0.1	0.1	0.3	4.6	0.3	93.7	0.2	0.2
SLSC	3.2	8.9	2.7	3.1	1.6	8.4	0.0	2.7	4.2	64.9	0.2
THST	0.1	0.3	1.9	0.0	1.3	0.1	0.1	0.0	8.8	0.1	87.3

*ALBL – Alaska blackfish (*Dallia pectoralis*), AMPH – amphipod species, ARFL – Arctic flounder (*Liopsetta glacialis*), ARGR – Arctic grayling (*Thymallus arcticus*), BRWH – broad whitefish (*C. nasus*), FAIR – fairy shrimp species, LECI – least cisco (*Coregonus sardinella*), NIST – ninespine stickleback (*Pungitius pungitius),* RASM – rainbow smelt (*Osmerus mordax*), SLSC – slimy sculpin (*Cottus cognatus*), and THST – three-spined stickleback (*Gasterosteus aculeatus*).

Table 4.3: Diet estimates of individual yellow-billed loons based on a quantitative fatty acid statistical analysis using calibration coefficients from common murres (Iverson 2007).

	Prey Species[*]												
Loon	ALBL	AMPH	ARFL	ARGR	BRWH	BURB	FAIR	LECI	NIST	NOPI	RASM	SLSC	THST
1	0.03	0.00	0.00	0.00	0.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.38
2	0.00	0.29	0.00	0.00	0.39	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.30
3	0.53	0.07	0.02	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16
4	0.40	0.17	0.02	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09
5	0.00	0.00	0.01	0.35	0.03	0.00	0.20	0.38	0.04	0.00	0.00	0.00	0.00
6	0.00	0.01	0.00	0.34	0.10	0.00	0.32	0.00	0.00	0.00	0.00	0.23	0.00
7	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.77	0.00	0.00	0.12	0.00	0.00
8	0.00	0.00	0.00	0.28	0.00	0.00	0.19	0.00	0.41	0.00	0.00	0.00	0.12
9	0.59	0.36	0.00	0.00	0.02	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
10	0.50	0.00	0.00	0.00	0.00	0.08	0.00	0.03	0.13	0.19	0.03	0.00	0.04
11	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33
12	0.40	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.52	0.03	0.00	0.03
13	0.14	0.07	0.00	0.00	0.65	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15
14	0.00	0.00	0.00	0.00	0.78	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22
15	0.36	0.22	0.01	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27
16	0.72	0.08	0.00	0.05	0.10	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00
17	0.34	0.00	0.00	0.04	0.07	0.00	0.01	0.00	0.32	0.00	0.00	0.07	0.15
18	0.47	0.00	0.00	0.00	0.05	0.16	0.00	0.00	0.07	0.00	0.24	0.00	0.00
19	0.37	0.00	0.03	0.00	0.04	0.00	0.00	0.00	0.00	0.38	0.12	0.00	0.06
20	0.41	0.08	0.05	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.29
21	0.00	0.00	0.09	0.00	0.02	0.19	0.13	0.00	0.25	0.00	0.00	0.31	0.00
22	0.19	0.33	0.01	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18
23	0.00	0.00	0.00	0.00	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.62
24	0.68	0.08	0.03	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.14
25	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
26	0.38	0.07	0.00	0.00	0.46	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00

[*] ALBL – Alaska blackfish (*Dallia pectoralis*), AMPH – amphipod species, ARFL – Arctic flounder (*Liopsetta glacialis*), ARGR – Arctic grayling (*Thymallus arcticus*), BRWH – broad whitefish (*C. nasus*), BURB – burbot (*Lota lota*), FAIR – fairy shrimp species, LECI – least cisco (*Coregonus sardinella*), NIST – ninespine stickleback (*Pungitius pungitius),* NOPI – northern pike (*Esox lucius*), RASM – rainbow smelt (*Osmerus mordax*), SLSC – slimy sculpin (*Cottus cognatus*), and THST – three-spined stickleback (*Gasterosteus aculeatus*).

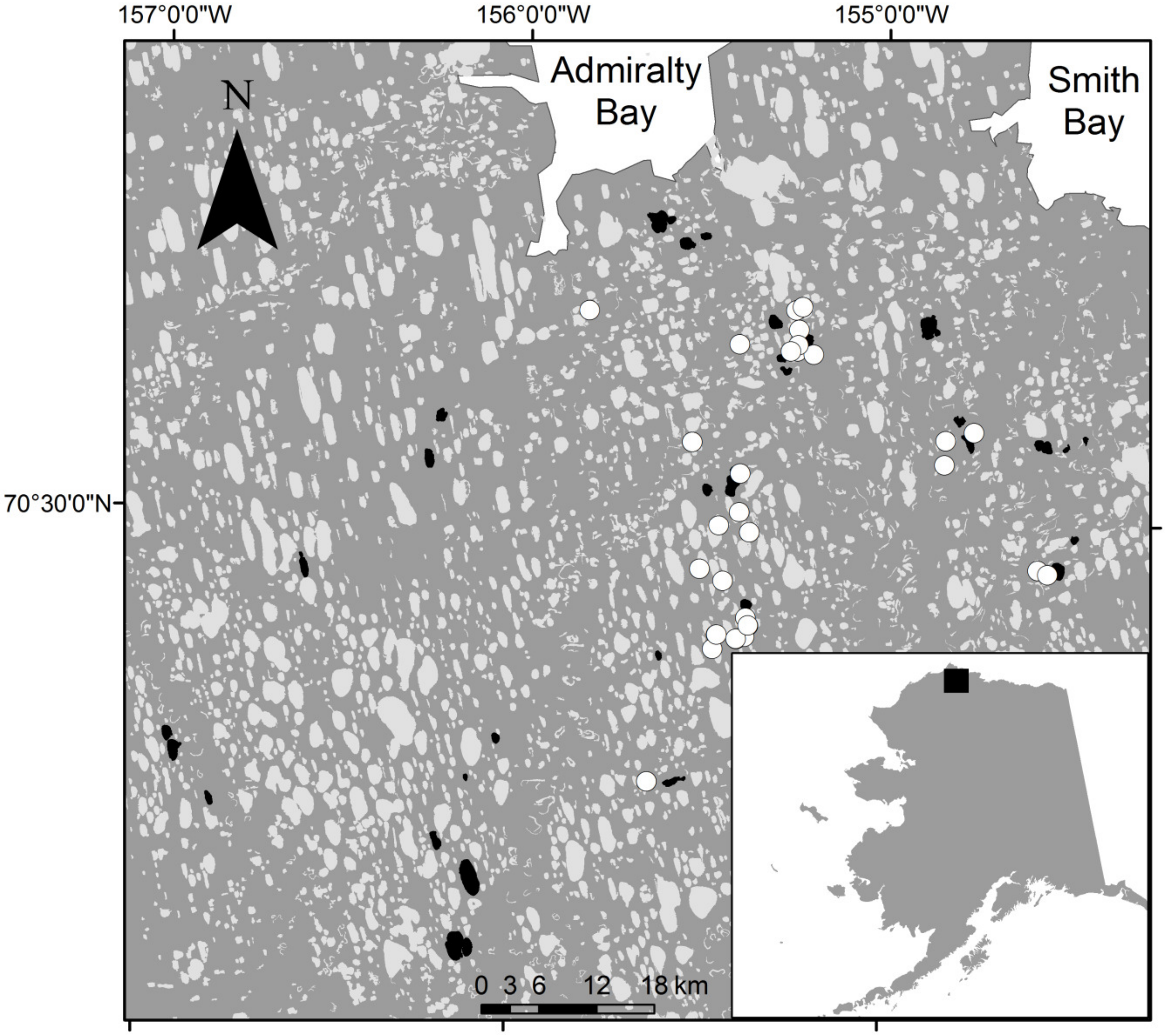


Figure 4.1: Locations where yellow-billed loons were captured for tissue sampling (white circles) and lakes sampled for prey (black polygons) on the Arctic Coastal Plain. Inset shows the study region (black square) relative to the state of Alaska.

Fig 4.2 - Panel A

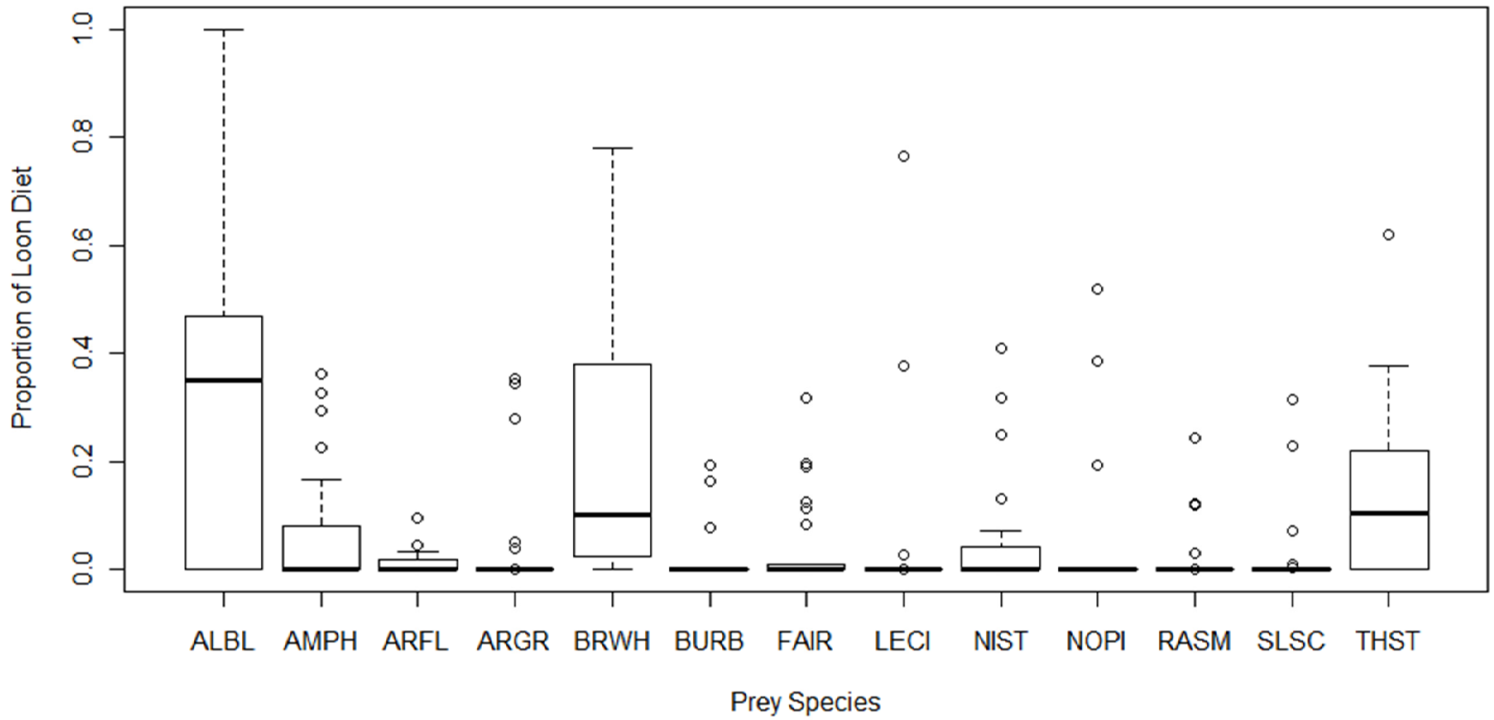


Fig 4.2 - Panel B

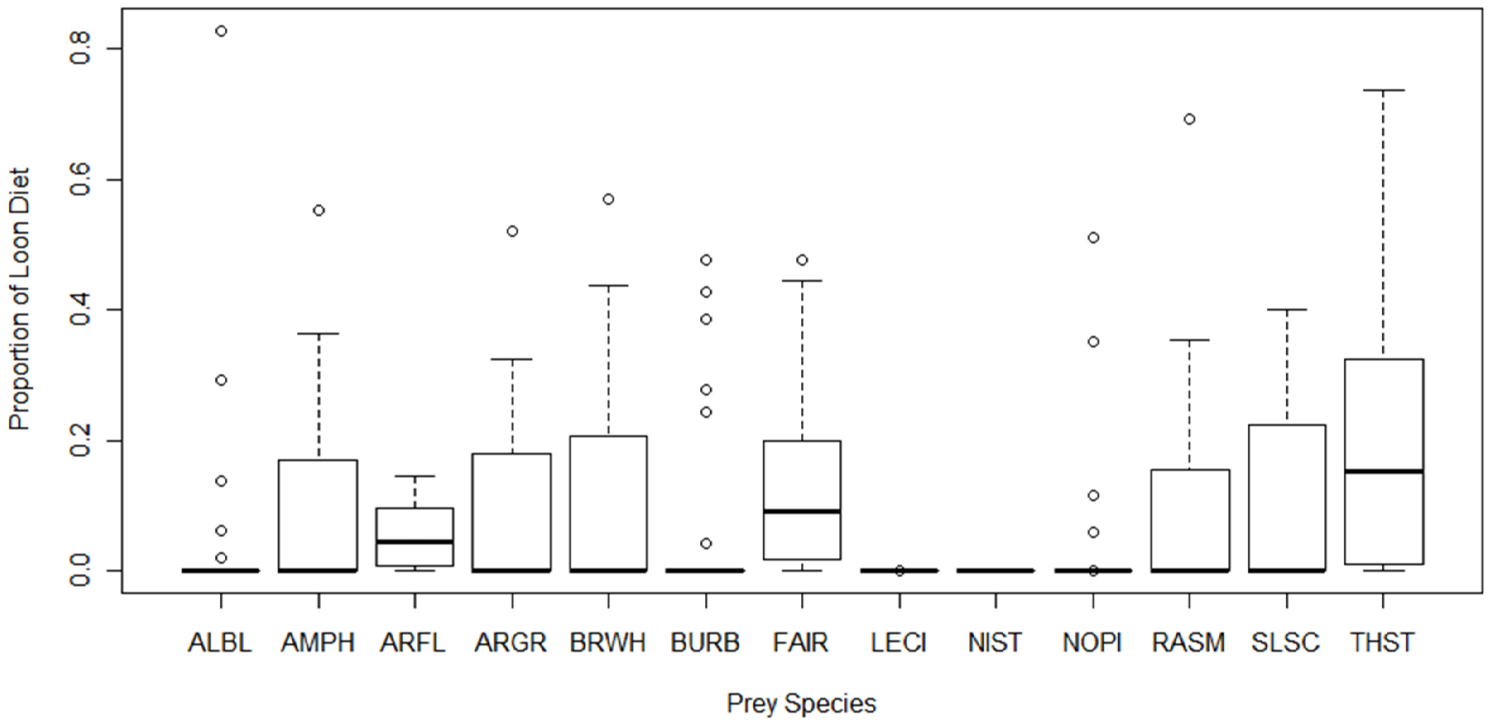


Fig 4.2 - Panel C

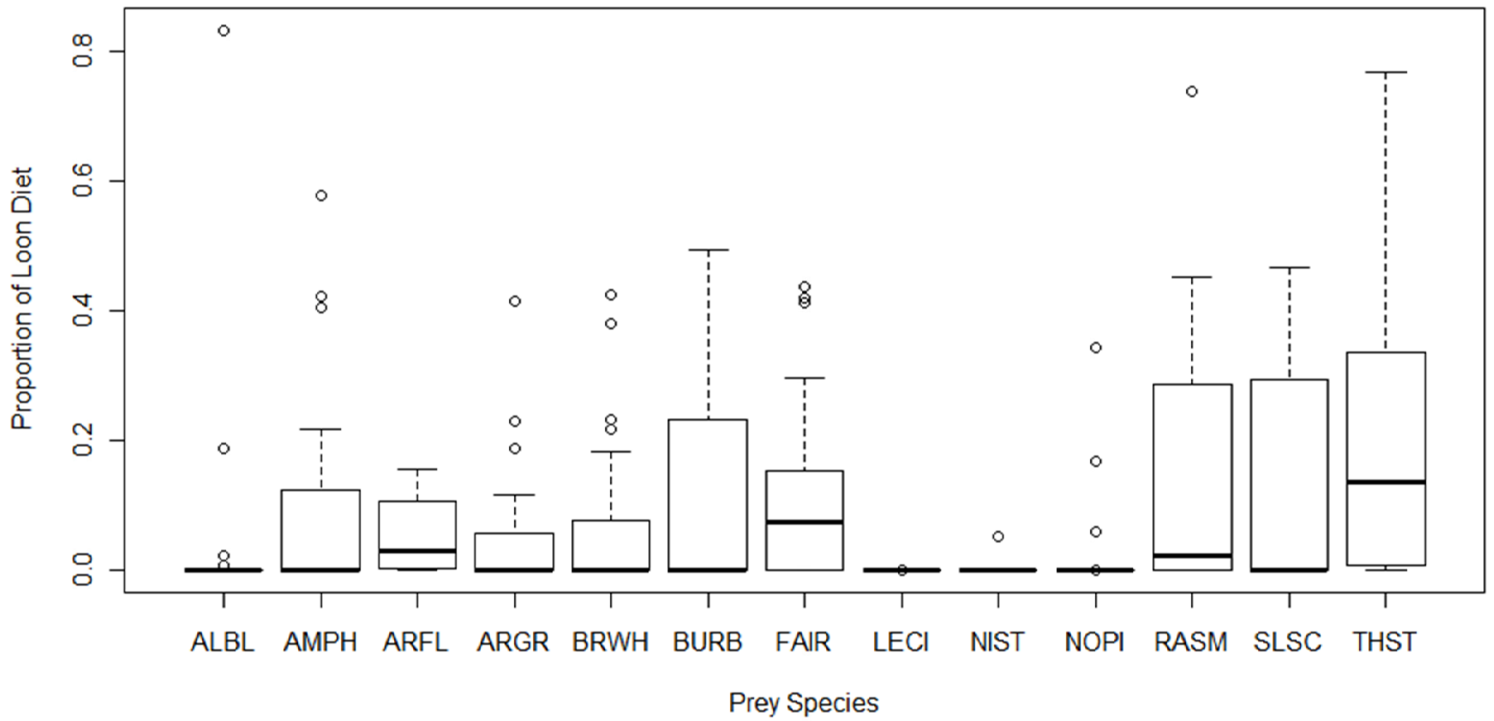
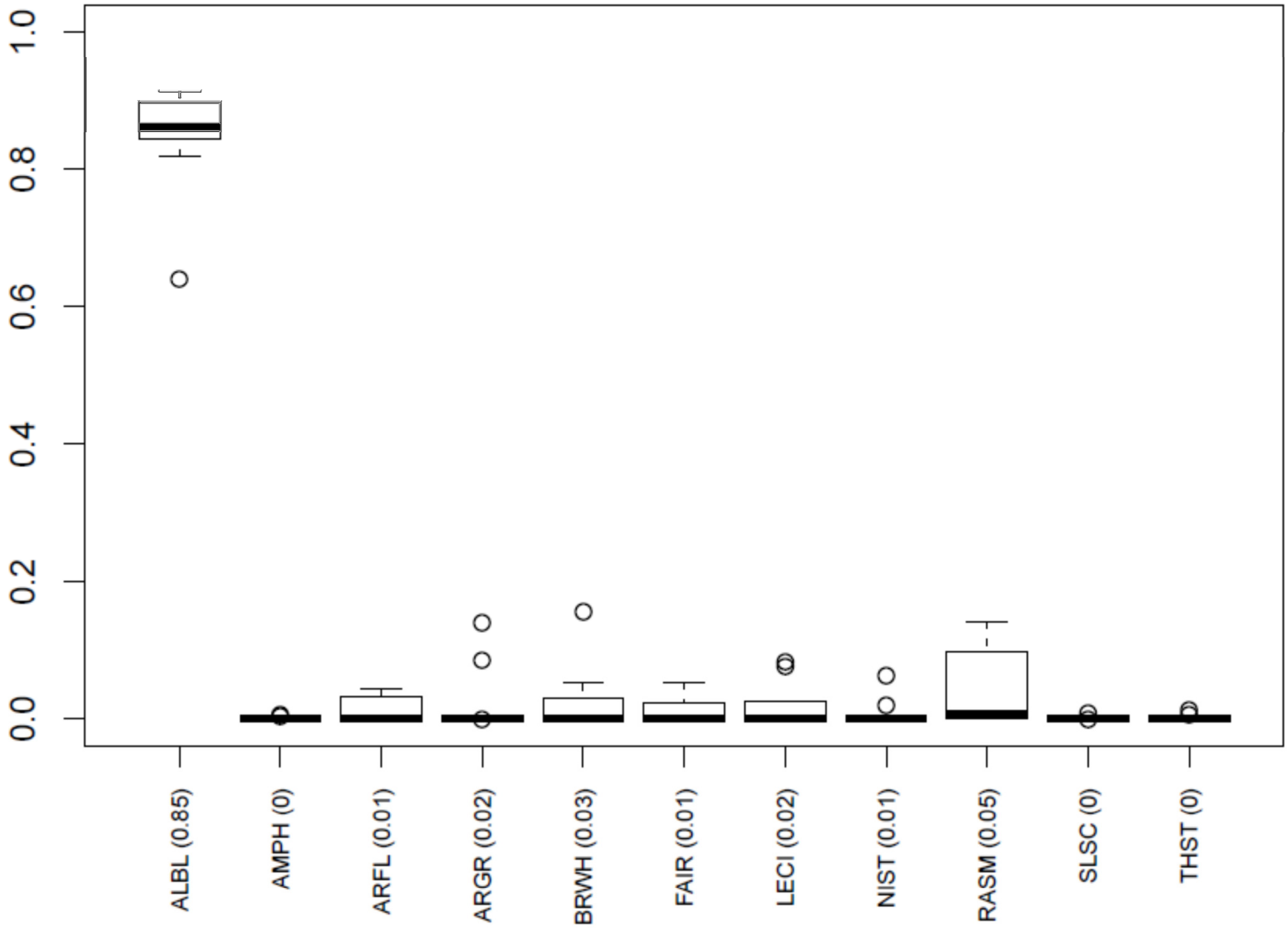
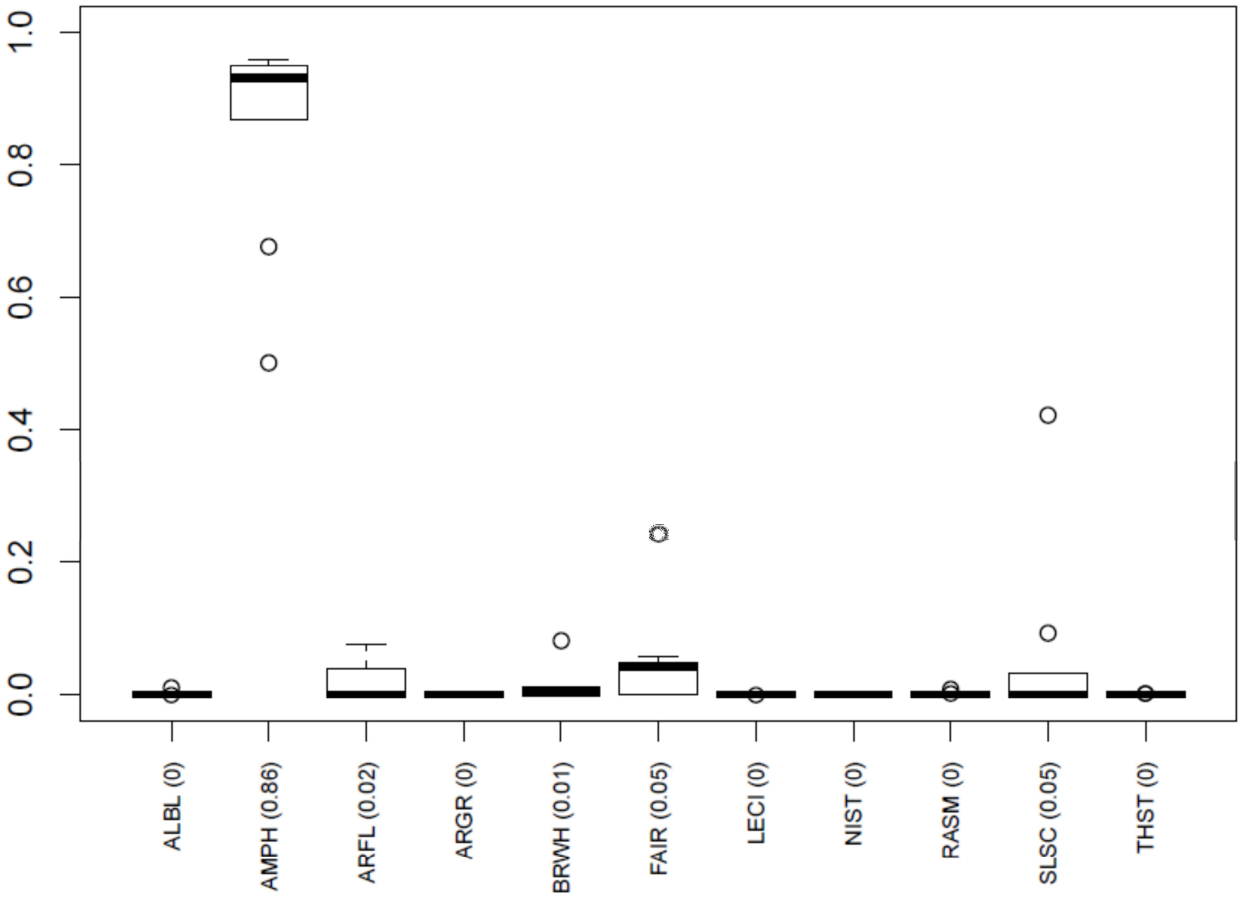


Figure 4.2: Mean diet estimate of 26 yellow-billed loons from the Arctic Coastal Plain, Alaska, based on fatty acid analysis of loon and prey tissues using common murre (Panel A), Steller’s eider (Panel B) and spectacled eider (Panel C) calibration coefficients. Boxes represent first and third quartiles around the mean (thick black line), whiskers represent the range (the interquartile range multiplied by 1.5) and the dots represent outliers (falling outside the range). Estimates of the proportions of 13 prey items (sources) in the loon diet were derived using a quantitative fatty acid signature analysis (QFASA; Iverson et al. 2004). See Table 1 for species abbreviations.

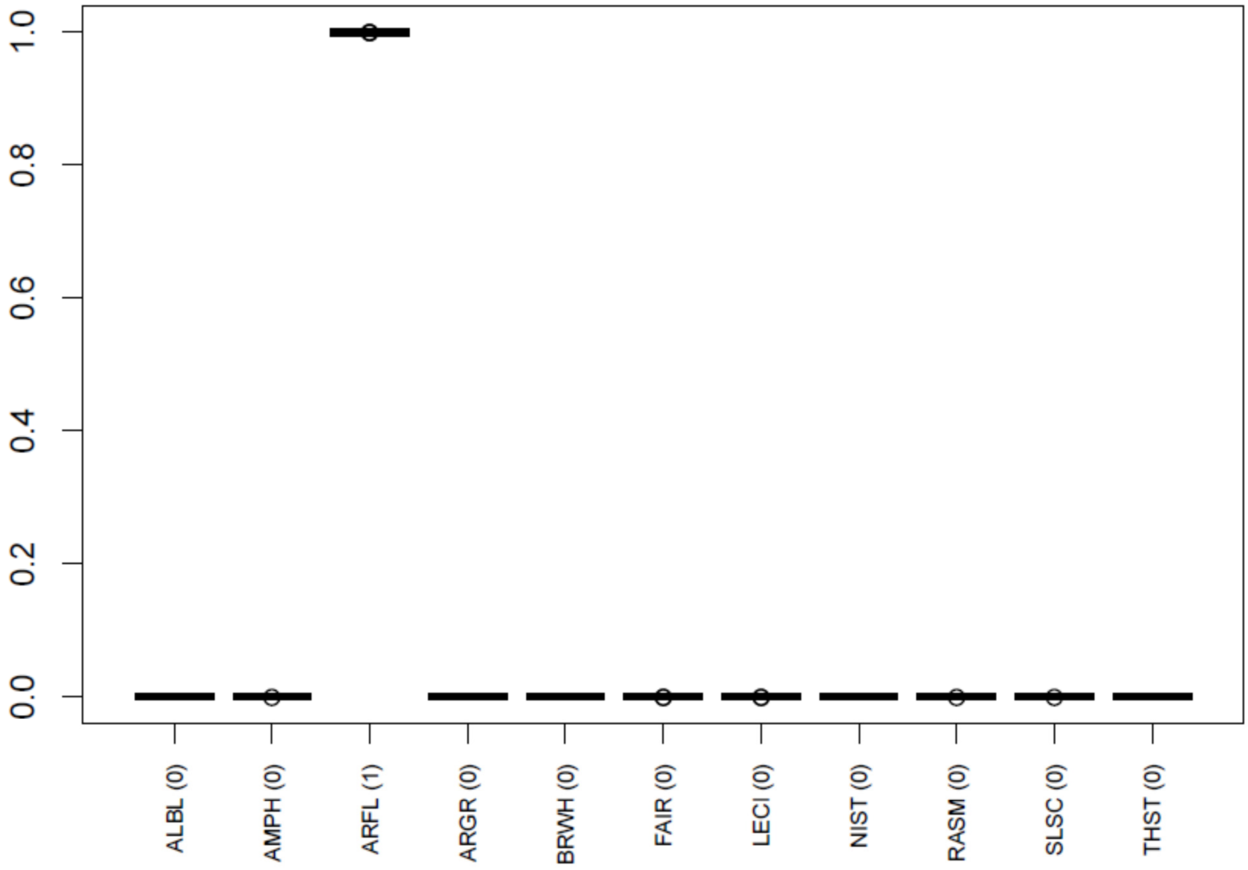
Appendix Figure A4.1a - Alaska Blackfish (ALBL)



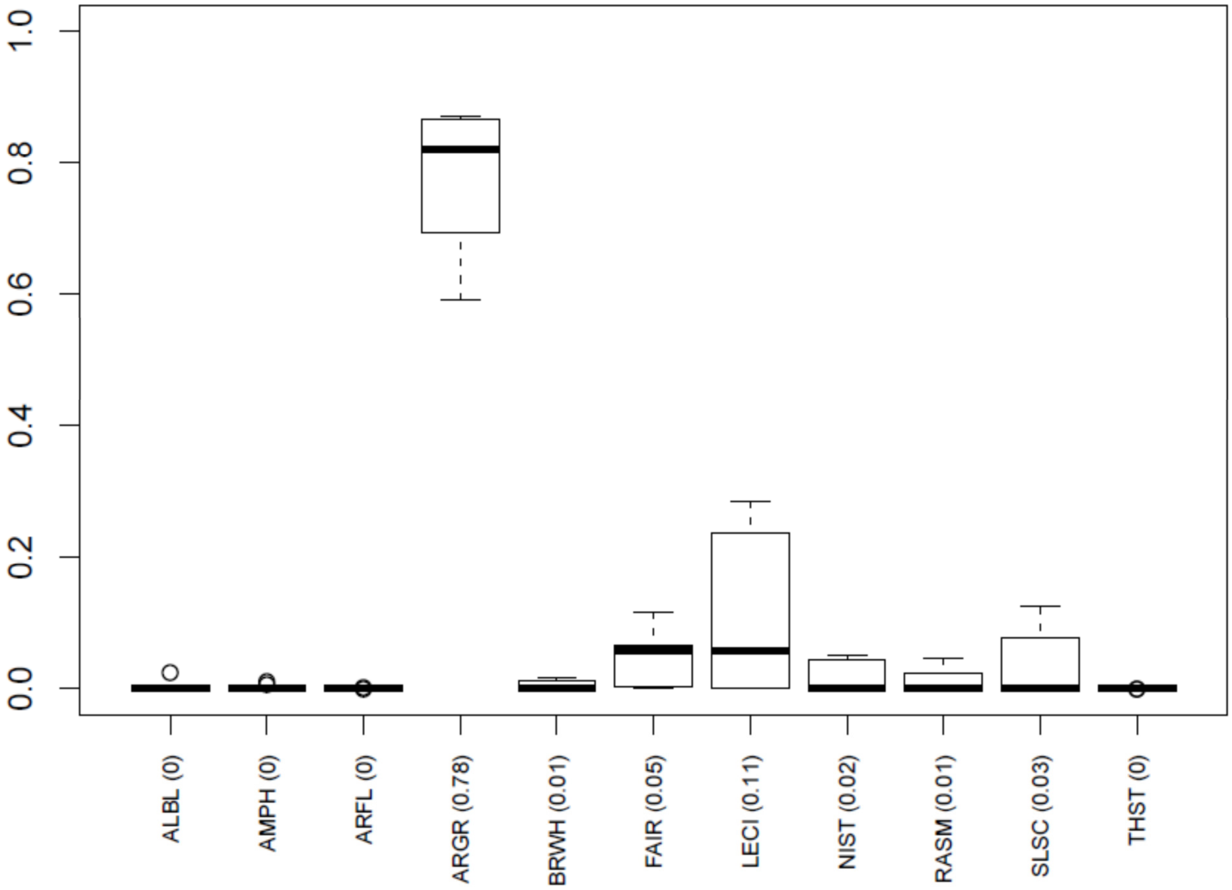
Appendix Figure A4.1b - Amphipod (AMPH)



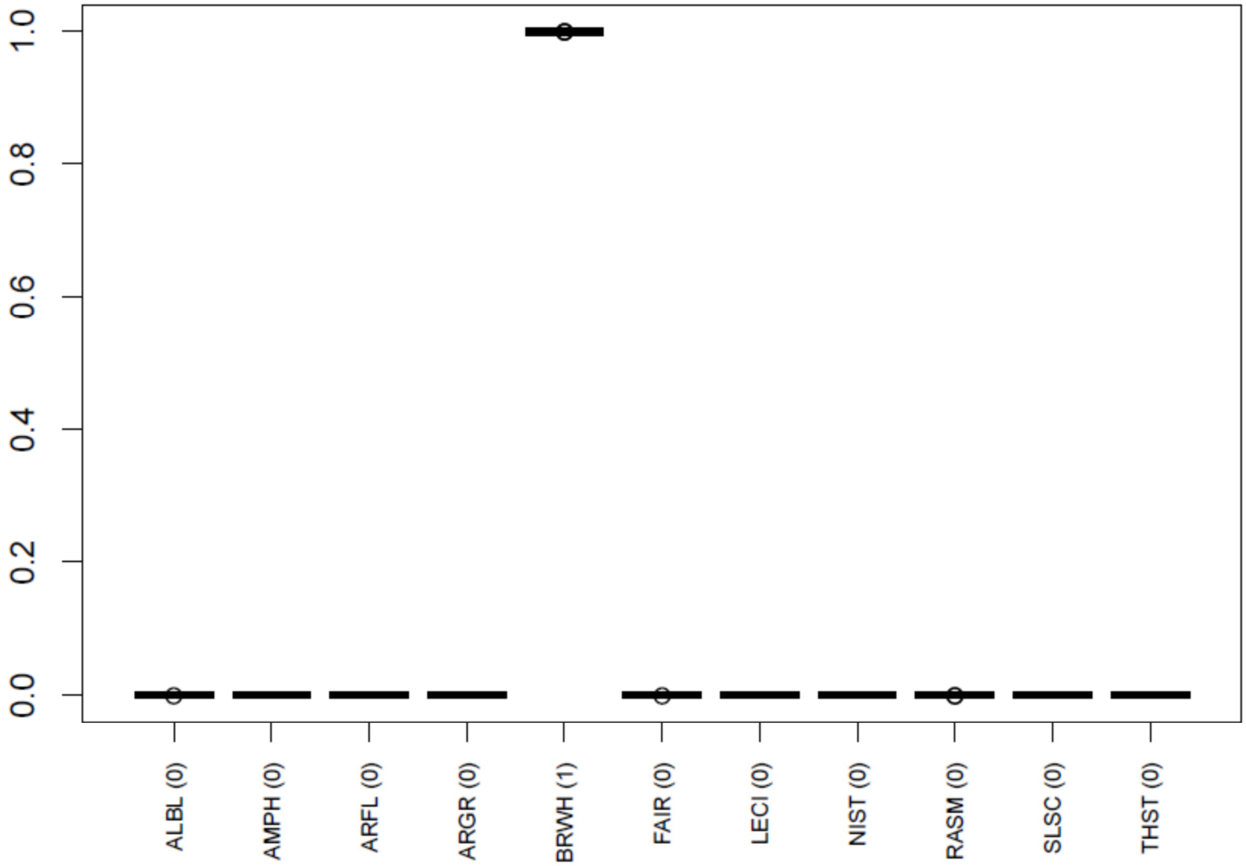
Appendix Figure A4.1c - Arctic Flounder (ARFL)



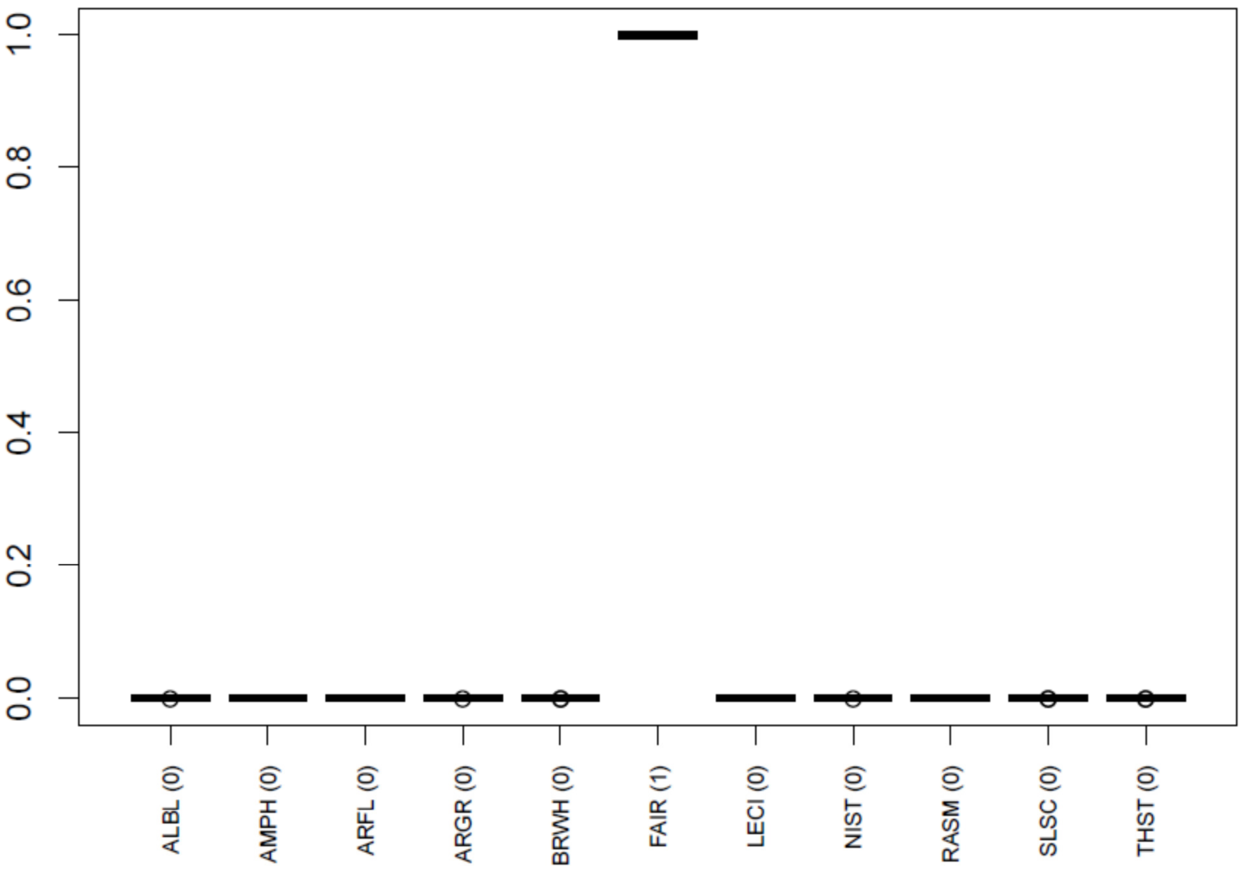
Appendix Figure A4.1d - Arctic Grayling (ARGR)



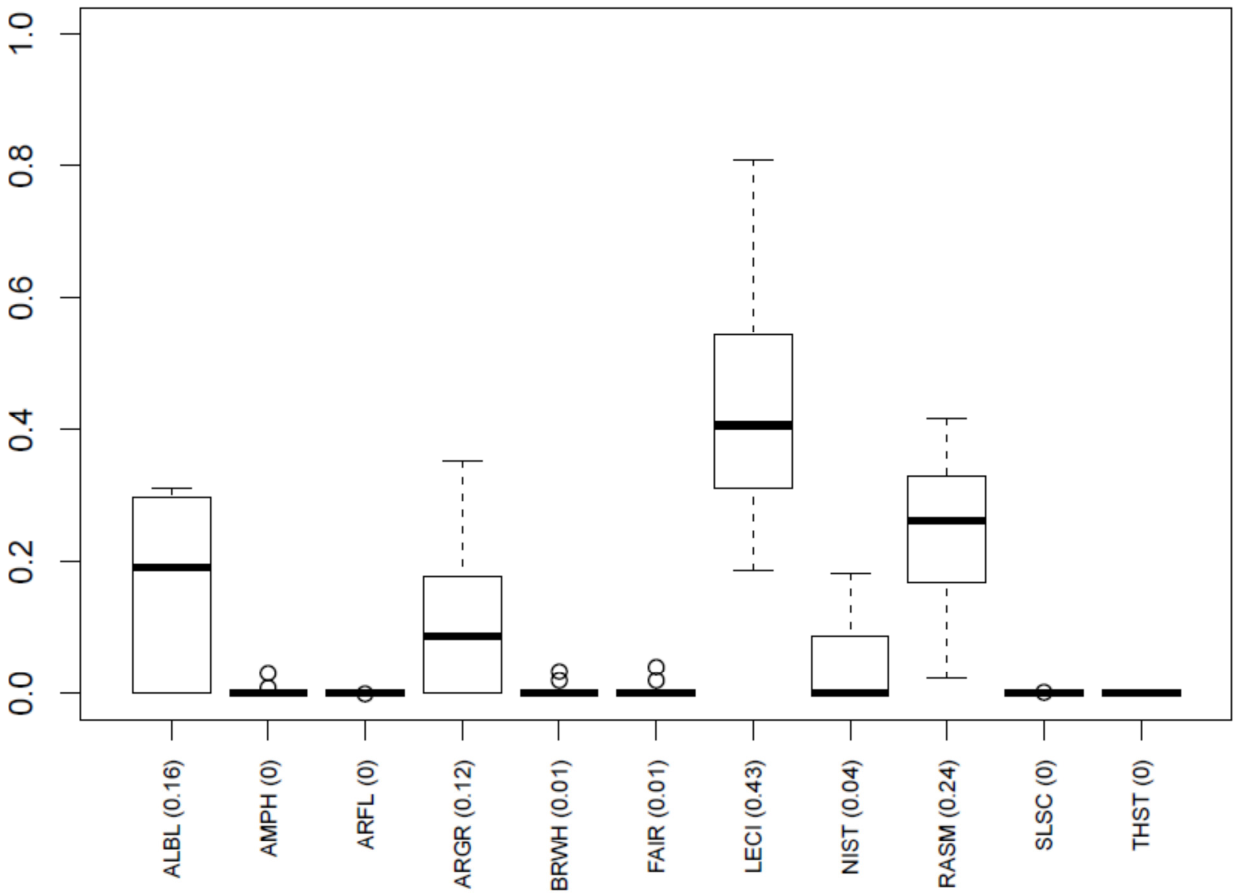
Appendix Figure A4.1e - Broad Whitefish (BRWH)



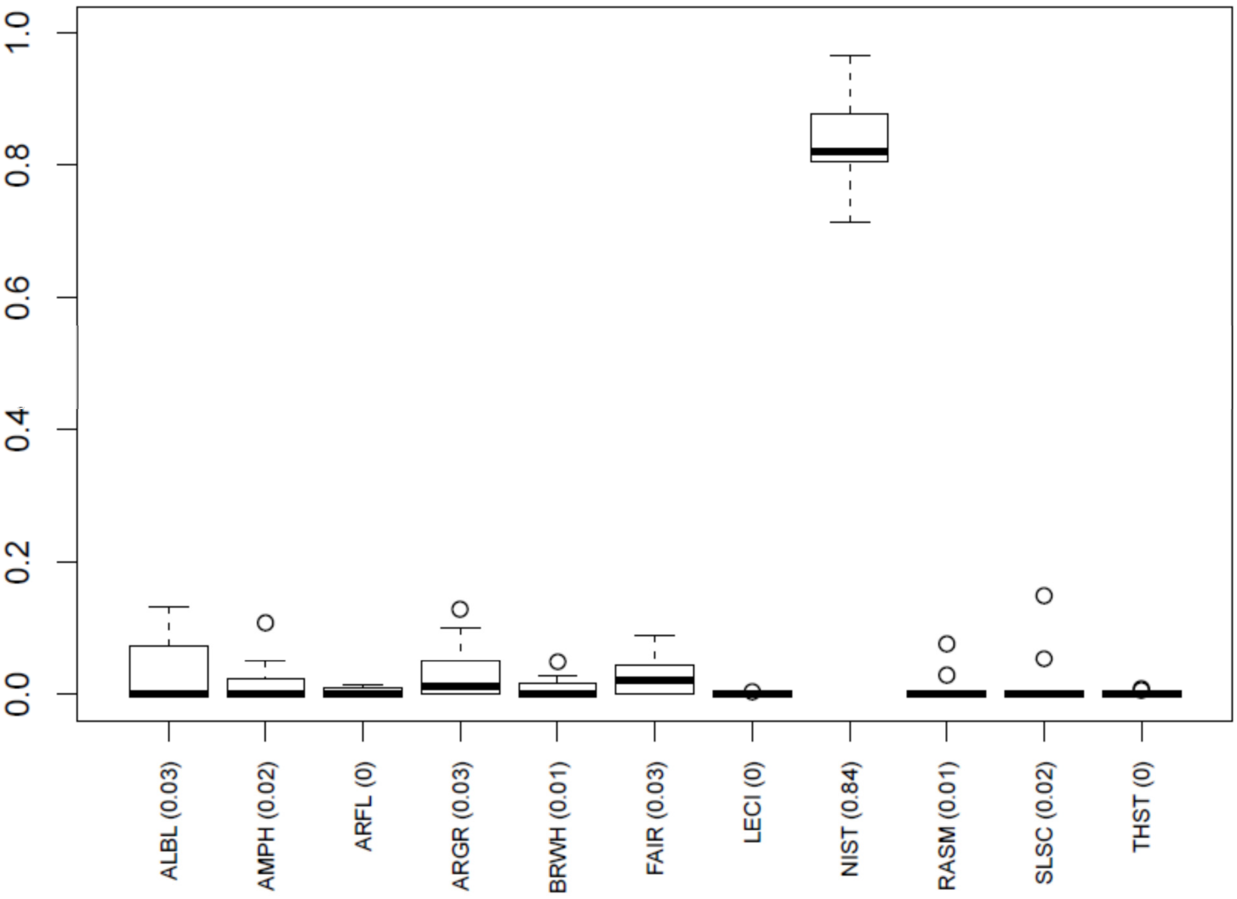
Appendix Figure A4.1f - Fairy Shrimp (FAIR)



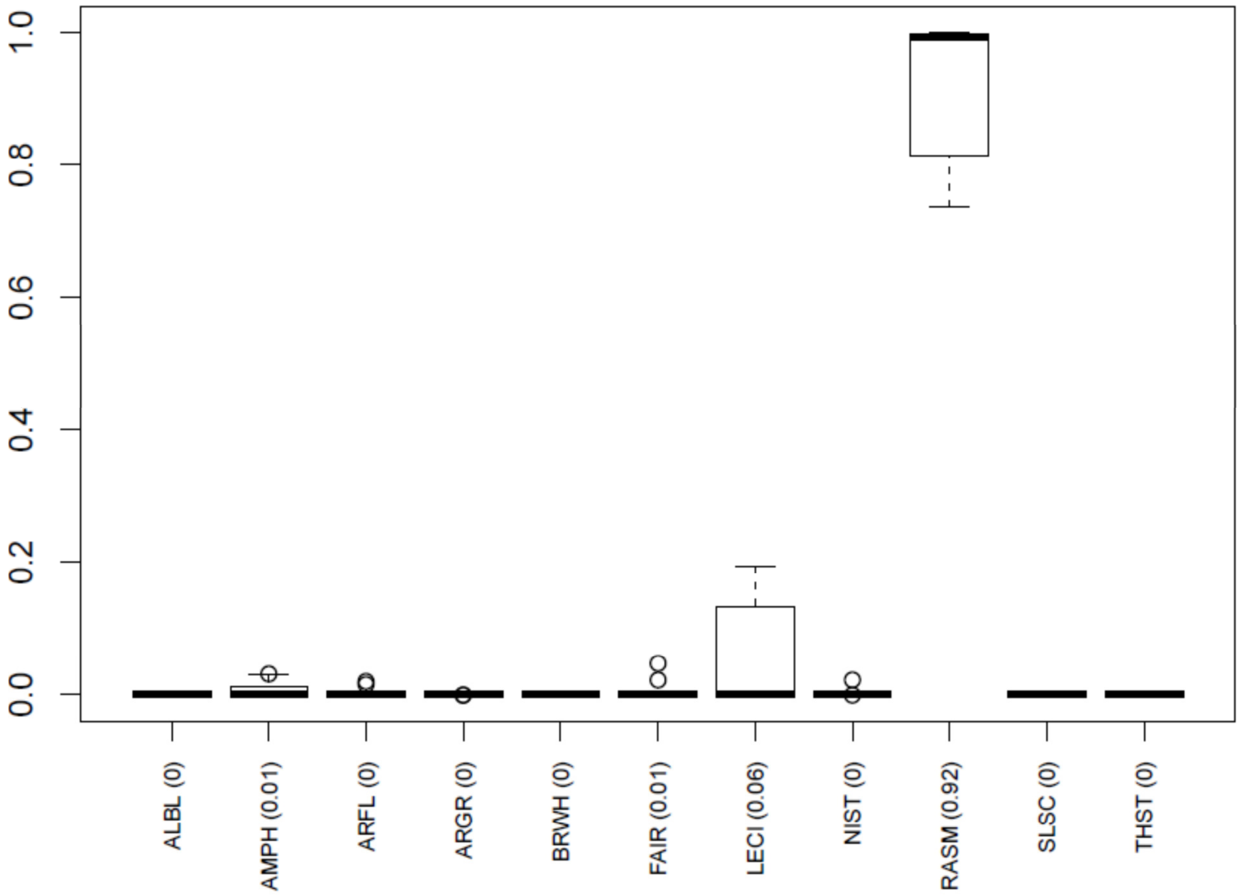
Appendix Figure A4.1g - Least Cisco (LECI)



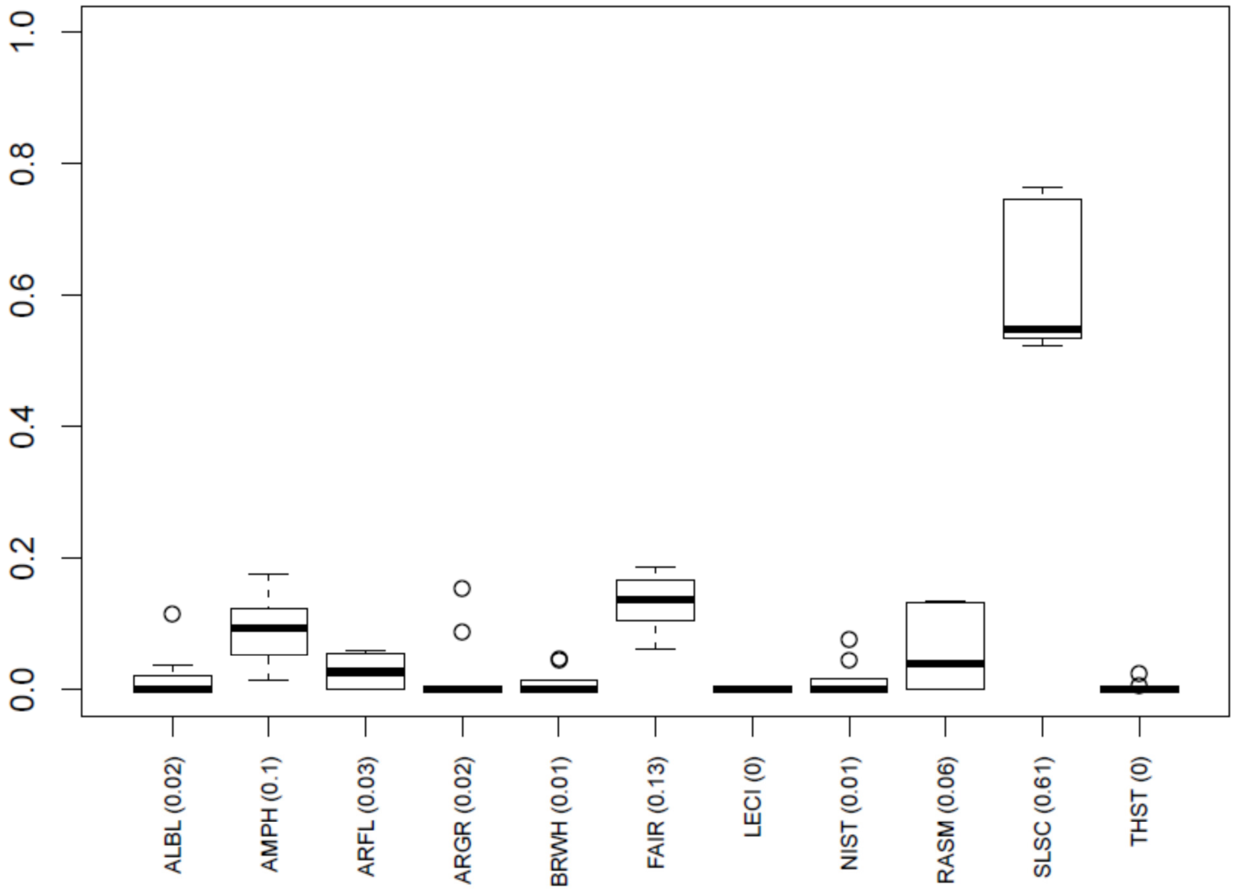
Appendix Figure A4.1h - Ninespine Stickleback (NIST)



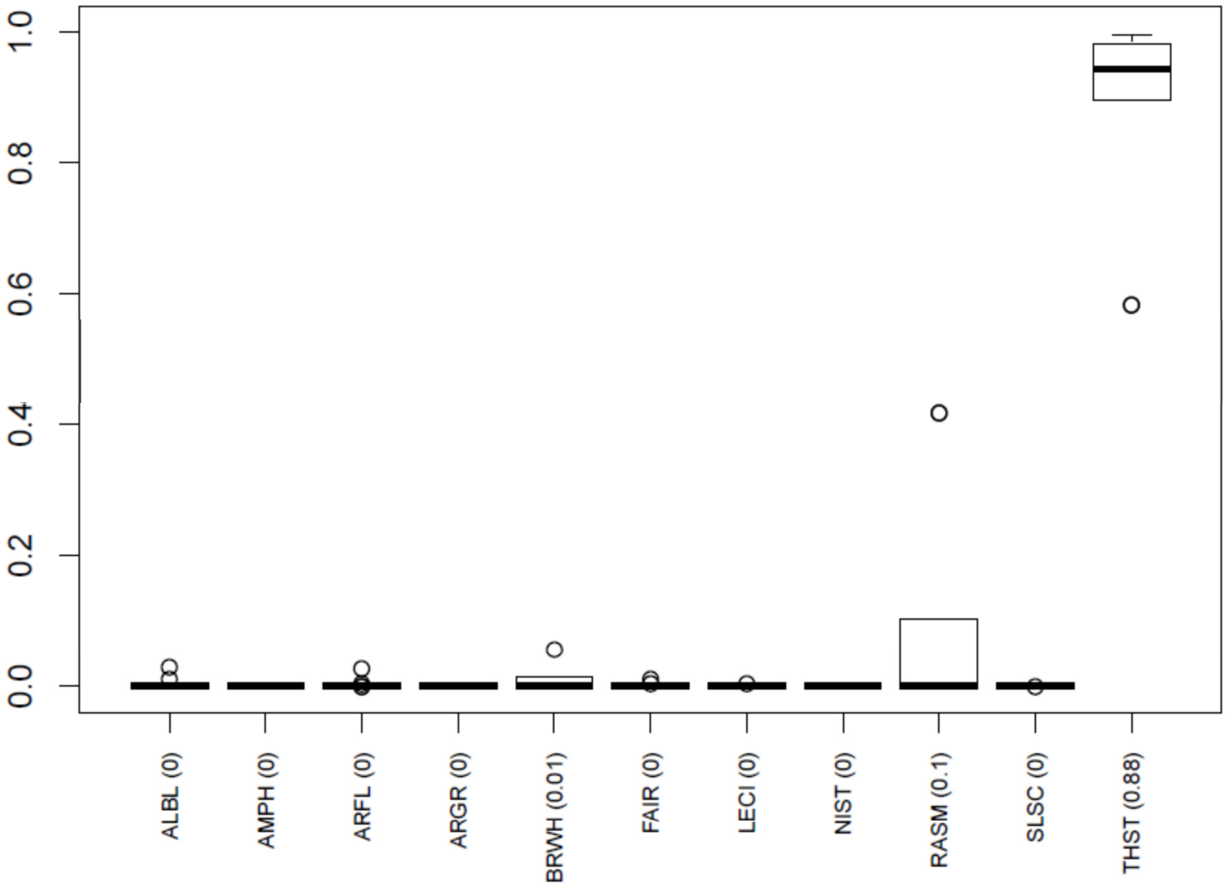
Appendix Figure A4.1i - Rainbow Smelt (RASM)



Appendix Figure A4.1j - Slimy Sculpin (SLSC)



Appendix Figure A4.1k - Threes-spined Stickleback (THST)



Appendix Figure A4.1: Results from prey-on-prey simulations using Quantitative Fatty Acid Statistical Analysis methods. The prey-on-prey analysis is an iterative process (in our case performed 100 times) where the prey data are randomly split into two sets for each prey type – a set that acts as the prey data and a set that is modeled as the predator data without calibration coefficients (Iverson et al. 2004). The simulation output can be used to determine how well QFASA can distinguish among prey item types based on how well QFASA correctly classifies the FA signatures of each prey type. Prey codes include: ALBL – Alaska blackfish (*Dallia pectoralis*), AMPH – amphipod species, ARFL – Arctic flounder (*Liopsetta glacialis*), ARGR – Arctic grayling (*Thymallus arcticus*), BRWH – broad whitefish (*C. nasus*), FAIR – fairy shrimp species, LECI – least cisco (*Coregonus sardinella*), NIST – ninespine stickleback (*Pungitius pungitius*), RASM – rainbow smelt (*Osmerus mordax*), SLSC – slimy sculpin (*Cottus cognatus*), and THST – three-spined stickleback (*Gasterosteus aculeatus*).

Chapter 5: Occupancy of nesting yellow-billed loons: evidence of habitat saturation and a stable breeding population?

Abstract

Yellow-billed loons (*Gavia adamsii*), a recent candidate for listing under the U.S. Endangered Species Act, have some of its highest known nesting densities on the Arctic Coastal Plain. The breeding dynamics of this population segment is relevant to the overall conservation of the species. We investigate the occupancy dynamics of nesting yellow-billed loons (late June) and yellow-billed loon chicks (late August) in lakes greater than 7 hectares from four years of data collected over a period of nine years for nests and seven years for chicks. We examined how environmental drivers affected loon distribution on ACP lakes and hypothesized the importance of fish prey availability. Yellow-billed loons exhibited a relatively low nesting lake occupancy over the years examined (2003-2011), ranging from 20-29%. Occupancy was relatively stable to increasing, with an average annual rate of change in occupancy (λ) among years estimated to be 1.06 ± 0.08 (mean ± SE). For lakes with nesting loons, local extinction (probability of an occupied lake becoming unoccupied in the subsequent year) and colonization probabilities (probability of an unoccupied lake becoming occupied in the subsequent year) were also relatively stable, suggesting that the nesting population is at or near equilibrium. Stable to increasing nest occupancy was accompanied by a decrease in the annualized rate of chick occupancy ($\lambda_{\text{chick 2005-2008}} = 0.988 \pm 0.194$, $\lambda_{\text{chick 2008-2009}} = 0.836 \pm 0.235$, $\lambda_{\text{chick 2009-2011}} = 0.784 \pm 0.100$). The increase in nesting occupancy may have intensified intraspecific competition, which, in turn, may have negatively influenced chick production over time. The occupancy probability of least cisco, a potential prey item, corresponded with an increased probability of colonization of unoccupied lakes. We confirm that lake size and lake depth were not only positively associated with nesting occupancy but also related to chick production. The largest lakes had occupancy probabilities near one for nesting and chicks; however the saturation point (when occupancy approaches 1) for nest occupancy occurred at smaller lake sizes than for chick occupancy. This disparity between saturation points for nesting and chicks, together with apparent population equilibrium and the relative rarity of large lakes, suggests high quality habitat for yellow-billed loons may be near saturation and limiting population size.

Introduction

Identifying ecological relationships and dynamic processes that affect a species distribution provides a basis for species management into the future (Young and Hutto 2002, MacKenzie et al. 2006). Species distributions can be related to environmental features to characterize mechanistic species-environment relationships (Hochachka et al. 2007), which, in turn, can be used to manage activities that could impact the species (e.g., land use or harvest practices). Such information is particularly useful for species of conservation concern or species with poorly described distributions.

The yellow-billed loon (*Gavia adamsii*) is the rarest and least studied of the five loon species (North 1994). Yellow-billed loons breed on Arctic lakes in the low-lying tundra regions of Canada, Russia and Alaska. In early spring, loons migrate from marine wintering areas to Arctic breeding regions. Shortly after lake ice recedes, breeding loons move from coastal staging areas to nesting lakes, while the majority of non-breeding loons arrive on the breeding grounds after nest initiation by breeders (Earnst et al. 2005, Schmutz et al. 2014). Upon arrival at the breeding lake, loon pairs establish territories and commence nesting activities. Yellow-billed loons are highly territorial and defend their nesting lake from smaller loon species and conspecifics (Sjölander and Ǻgren 1976, North 1994, Haynes et al. 2014c).

About 6,000 yellow-billed loons occur in Alaska during the summer, greater than 70% of which occur within the National Petroleum Reserve on the Arctic Coastal Plain (hereafter "ACP", Earnst et al. 2005). Breeding yellow-billed loons on the ACP (< 1,000 pairs, Earnst et al. 2005) occur in relatively low densities across a large landscape, with some of the highest densities in areas available for oil and gas development (U.S. Fish and Wildlife Service 2009). Potential conflict with development on the breeding grounds, along with concerns about effects of climate change, overfishing, pollution, and subsistence harvest and bycatch in its wintering range, prompted a petition to list the yellow-billed loon as a threatened or endangered species under the U.S. Endangered Species Act (Center for Biological Diversity 2004).

Given that the ACP is vast, remote, and difficult to survey, species distribution models have potential to describe lake-scale spatial distribution and temporal trends of yellow-billed loons. Two studies (Stehn et al. 2005, Earnst et al. 2006) have provided information on the habitat use of yellow-billed loons on the ACP, both finding that yellow-billed loons prefer large, deep, and hydrologically connected lakes with complex shorelines and emergent vegetation. These studies also reported a lower probability of loons on lakes occupied by Pacific loons (*G. pacifica*), most likely due to exclusion of Pacific loons by larger yellow-billed loons (Haynes et al. 2014b). Additionally, Stehn et al. (2005) found that yellow-billed loons were less likely to be found on lakes with relatively higher elevation or lakes surrounded by upland-tundra landcover. Although these studies have identified important landscape features corresponding with the distribution of yellow-billed loons, models were based entirely on remotely sensed data, did not discriminate between non-breeding and breeding loons (i.e., loons establishing territories, nesting, and rearing chicks) and included only a single breeding season.

In this study, we investigate the occupancy dynamics (changes in occupancy over time) of yellow-billed loons with discontinuous data collected over 9 years. We examine the habitat use of nesting loons and successful breeders (i.e., loons that produce chicks) with the goal of identifying influences on their distribution. Measures of prey were likely one of the most important missing variables in past models (Earnst et al. 2006). We therefore build on previous efforts by incorporating prey occupancy dynamics (Haynes et al. 2014a) into loon occupancy models. We predict that, based on an expected spatial concordance between avian predators and their prey (Fauchald 2009), the distribution of prey species will influence yellow-billed loon occupancy. Also, in contrast with previous work, we focus entirely on nesting loons and loon chicks in a region with some of the highest known densities – a population segment that is important for loon conservation. We define breeding loons (breeders) as loons that attempted to nest in late June/early July. Many non-breeders occur on the ACP (Stehn et al. 2013), most of which may be younger individuals (3-5 year olds), assuming a similar ecology to the closely related common loon (*G. immer*; Evers et al. 2010). Nesting birds likely have stronger habitat associations compared with non-breeders because they are more spatially restricted (Campioni et al. 2010), and habitat associations for nesting loons should be relatively static because they remain on the lake throughout the nesting season (Schmutz et al. 2014). By examining nesting and chick occupancy over multiple seasons, we can better understand the temporal dynamics of occupancy at lake territories and can estimate occupancy vital rates such as local extinction (the probability an occupied lake is unoccupied in the subsequent season) and colonization (the probability that an unoccupied lake becomes occupied in the subsequent season) (Hammond et al. 2012), production of chicks, and the annual rate of change in occupancy for the nests and chicks. Also, by examining nesting and chick occupancy, we can begin to understand habitat use in relation to fitness, and can thus gauge habitat quality (VanHorne 1981). Our results provide insight into the processes that govern these patterns and offer a broader understanding of yellow-billed loon occupancy dynamics, including dynamics of population growth and how it may be linked to habitat.

Methods

The ACP is a 98,200 km^2 region of low relief tundra across the entire northern coast of Alaska, of which 61,681 km^2 have been surveyed annually by aircraft since 1985. Stehn et al. (2005) used an objective analysis of these long-term transect data and categorized the distribution of yellow-billed loons into two density strata – a high density stratum of 20,546 km^2 and a lower density stratum of 41,135 km^2. We then randomly selected 16 7 x 7 km plots within the high density stratum, with the constraint that no plots fell within 2 km of another plot. Our study area is bounded to the south by the Brooks Mountain Range and bounded longitudinally by the Meade and Ikpikpuk Rivers (Figure 5.1). This low relief landscape is dominated by shallow lakes, (Arp and Jones 2009) and, depending on lake depth, lake volumes can freeze partially or entirely during the winter months (1.5-2.0 m over a winter season, Jefferies et al. 1996, Arp et al. 2011).

The sampling focused on two breeding stages: early spring nesting and late summer brood rearing. Lakes were sampled for yellow-billed loon nests from late June to early July by ground or aerial surveys over four seasons: 2003/2004, 2009, 2010 and 2011. The 2003/2004 survey data were from Stehn et al. (2005), and we treated these data as one season due to no between-season replication. Lakes were surveyed for yellow-billed loon chicks using aerial surveys in late August (all sampling occurred between 23-Aug and 1-Sep) in 2005, 2008, 2009 and 2011. For all years except 2008, a subset of lakes was surveyed within 16 plots measuring 7 × 7 km (342 lakes available) randomly distributed within the study region (Stehn et al. 2005). In 2008, lakes were sampled from 6 × 6 km plots randomly placed across our study area, with some spatial overlap with the other years. Within each plot, we surveyed every lake > 7 ha in surface area, omitting smaller lakes because yellow-billed loons tend to select larger lakes for nesting (Earnst et al. 2006). For both nest and chick surveys, crews conducted repeat sampling within the same season over a short time span in a subset of lakes (generally less than 48 hrs). Nest surveys at the lakes were replicated either with two aerial surveys, one aerial and one ground survey, or two aerial and one ground survey (Haynes et al. 2014c), while chick surveys were replicated with two aerial surveys.

Loon specific aerial surveys were conducted in a Cessna 206 (2003/2004, 2008, 2009) or a Kodiak (2011) amphibious fixed-wing plane with two observers (left side pilot and right side passenger). The plane circled shorelines to locate loons on the water and loon nests on shore, and for larger lakes, flew transects across the lake (Stehn et al. 2005). Loons sitting immobile on land were considered to be nesting, even if a nest scrape or eggs were not evident. Loons on the water were recorded but not used in analysis. All observations were made by US Fish and Wildlife Service pilots and biologists with a decade or more of experience conducting aerial surveys for birds on the ACP (Larned et al. 2006, Mallek et al. 2007).

We conducted ground surveys for nests in late June to early July in 2009 (82 lakes), 2010 (136 lakes), and 2011 (145 lakes; Haynes et al. 2014c). Observers accessed plots with an amphibious fixed-wing plane or a helicopter and accessed lakes within a plot on foot. One or two observers surveyed for nests by walking the perimeter of each lake, about 1 m from the water's edge (about the mean distance of a loon nest from the water, Haynes et al. 2014b). In the case of two observers, each walked a portion of the lake with no overlap such that the whole lakeshore was surveyed, including islands. Nest locations were recorded on GPS units and loon species associated with the nest by identifying adults or from species-specific egg size (Bowman 2008).

We used an occupancy modeling approach (MacKenzie et al. 2002, 2006) to examine factors affecting nesting loon or chick distribution and provide estimates of the probability of lake occupancy, local extinction, colonization, and rate of change in occupancy between seasons (colonization divided by extinction). Given that yellow-billed loons are not detected perfectly during surveys (Stehn et al. 2005, Haynes et al. 2014c), we also modeled detection probability (the probability of detecting loon nests or chicks with a single survey, given a lake is occupied) to avoid underestimation of occupancy and bias in colonization and extinction estimates (MacKenzie et al. 2003). We considered a lake occupied by nesting loons if it contained one pair of loons defending a territory with an active nest, and we considered a lake occupied by chicks if at least one loon chick was present.

Because incomplete site coverage among years resulted in missing survey data, we used different subsets of data to conduct three analyses related to loon breeding occupancy: 1) multi-season nest occupancy, 2) single-season chick occupancy and, 3) multi-season chick occupancy. We examined chick occupancy in two separate analyses because chick occupancy was generally low and we had a smaller sample size, which inhibited simultaneous examination of environmental covariates and across-year dynamics (i.e., colonization and extinction). There was enough data, however, to examine environmental covariates (single season) and dynamics (multi-season) separately. We used an information-theoretic approach to evaluate models in multi-season nest occupancy and single-season chick occupancy analyses, but not for the third analysis because we only ran a single model to obtain multi-season estimates for occupancy parameters. For the first two analyses, we fitted *a priori* models, which we competed against each other by ranking the models using Akaike's Information Criterion, corrected for sample size (AIC_c; Burnham and Anderson, 2002). Determining sample size for occupancy models is still a topic of debate (MacKenzie et al. 2006) and thus we adjusted the sample size by using the mean value between the number of sites and the number of surveys (multi-season nest occupancy = 965, single-season chick occupancy = 518; MacKenzie et al. 2012). In the case of substantial model selection uncertainty, we adjusted parameter estimates by presenting model averaged estimates based on models within 90% of the AIC weight (Burnham and Anderson 2002). For analysis, we standardized all continuous covariates by calculating z-scores and fit all models in the program PRESENCE (version 6.4; Hines 2006) using the logit link function. Parameter estimates are presented in results ± standard error unless otherwise indicated.

Multi-season nest occupancy

We used a multi-season occupancy approach to estimate the annual proportion of lakes occupied by nesting yellow-billed loons and the dynamics of loon territory occupancy including the probability of local extinction (ε) and colonization (γ; MacKenzie et al. 2003). To allow for a manageable set of *a priori* models, we examined occupancy model parameters in three steps: 1) detection probability (p), 2) initial occupancy in first year (ψ^1) and 3) local extinction (ε) and colonization (γ). We considered detection probability models using a saturated initial occupancy model that incorporates all landscape variables (but not fish occupancy probabilities; see below) and no covariates for ε and γ. We were primarily interested in examining difference in ε and γ probabilities for the 2003/2004 to 2009 timestep and the 2009-2011 timesteps because we predicted that the differences in ε and γ would occur for the largest timestep. Thus, we allowed ε

and γ to differ between the 2003/04 to 2009 and the 2009 to 2011 timesteps, but not between the 2009 to 2010 and 2010 to 2011 timesteps. We scaled all intervals to be annualized.

Models of detection probability included survey platform (Cessna 206, Kodiak, ground surveys) due to its known effect on the observability of breeding loons (Haynes et al. 2014c). We also included models with combinations of the covariates "LakeArea" – the surface area of the lake, and "Shore" – a measure of shoreline convolution calculated as the ratio of the perimeter of the lake to the circumference of a circle of equal area (Stehn et al. 2005). We included detection models for which the influences of LakeArea and Shore varied by aerial and ground surveys and models for which covariate influence was constant among survey platforms (total of 6 detection models).

Using the best detection model from the first step, we examined ψ^1 (loon nesting occupancy in 2003/2004) using two groups of variables – landscape level environmental variables important for loons (Stehn et al. 2005, Earnst et al. 2006) and occupancy probabilities of potential prey fishes (Haynes et al. 2014a). We did not include variables from both groups in the same model because fish occupancy probabilities were based on many (but not all) of the landscape variables. Landscape variables considered for nest occupancy included LakeArea, Shore, lake elevation above sea level ("Elev"; Stehn et al. 2005), the proportion of the lake area that has liquid water below the ice in spring ("Unfroz"; Grunblatt and Atwood 2014), hydrologic connectivity ("Connect") and an interaction between lake surface area and hydrologic connectivity (LakeArea*Connect, Earnst et al. 2006). The Unfroz variable was based on a Synthetic Aperture Radar imagery model that estimates the proportion of a lake's surface area that is deep and does not freeze to the bottom by the end of winter (Grunblatt and Atwood 2014). We defined Connect as the existence of a surface waterway (generally a stream) connecting a lake to another water body (stream, river, lake, pond or wetland). We determined whether a lake had a connection by a combination of digital map (i.e. National Hydrography Dataset), aerial photograph, and ground-observation. Combinations of landscape level environmental variables resulted in 33 models for ψ^1.

We also modeled ψ^1 using the occupancy probability of fish prey species as covariates (Haynes et al. 2014a), including the occupancy probability of Alaska blackfish (*Dallia pectoralis*, "ALBL"), least cisco (*Coregonus sardinella*, "LECI") and at least one large-bodied

(“LB”) species (least cisco, arctic grayling- *Thymallus arcticus* or broad whitefish - *Coregonus nasus*). This model set included combinations of ALBL and either LB or LECI, but not a combination of LB and LECI (5 models in total). To determine whether fish distributions might have a more direct relationship with loon occupancy than landscape characteristics, we competed ψ^1 models that used landscape covariates against the models that used fish occupancy probabilities as covariates.

We estimated occupancy probabilities for ALBL, LECI, and LB by applying models from Haynes et al. (2014a). We used the same occupancy models from Haynes et al. (2014a) to estimate the occupancy probabilities for ALBL and LECI at the sample lakes. Haynes et al. (2014a) created models for individual large bodied species; however, we were interested in an occupancy model for large bodied species as a group (i.e., lake occupancy by at least one large bodied species). We used data from Haynes et al. (2014a) to create a model for LB using parameters that were generally important for large-bodied species. Covariates that were important for at least one large-bodied species and had the same direction of relationship for all large-bodied species included Unfroz, Connect, regional distance of the lake to the Beaufort Sea, and the distance of the lake to the next closest lake (Haynes et al. 2014a). For the large-bodied model, we used the detection probability structure from Haynes et al. (2013); we let detection probability vary by sampling method and four site covariates: LakeArea, Unfroz, Day and Year, where Day was the number of days from the beginning of sampling and Year was binary (representing 2009 or 2010).

In the third step, we examined ε and γ using the best detection probability model structure from the first step and the best ψ^1 model structure from the second step. Rather than test models of ε and γ with a large set of covariates, as we did for ψ^1, we selected four covariates that we thought would most likely influence each parameter. We modeled ε and γ with only one covariate at a time because local extinction and colonization were relatively rare. We modeled ε with the variables we hypothesized may be related to extinction including Unfroz, Shore, LakeArea and ALBL. Unfroz is related to local extinction of fish populations (Haynes et al. 2014a) which may in turn affect local extinction of loons. Shore is related to available nesting habitat and territoriality, with an increase in shoreline convolution providing a more defensible territory and better nest sites and potentially decreasing local extinction probability (Haynes et al. 2014c). LakeArea is positively related to fish occupancy and available nesting habitat (Haynes et al. 2014a, c) and large lakes may be less likely to have local extinction of fish species and can provide larger territory size, thus potentially decreasing local extinction probability. Alaska Blackfish is a species which may be an important food source during nest initiation, before the arrival of migratory fishes to the nesting lake, (Chapter 4) and an increase in ALBL may be related to a decrease extinction probability. We modeled γ with of Connect, LB, LECI and Shore. Connect, LB and LECI are all related to the colonization potential of migratory species (Haynes et al. 2014a), which may be an important cue for late-season prospecting loons that the lake has sufficient prey resources. Shore is important for common loon colonization (Hammond et al. 2012). After determining the best covariate structure for both ε and γ, we ran a final model that included the best model for ε and γ, ψ_1 and p.

Single-Season Chick occupancy

Although we obtained data from multiple years, our data were too sparse to run multi-season models with covariates while simultaneously estimating ψ^1, ε and γ. Local extinction and colonization of broods are relatively rare events and preliminary analysis using a multi-season approach had difficulty estimating γ when covariates were included. We therefore examined how covariates affected chick occupancy via a single-season chick occupancy model (MacKenzie et al. 2002) and using data from all years but not specifying individual years (i.e., treated all data as one season of data).

We combined multiple seasons into a single season analysis by including only one season's data for each site. When a lake had data from more than one season, we included data from the season with the most survey replicates. For lakes with an equal number of surveys, we randomly selected the season for which data were used. We included 409 lakes that were surveyed at least once for chicks in 2008, 2009 or 2011. Of these, 141 lakes had only one survey replicate within a season and the rest were surveyed twice a season. We used a similar stepwise approach as with the multi-season nest occupancy except we did not model ε and γ. We tested the goodness-of-fit of the saturated model using a bootstrap approach (MacKenzie and Bailey 2004).

Multi-Season Chick Occupancy

To obtain estimates for multi-season parameters, we used the seasonal data to run a multi-season chick occupancy model without covariates for ψ^1, ε and γ. Using the best detection model covariates from the single-season chick occupancy analysis, we ran a null model for ψ^1, ε and γ (i.e., no covariates). We used chick occupancy data from 2005, 2008, 2009, and 2011 (413 lakes). We allowed ε, but not γ, to vary annually because preliminary analysis suggested that γ was close to zero; thus, estimating one overall value for γ, rather than estimates of γ for each year, reduced the number of parameters in the model.

Results

Multi-season nest occupancy

The top two models for multi-season nest occupancy had 99% of the AIC model weight. These two models differed only by one parameter – the top model had no covariate for extinction, while Unfroz was a covariate for extinction in the second ranked model. Due to minimal model selection uncertainty, we focused on estimates from the top two models but also gained insights from model selection at each step (p, ψ^1, ε and γ)

The top ranked detection (p) model included Shore and platform specific detection probabilities (Table 5.1). Shore had a positive influence on nest detection probability, with an increasing probability of detecting breeding loons as the shoreline became more complex (logit $\beta_{\text{Shore}} = 0.56 \pm 0.16$). Ground surveys had the highest detection probability for nests ($p_{\text{Ground}} = 0.620 \pm 0.071$) with a similar detection probability to the Cessna aerial surveys ($p_{\text{Cessna}} = 0.557 \pm 0.056$), both of which were about twice as high as the Kodiak aerial surveys ($p_{\text{Kodiak}} = 0.303 \pm 0.064$).

The top ranked model for ψ_1 included the covariates LakeArea and Unfroz, both of which positively corresponded with the probability of initial occupancy by nesting loons ($\beta_{\text{LakeArea}} = 3.26 \pm 0.80$; $\beta_{\text{Unfroz}} = 0.76 \pm 0.26$; Figure 5.2). The probability of lake occupancy for nesting yellow-billed loons was generally low relative to available habitat, with breeders occupying less than a third of lakes >7 ha, and increased through the study duration ($\psi_{\text{nest 2003/2004}} = 0.204 \pm 0.029$, $\psi_{\text{nest 2009}} = 0.260 \pm 0.033$, $\psi_{\text{nest 2010}} = 0.278 \pm 0.033$, $\psi_{\text{nest 2011}} = 0.29 \pm 0.046$).

LECI was the most important variable related to loon colonization probability (γ) with the probability of least cisco occupancy having a positive influence on colonization of a lake by nesting loons ($\beta_{\text{LECI}} = 1.31 \pm 0.37$; Figure 5.3). In the second ranked model, Shore was weakly related to the probability of extinction ($\beta_{\text{Shore}} = -0.31 \pm 0.50$), such that an increasing complexity of lake shoreline decreases the probability of extinction of nesting loons at the lake. Local extinction probabilities ($\varepsilon_{2003/2004\text{-}2009} = 0.23 \pm 0.09$; $\varepsilon_{2009\text{-}2011} = 0.14 \pm 0.07$) were almost double the colonization probabilities ($\gamma_{2003/2004\text{-}2009} = 0.13 \pm 0.03$; $\gamma_{2009\text{-}2011} = 0.07 \pm 0.02$); however, these parameters were estimated with relatively low precision. Estimates of lambda (λ = the rate of change in occupancy) for the individual years were all greater than one ($\lambda_{\text{nest } 2003/2004\text{-}2009} = 1.05 \pm 0.08$, $\lambda_{\text{nest } 2009\text{-}2010} = 1.07 \pm 0.10$, $\lambda_{\text{nest } 2010\text{-}2011} = 1.05 \pm 0.07$), but estimates had large 95% confidence intervals that included one.

Single-Season Chick Occupancy

We did not find evidence of overdispersion from the goodness-of-fit test ($\hat{c} = 0.797$). The top models had similar AIC scores (top 6 models had 89.5% of AIC weight). We therefore accounted for model selection uncertainty in parameter estimates by model averaging across these six models (Burnham and Anderson 2002). Although we used model averaging for estimation, we discuss model rankings in the context of our stepwise approach.

The best model for detection included LakeArea and survey platform (Table 5.2). As lake surface area increased, the probability of detecting a yellow-billed loon chick decreased ($\beta_{\text{LakeArea}} = -0.346 \pm 0.155$), and chicks had a higher detection probability in the survey by the Kodiak aircraft in 2011 ($\beta_{\text{Platform}} = -0.671 \pm 0.460$) than in the Cessna 206 in 2008 or 2009, (however, platform is confounded by year). The Kodiak aircraft had a detection probability for chicks of 0.639 ± 0.107 on an average sized lake.

The best model for occupancy included LakeArea and Unfroz with the probability of a yellow-billed loon chick occupying a lake increasing with lake size ($\beta_{\text{LakeArea}} = 2.329 \pm 0.593$) and the proportion of the lake unfrozen through winter ($\beta_{\text{Unfroz}} = 1.618 \pm 0.415$). Other occupancy covariates from the top models had beta estimates near zero and with low precision ($\beta_{\text{Elev}} = -0.037 \pm 0.054$, $\beta_{\text{Shore}} = 0.061 \pm 0.085$, $\beta_{\text{Connect}} = 0.164 \pm 0.191$). The occupancy probability for chicks ($\psi_{\text{chick}} = 0.191 \pm 0.053$) was slightly lower than the nesting occupancy probability. Based on overall chick occupancy probability (late Aug./early Sept.) and mean annual nest occupancy probability (late June/early July), about three quarters of the nests present in the early season produced chicks ($\psi_{\text{chick}}/\psi_{\text{nest}} = 0.191/0.259 = 0.74 \pm 0.32$).

Both nest and chick occupancy were positively influenced by LakeArea and Unfroz (Figure 5.2). Based on the shape of the curves, lakes that have a high probability of producing chicks are generally larger and deeper (more area unfrozen in the spring) than the lakes that have a high probability of nests, suggesting that nests that fail to produce chicks are more commonly found on smaller, shallower lakes. For the largest lake sizes, occupancy approaches one (i.e., approaches saturation). For example, lakes with surface areas greater than 258 ha (z-value = 1.2) had a nesting occupancy probability > 0.95 and lakes greater than 410 ha (z-value = 2.2) had a >0.95 probability of producing a chick.

Multi-Season Chick Occupancy

Annual chick occupancy probability decreased over time ($\psi_{\text{chick 2005}} = 0.229 \pm 0.078$, $\psi_{\text{chick 2008}} = 0.221 \pm 0.065$, $\psi_{\text{chick 2009}} = 0.185 \pm 0.039$, $\psi_{\text{nest 2011}} = 0.113 \pm 0.022$), which was reflected in the rate of change in chick occupancy ($\lambda_{\text{chick 2005-2008}} = 0.988 \pm 0.194$, $\lambda_{\text{chick 2008-2009}} = 0.836 \pm 0.235$, $\lambda_{\text{chick 2009-2011}} = 0.784 \pm 0.100$). Colonization probability for chicks in August were very close to zero ($\gamma = 0.030 \pm 0.020$) while extinction probabilities varied considerably by year; estimates of extinction probability between 2009 and 2011($\varepsilon_{2009\text{-}2011} = 0.517 \pm 0.104$) was over twice that of other timesteps ($\varepsilon_{2005\text{-}2008} = 0.136 \pm 0.296$, $\varepsilon_{2008\text{-}2009} = 0.268 \pm 0.218$).

Discussion

Occupancy of territorial species, such as the yellow-billed loon, is a result of combining social, behavioral and habitat factors. Without controlled experiments (e.g., Sjöberg et al. 2000), it is difficult to confirm mechanistic relationships suggested by empirically derived models. However, our approach was based on *a priori* hypotheses, derived from previous study and current understanding of loon ecology. Our study had a different scope than previous work on yellow-billed loons (Stehn et al. 2005, Earnst et al. 2006), but habitat associations for occupancy were similar – yellow-billed loons prefer to nest on large, deep lakes (i.e., lakes with large areas > 2 m in depth). Further, our models indicate that these large, deep lakes are most likely to produce chicks; however, these lakes are relatively rare on the landscape (Figure 5.4). Lake elevation, connectivity, or the interaction between lake area and connectivity were not associated with occupancy, as previous studies suggest (Stehn et al. 2005, Earnst et al. 2006). However, differences in modeling results are likely due to differences in scale (our study extent was smaller, precluded to the core breeding region) and focus (specific to breeding loons).

Despite our focus on the high density stratum for breeding yellow-billed loons, nesting loon occupancy was low relative to the available lake habitat. In late June, nesting yellow-billed loons occupied 20-30% of the available lakes >7 ha and only about 19% of available lakes produce chicks. This occupancy is much higher than that for the broader ACP (occupancy of about 15% for breeding and non-breeding yellow-billed loons combined, Earnst et al. 2006) but is still low relative to the number of potential nesting lakes based on lake size alone (i.e. >7 ha). The apparent low occupancy of nesting yellow-billed loons on the ACP raises the question – Why are loons not breeding on a higher proportion of available lakes (Stehn et al. 2005, Earnst et al. 2006)?

We provide two main explanations as to why nesting yellow-billed loons do not occupy more lakes: 1) loons may not be at a population level such that all suitable habitat is occupied because factors outside of the nesting season limit their population, or 2) suitable habitat is saturated and the remaining lakes are unsuitable for breeding. Understanding which of these two explanations produced the observed occupancy patterns has clear conservation implications; if habitat is not saturated, the population of yellow-billed loons breeding on the ACP may be limited during another stage of the life cycle (e.g., on the wintering grounds or during migration). Conversely, if yellow-billed loons saturate the high-quality nesting habitat, their population is likely close to equilibrium and the availability of breeding habitat may limit population growth. It is difficult to answer this question based on previous single-season work because information on reproductive success or habitat use over time was lacking.

This study adds to the growing evidence that quality nesting habitat for yellow-billed loons may be saturated in various parts of their range (North 1986, Schmidt et al. 2014 Schmutz et al. 2014). Although our evidence is indirect, our results suggest that the high quality habitat in this core area may be close to saturation. Large, deep lakes are high quality breeding habitat because they are not only more likely to be occupied by nesting loons, but also have the highest probability of producing chicks. Lake size was the most influential variable on occupancy probability, large lakes are saturated by nesting loons, and the largest lakes are saturated by loon chicks. The differences between nesting and chick occupancy probabilities across values of LakeArea and Unfroz also suggest that the highest quality habitat is close to saturation. Across the range of values of LakeArea and Unfroz, chick occupancy increases at higher values relative to nest occupancy. Many lakes with lower values of LakeArea and Unfroz support nests but they do not have a high probability of producing chicks. For example, lakes with an area of 240 ha have >0.95 probability of occupancy for nests with only a 0.68 probability of producing a chick. Although the fish covariates were not strongly supported for nesting occupancy, the positive relationship between nesting occupancy and lake size may be related to the availability of fish prey, as larger lakes generally have a higher occupancy probabilities for fish species (Haynes et al. 2014a). The selection of the largest lakes by yellow-billed loons may also be in response to the availability of nesting habitat, with large lakes having proportionally more shoreline and thus potentially more suitable nesting locations (Haynes et al. 2014b). Large lakes may also have a higher likelihood of support more than one yellow-billed loon nest, although this is generally rare on the ACP (Haynes et al. 2014b).

The hypothesis that high quality habitat is saturated within the core area of density in the ACP is supported by other lines of evidence: observations that large, deep lakes are able to support multiple loon nests (Haynes et al. 2014b, Haynes et al. 2014c); the presence of large numbers (a third of the total population) of “floating” non-breeders on the ACP breeding grounds (Earnst et al. 2005, Schmutz et al. 2014); and a stable to increasing occupancy for nesting loons over a nine year period (this study). Hammond et al. (2012) found similar dynamics (loon occupancy at equilibrium in time) for annual territorial occupancy of common loons.

Yellow-billed loons have high territory retention between breeding seasons. In a study on the ACP, Schmutz et al. (2014) found that 12 of 16 (75%) breeding yellow-billed loons that were fixed with satellite tags reused the same nesting lake in the next season. Schmidt et al. (2014) found the probability of nest lake reuse was 0.72 for breeding yellow-billed loons on the Seward Peninsula. These values are similar to our estimate of probability of reuse (1- ε) at the population level of 0.83 between 2003/2004 and 2009, and 0.84 from 2009-2011. Although we allowed ε to vary between the two timesteps, local extinction probabilities were similar, indicating that extinction rates varied little over the study period. The relatively stable local extinction probabilities, along with the stable colonization probabilities and occupancy rates suggest the breeding population of yellow-billed loons were near equilibrium over the past nine years.

Increases in yellow-billed loon nesting occupancy over time corresponded with a substantial decrease in chick occupancy; each timestep had a lambda value for chick occupancy less than one, and the 2011 season had about half the chick occupancy probability of 2005. Although our analysis does not provide any causal linkage between the increase in nesting density and the decrease in chick production, increasing breeding densities can cause decreased reproductive success in birds (e.g., Page et al. 1983, Vickery et al. 1992) and increased breeding territory abandonment in loons (Hammond et al. 2012). Similar dynamics on the ACP could be taking place, where densities of nesting yellow-billed loons may be negatively affecting breeding success. Yellow-billed loons on the ACP must also compete with abundant nesting Pacific loons (Haynes et al. 2014c). Higher densities of loons would increase potential for territorial conflicts, especially considering that loons prospecting for nesting habitat target territories that produced chicks in the previous season (Piper et al. 2006). Increases in territorial conflicts would lead to increased exposure to conspecific chick mortality (Evers et al. 2010) and more time spent defending a territory rather than performing other breeding duties such as guarding a nest from predators or caring for chicks.

The occupancy probabilities of chosen fish were not important for initial nesting or chick occupancy. We chose fish species that we knew (Chapter 4) or suspected (i.e., common inland species; Chapter 3) as being important for diet. Although not important for initial occupancy, the occupancy probability of least cisco was an important covariate for territory acquisition (colonization) by nesting loons. Least cisco are a high energy prey item (Ball et al. 2007) and generally locally abundant when present in a lake (Haynes et al. 2014a). Lakes with high occupancy probabilities for least cisco may have the prey reserves necessary to support breeding through to fledging. Thus, the presence of least cisco may be an indication of the quality of a nesting lake to prospecting loons. However, understanding how prey distributions influence loons is difficult. Loons are likely responding to the local fish communities in aggregate and to abundance of key species in complex ways. Beyond the expected spatial concordance between piscivorous birds and prey fish (Paszkowski and Tonn 2006), some fish species may have negative associations with birds because fish may compete for similar prey (Wagner and Hansson 1998, Haas et al. 2007), alter the trophic characteristics of the lake (Scheffer et al. 2006, Elmberg et al. 2010, McParland et al. 2010), or even depredate chicks (Gunnarsson et al. 2006). In addition, fish and aquatic birds may show a high spatial concordance because they are responding to similar environmental factors (Paszkowski and Tonn 2000). In our case, it is difficult to determine whether loons are responding to the presence of least cisco or whether the two species have similar habitat associations. Regardless, because of their body size, abundance and energy content, it is likely that when least cisco are present at a nesting lake, they are an important food source for breeding loons.

Our analysis also revealed an interesting dynamic in the aerial surveys; the Cessna surveys had a higher detection probability during nesting surveys, whereas the Kodiak had a higher detection probability during chick rearing. Differences in aircraft performance during the surveys are likely responsible for the contrasting detection results. The Kodiak is designed for good visibility, but does not turn as quickly as the Cessna. Thus, the Kodiak performs better when surveying for chicks, as most chicks in late August are out in the middle of the lake. The Cessna can follow shorelines more closely which likely gives it an advantage for surveying nests. It is worthy to point out that this comparison is confounded by year (no seasons when both Cessna and Kodiak used); however, we are unaware of any major annual differences that would otherwise lead to such contrasting results in detection.

If habitat is saturated and the availability of quality breeding habitat is limiting the population of yellow-billed loons on the ACP in the core area, managing potential breeding lakes may be one of the most effective ways to conserve the species (US Fish and Wildlife Service 2006). Focusing on areas of the ACP that have the highest loon densities (i.e., our study extent and the Colville River Delta; North 1986, Earnst et al. 2005) would be an efficient management strategy considering these regions constitute important population segments, and encompass regions open to oil and gas development. We confirm prior research (Stehn et al. 2005, Earnst et al. 2006); deep lakes with large surface area and adequate fish prey represent high quality habitat for yellow-billed loons. Managers should be aware that an increase in nesting occupancy is not necessarily a good indicator of increasing reproductive output. Rather, our estimates suggest that a recent decline in total productivity despite the increase in nesting occupancy. Because one and two year old loons likely do not return to the ACP in summer, low chick production would not manifest in observed population trend data until several years after ecological conditions have changed to affect chick success. Thus, our results may portend a near-future reduction in population growth unless an increase in nesting occupancy offsets a reduction in per-capita chick survival.

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Table 5.1: Ranking of candidate models of multi-year occupancy of nesting yellow-billed loons on Arctic Coastal Plain lakes in late June. Inference about best fitting models was based on ranking of Akaike's Information Criterion adjusted for sample size (AIC$_c$), differences in AIC$_c$ (ΔAIC$_c$), model weight (*w*), and model likelihood, given the number of estimated parameters (K).

Model[1]	Step[2]	AIC$_c$	ΔAIC$_c$	*w*	Likelihood	K
ψ(LakeArea,Unfroz),ɣ(LECI),ε(.),p(Platform,Shore)	ɣ	972.80	0.00	0.693	1	12
ψ(LakeArea,Unfroz),ɣ(LECI),ε(PUnfroz),p(Platform,Shore)	Final	974.47	1.67	0.301	0.434	13
ψ(LakeArea,Unfroz),ɣ(LB),ε(.),p(Platform,Shore)	ɣ	982.10	9.30	0.007	0.010	12
ψ(LakeArea,Unfroz),ɣ(Connect),ε(.),p(Platform,Shore)	ɣ	989.07	16.27	0.000	0.000	12
ψ(LakeArea,Unfroz),ɣ(Shore),ε(.),p(Platform,Shore)	ɣ	991.32	18.52	0.000	0.000	12
ψ(LakeArea,Unfroz),ɣ(.),ε(PUnfroz),p(Platform,Shore)	ε	993.26	20.46	0.000	0.000	12
ψ(LakeArea,Unfroz),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	993.47	20.67	0.000	0.000	11
ψ(LakeArea,Unfroz),ɣ(.),ε(Shore),p(Platform,Shore)	ε	994.34	21.54	0.000	0.000	12
ψ(LakeArea,Unfroz),ɣ(.),ε(LakeArea),p(Platform,Shore)	ε	994.72	21.92	0.000	0.000	12
ψ(LakeArea,Connect,Unfroz),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	995.03	22.23	0.000	0.000	12
ψ(LakeArea,Unfroz),ɣ(.),ε(ALBL),p(Platform,Shore)	ε	995.18	22.38	0.000	0.000	12
ψ(LakeArea,Elev,Unfroz),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	995.52	22.72	0.000	0.000	12
ψ(LakeArea,Shore,Unfroz),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	995.52	22.72	0.000	0.000	12
ψ(LakeArea,Elev,Unfroz,Connect),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	997.06	24.26	0.000	0.000	13
ψ(LakeArea,Shore,Unfroz,Connect),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	997.07	24.27	0.000	0.000	13

Table 5.1 Continued

ψ(LakeArea,Elev,Shore,Unfroz),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	997.57	24.77	0.000	0.000	13
ψ(Saturated - no interaction),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	999.12	26.32	0.000	0.000	14
ψ(Saturated),ɣ(.),ε(.),p(Platform,Shore)	p	999.24	26.44	0.000	0.000	15
ψ(Saturated),ɣ(.),ε(.),p(Platform,LakeArea, Shore)	p	999.58	26.78	0.000	0.000	16
ψ(Saturated),ɣ(.),ε(.),p(Platform,Shore*Platform)	p	1001.25	28.45	0.000	0.000	16
ψ(Saturated),ɣ(.),ε(.),p(Platform,LakeArea)	p	1002.95	30.15	0.000	0.000	15
ψ(Saturated),ɣ(.),ε(.),p(Platform,LakeArea*Platform)	p	1003.44	30.64	0.000	0.000	16
ψ(LakeArea),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	1006.83	34.03	0.000	0.000	10
ψ(LakeArea,Connect),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	1007.77	34.97	0.000	0.000	11
ψ(LakeArea,Elev),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	1008.81	36.01	0.000	0.000	11
ψ(LakeArea,Shore),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	1008.83	36.03	0.000	0.000	11
ψ(LakeArea*Connect),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	1009.20	36.40	0.000	0.000	12
ψ(saturated),ɣ(.),ε(.),p(Platform)	p	1009.55	36.75	0.000	0.000	14
ψ(LakeArea,Shore,Connect),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	1009.60	36.80	0.000	0.000	12
ψ(LakeArea,Elev,Connect),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	1009.82	37.02	0.000	0.000	12
ψ(LakeArea,Elev,Shore),ɣ(.),eps(.),p(Platform,Shore)	ψ_1	1010.75	37.95	0.000	0.000	12
ψ(LakeArea,Elev,Shore,Connect),ɣ(.),eps(.),p(Platform,Shore)	ψ_1	1011.62	38.82	0.000	0.000	13
ψ(LECI,ALBL),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	1039.79	66.99	0.000	0.000	11
ψ(LECI),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	1044.82	72.02	0.000	0.000	10
ψ(LB,ALBL),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	1045.53	72.73	0.000	0.000	11

Table 5.1 Continued

ψ(ALBL),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	1046.54	73.74	0.000	0.000	10
ψ(LB),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	1048.28	75.48	0.000	0.000	10
ψ(Unfroz,Connect),ɣ(.),ε(.), p(Platform,Shore)	ψ_1	1049.31	76.51	0.000	0.000	11
ψ(Shore,Unfroz,Connect),ɣ(.),ε(.), p(Platform,Shore)	ψ_1	1050.47	77.67	0.000	0.000	12
ψ(Elev,Unfroz,Connect),ɣ(.),ε(.), p(Platform,Shore)	ψ_1	1051.10	78.30	0.000	0.000	12
ψ(Shore,Unfroz),ɣ(.),ε(.),p(Platform, Shore)	ψ_1	1051.82	79.02	0.000	0.000	11
ψ(Unfroz),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	1051.82	79.02	0.000	0.000	10
ψ(Elev,Shore,Unfroz,Connect),ɣ(.), ε(.),p(Platform,Shore)	ψ_1	1051.89	79.09	0.000	0.000	13
ψ(Elev,Shore,Unfroz),ɣ(.),ε(.), p(Platform,Shore)	ψ_1	1053.75	80.95	0.000	0.000	12
ψ(Elev,Unfroz),ɣ(.),ε(.),p(Platform, Shore)	ψ_1	1053.85	81.05	0.000	0.000	11
ψ(Connect),ɣ(.),ε(.),p(Platform, Shore)	ψ_1	1056.17	83.37	0.000	0.000	10
ψ(Shore,Connect),ɣ(.),ε(.),p(Platform, Shore)	ψ_1	1057.95	85.15	0.000	0.000	11
ψ(Elev,Connect),ɣ(.),ε(.),p(Platform, Shore)	ψ_1	1058.21	85.41	0.000	0.000	11
ψ(.),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	1058.82	86.02	0.000	0.000	9
ψ(Shore),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	1059.81	87.01	0.000	0.000	10
ψ(Elev,Shore,Connect),ɣ(.),ε(.), p(Platform,Shore)	ψ_1	1059.95	87.15	0.000	0.000	12
ψ(Elev),ɣ(.),ε(.),p(Platform,Shore)	ψ_1	1060.58	87.78	0.000	0.000	10
ψ(Elev,Shore),ɣ(.),ε(.),p(Platform, Shore)	ψ_1	1061.81	89.01	0.000	0.000	11

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[1] “LakeArea” – the surface area of the lake; “Shore” – a measure of shoreline convolution calculated as the ratio of the perimeter of the lake to the circumference of a circle of equal area. “Elev” – elevation above sea level; “Unfroz” – the area of the lake that has liquid water below the ice in spring; “Connect” hydrologic connectivity; “LakeArea*Connect” – interaction between lake surface area and hydrologic connectivity; “ALBL” – occupancy probability of Alaska blackfish (*Dallia pectoralis*); “LECI” – occupancy probability of least cisco (*Coregonus sardinella*); “LB” – occupancy probability of at least one large-bodied species (least cisco, arctic

grayling- *Thymallus arcticus* or broad whitefish - *Coregonus nasus*); “Platform” – survey type (Cessna 206, Kodiak, ground); “Saturated” – all landscape variables, but not fish occupancy probabilities; “Shore*Platform” and “LakeArea*Platform” denotes models where the covariate (Shore or LakeArea) were allowed to vary by platform.

[2] To allow for a manageable set of *a priori* models, we examined occupancy model parameters in three steps: 1) detection probability (p), 2) initial occupancy in first year (ψ^1) and 3) local extinction (ε) and colonization (γ) with the final step being the highest ranked model structure for each step.

Table 5.2: Rankings of models examining single-season occupancy of yellow-billed loon chicks on Arctic Coastal Plain lakes in late August. Inference about best fitting models was based on ranking of Akaike's Information Criterion adjusted for sample size (AIC_c), differences in AIC_c (ΔAIC_c), model weight (*w*), and model likelihood, given the number of estimated parameters (K).

Model[1]	Step[2]	AIC_c	ΔAIC_c	*w*	Likelihood	K
ψ(Unfroz,LakeArea),p(LakeArea,Platform)	ψ	309.38	0	0.284	1	6
ψ(Unfroz,Connect,LakeArea),p(LakeArea, Platform)	ψ	310.23	0.85	0.186	0.654	7
ψ(Unfroz,Elev,LakeArea),p(LakeArea, Platform)	ψ	310.65	1.27	0.151	0.53	7
ψ(Shore,Unfroz,LakeArea),p(LakeArea, Platform)	ψ	310.68	1.3	0.148	0.522	7
ψ(Unfroz,Connect,LakeArea,Shore), p(LakeArea,Platform)	ψ	311.76	2.38	0.086	0.304	8
ψ(Saturated),p(LakeArea,Platform)	p, ψ	313.32	3.94	0.04	0.14	9
ψ(Saturated),p(LakeArea)	p	313.44	4.06	0.037	0.131	8
ψ(Saturated,Interaction),p(LakeArea, Platform)	ψ	315.26	5.88	0.015	0.053	10
ψ(Saturated),p(LakeArea,Shore)	p	315.49	6.11	0.013	0.047	9
ψ(Saturated),p(.)	p	315.94	6.56	0.011	0.038	7
ψ(Saturated),p(Shore)	p	316.67	7.29	0.007	0.026	8
ψ(Saturated),p(Platform)	p	316.75	7.37	0.007	0.025	8
ψ(Saturated),p(Shore,Platform)	p	317.7	8.32	0.004	0.016	9
ψ(ALBL,LB),p(LakeArea,Platform)	ψ	318.91	9.53	0.002	0.009	6
ψ(Unfroz,Connect),p(LakeArea,Platform)	ψ	320.59	11.21	0.001	0.004	6
ψ(ALBL),p(LakeArea,Platform)	ψ	321.78	12.4	0.001	0.002	5
ψ(LB),p(LakeArea,Platform)	ψ	322.1	12.72	0	0.002	5
ψ(Connect,Unfroz,Shore),p(LakeArea, Platform)	ψ	322.24	12.86	0	0.002	7
ψ(Elev,Connect,Unfroz),p(LakeArea, Platform)	ψ	322.41	13.03	0	0.002	7
ψ(Saturated),p(LakeArea,Shore,Platform)	p	322.91	13.53	0	0.001	10
ψ(Unfroz),p(LakeArea,Platform)	ψ	323.03	13.65	0	0.001	5
ψ(Elev,Unfroz,Shore,Connect),p(LakeArea ,Platform)	ψ	324.11	14.73	0	0.001	8
ψ(Shore,Unfroz)p(LakeArea,Platform)	ψ	324.21	14.83	0	0.001	6
ψ(Elev,Unfroz),p(LakeArea,Platform)	ψ	324.61	15.23	0	0.001	6
ψ(Elev,Unfroz,Shore),p(LakeArea, Platform)	ψ	325.91	16.53	0	0	7

Table 5.2 Continued

ψ(LECI),p(LakeArea,Platform)	ψ	326.41	17.03	0	0	5
ψ(Connect,Elev,LakeArea),p(LakeArea, Platform)	ψ	334.76	25.38	0	0	7
ψ(LakeArea,Elev,Connect),p(LakeArea, Platform)	ψ	334.76	25.38	0	0	7
ψ(Connect),p(LakeArea,Platform)						
ψ(Interaction),p(LakeArea,Platform)	ψ	335.73	26.35	0	0	7
ψ(Shore,Connect,LakeArea),p(LakeArea, Platform)	ψ	335.74	26.36	0	0	7
ψ(LakeArea),p(LakeArea,Platform)	ψ	335.74	26.36	0	0	5
ψ(Elev,Connect),p(LakeArea,Platform)	ψ	336.04	26.66	0	0	6
ψ(LakeArea,Elev),p(LakeArea,Platform)	ψ	336.04	26.66	0	0	6
ψ(Shore,Elev,LakeArea,Connect), p(LakeArea,Platform)	ψ	336.6	27.22	0	0	8
ψ(Shore,Connect)p(LakeArea,Platform)	ψ	336.88	27.5	0	0	6
ψ(LakeArea,Connect),p(LakeArea, Platform)	ψ	336.89	27.51	0	0	6
ψ(Shore,Elev,LakeArea),p(LakeArea, Platform)	ψ	338.04	28.66	0	0	7
ψ(Elev,Connect,Shore),p(LakeArea, Platform)	ψ	338.07	28.69	0	0	7
ψ(Elev),p(LakeArea,Platform)	ψ	338.68	29.3	0	0	5
ψ(Shore,p(LakeArea,Platform)	ψ	339.72	30.34	0	0	5
ψ(Elev,Shore),p(LakeArea,Platform)	ψ	340.56	31.18	0	0	6

[1] "LakeArea" – the surface area of the lake; "Shore" – a measure of shoreline convolution calculated as the ratio of the perimeter of the lake to the circumference of a circle of equal area. "Elev" – elevation above sea level; "Unfroz" – the area of the lake that has liquid water below the ice in spring; "Connect" hydrologic connectivity; "LakeArea*Connect" – interaction between lake surface area and hydrologic connectivity; "ALBL" – occupancy probability of Alaska blackfish (*Dallia pectoralis*); "LECI" – occupancy probability of least cisco (*Coregonus sardinella*); "LB" – occupancy probability of at least one large-bodied species (least cisco, arctic grayling- *Thymallus arcticus* or broad whitefish - *Coregonus nasus*); "Platform" – survey type (Cessna 206, Kodiak, ground); "Saturated" – all landscape variables, but not fish occupancy probabilities.

[2] To allow for a manageable set of *a priori* models, we examined occupancy model parameters in two steps: 1) detection probability (p), 2) occupancy (ψ), with the final step being the highest ranked model structure for each step.

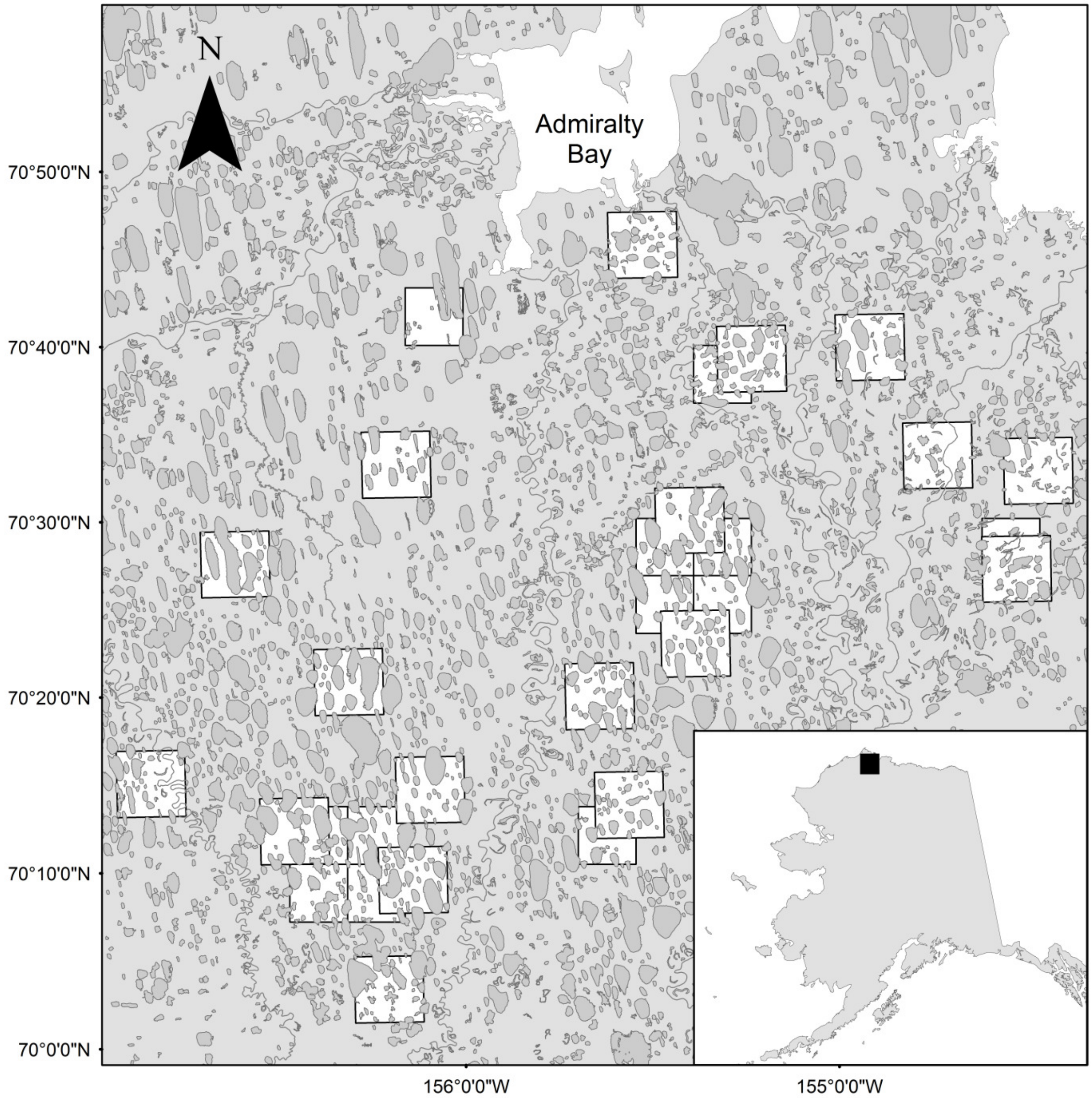
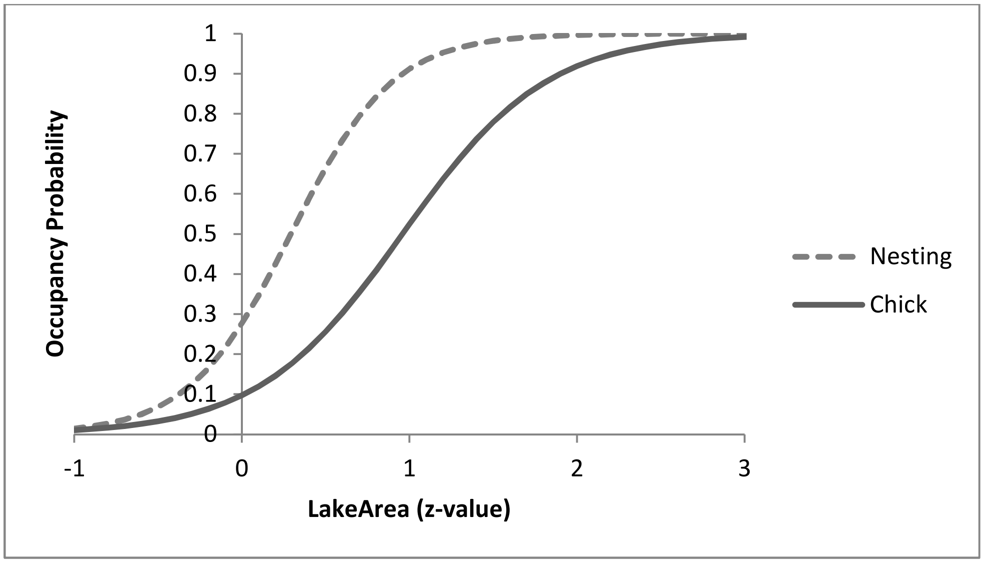


Figure 5.1: Survey plots (white squares) for breeding yellow-billed loons on the Arctic Coastal Plain. Data were collected under two survey designs including 7x7 km and 6x6 km plots. Inset map shows study extent (black rectangle) relative to Alaska.



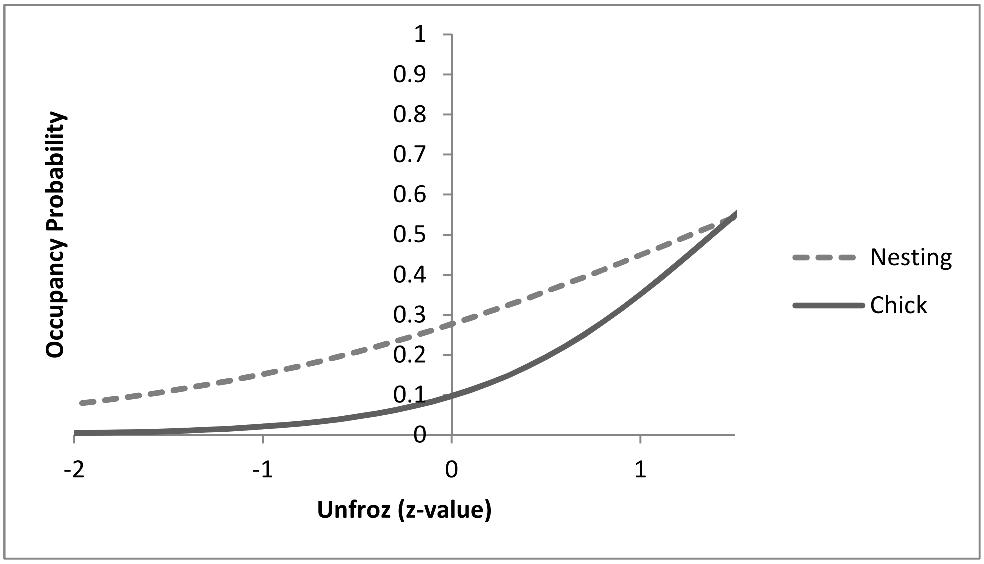


Figure 5.2: Probability of nesting occupancy (in late June/early July) and chick occupancy (in late August/early Sept) at lakes on the Arctic Coastal Plain of Alaska, relative to lake area (LakeArea) and the proportion of the lake surface area that is deep enough to contain liquid water at the end of winter (Unfroz). LakeArea (range 20-414 ha) and Unfroz (range 0-100%) were standardized to have a mean of 0.0 and standard deviation of 1.0. Increasing values represent larger lake surface area (LakeArea; logit $\beta_{\text{LakeArea}} = 2.329 \pm 0.593$) or a higher proportion of lake area that is deeper than maximum winter ice thickness (Unfroz; logit $\beta_{\text{Unfroz}} = 1.618 \pm 0.415$).

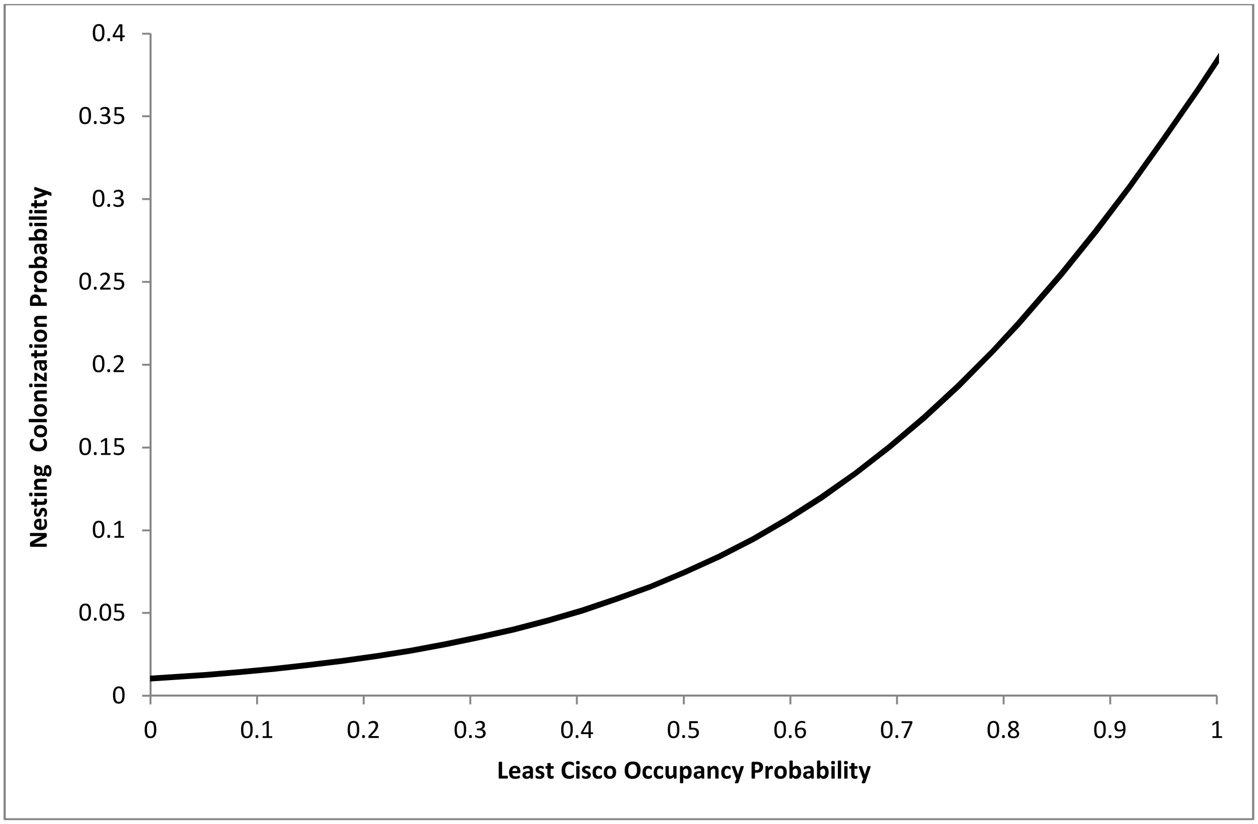


Figure 5.3: Probability of lake colonization for nesting yellow-billed loons relative to least cisco occupancy probability (logit $\beta_{LECI} = 1.31 \pm 0.37$).

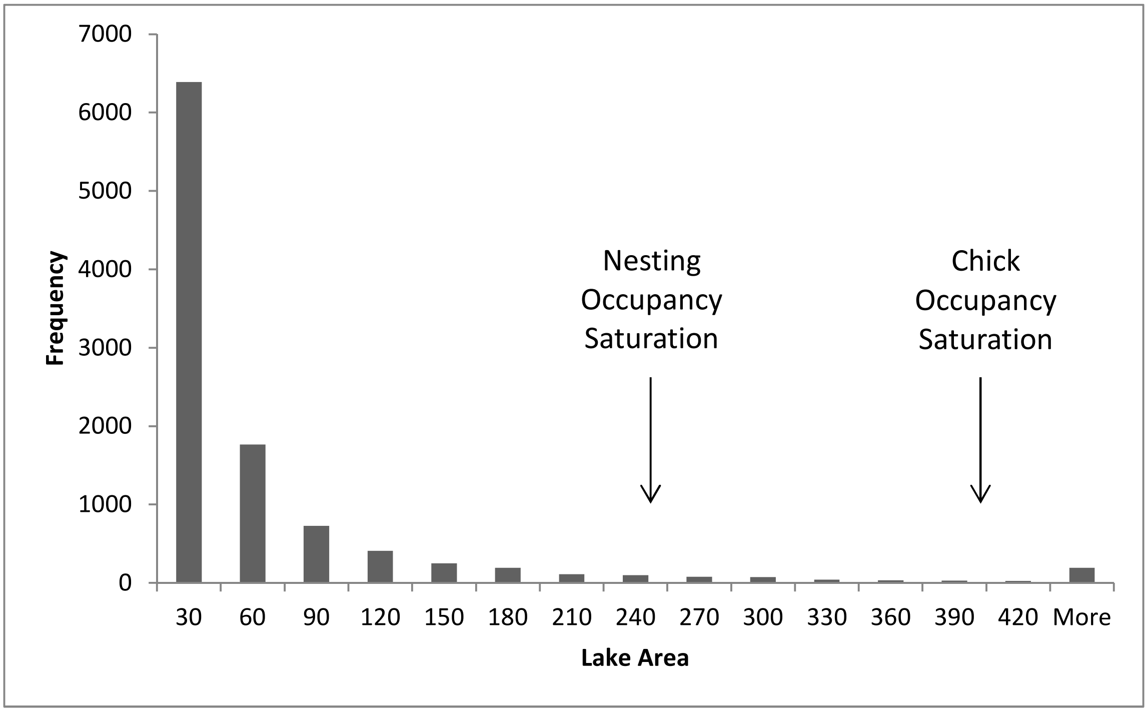


Figure 5.4: Frequency of lake area across the study region. Arrows indicate points at which lakes approach saturation (ψ ~ 1) for nest and chick occupancy.

Chapter 6: Conclusions

The Arctic Coastal Plain (ACP) is an expansive area, spanning over 98,200 km^2 , representing important habitat for Arctic flora and fauna (Hobbie 1984, Leibezeit et al. 2009). For example, the National Petroleum Reserve-Alaska (NPR-A), which covers a large portion of the ACP, including our study region, is one of the most important areas for breeding aquatic birds in the holarctic (Bart et al. 2013). The majority of ACP remains undeveloped; however, substantial oil and gas extraction remains a part of the current landscape (>2000 wells drilled since 1977; Fuller et al. 2008), and much of the ACP region remains open to development with the U.S. Bureau of Land Management expecting to offer annual lease sales (Bureau of Land Management 2014). The Arctic region also will experience some of the strongest effects of climate change (Post et al. 2009), which could have major ecological consequences for freshwater ecosystems on the ACP (Reist et al. 2006; Wrona et al. 2006). Given the potential impacts from increased development and a warming climate, study of the ACP ecosystems is key for detecting and predicting the potential effects of these impacts. However, due to its vast size and inaccessibility, the ACP remains poorly studied compared with other regions. The work included in this dissertation provides insights into important aspects of the freshwater ecosystem of the ACP, including important sampling considerations for the relatively unstudied fish communities, the ecological drivers of Arctic fish distributions, information gaps about yellow-billed loon diet, and occupancy dynamics parameters for breeding yellow-billed loons and loon chicks (i.e., productivity).

In Chapter 2, I examined how detection probability affects fish sampling in Arctic lakes. Detection probabilities were always less than one, suggesting that repeated sampling with multiple gear types provides the most efficient sampling regime when trying to detect fish species with a high level of confidence. Using results from Chapter 2, scientists and managers can design sampling schemes to target specific species or the entire fish communities. For example, the U.S. Bureau of Land Management and the U.S. Fish and Wildlife Service is currently using detection estimates from Chapter 2 to design fish research studies on the ACP. The results from this chapter are particularly relevant to the regulations set by the State of Alaska for industrial water withdrawal from Arctic lakes. The state sets strict guidelines for water withdrawal and withdrawal allowance depend on the fish species present in the lake. Although the state requires permit applicants to sample for fish in lakes targeted for water withdrawal, the state currently does not have standardized guidelines for fish sampling efforts. Results from Chapter 2 could be used by the State of Alaska to develop such guidelines, or used by permit applicants and consultants charged with sampling lakes to ensure there is a scientific basis for their sampling design. This will allow permit applicants to demonstrate that an appropriate level of sampling has occurred when applying for water withdrawal permits.

Chapter 3 makes an important addition to the modest amount of ecological information available on the freshwater fish communities of the ACP. Fish distributions are generally unavailable for thousands of lakes on the ACP and landscape characteristics that influence fish distributions are poorly understood. In Chapter 3, I examined the distributions of six of the most common fish species. These species had occupancy patterns that reflected their life history strategies, and I synthesized known ecological information with modeling results to create a conceptual model for fish distributions on the ACP. Models of fish distributions from Chapter 3 can be used to predict fish distributions in unsampled lakes (see Chapter 5) and should have utility for managing fish populations or provide *a priori* expectations for refining detectability models. For example, we have received requests by the U.S. Bureau of Land Management and the Arctic Landscape Conservation Cooperative for both sampled and modeled data on fish distributions. We expect that these data will be developed into tools that will give managers and policy makers the information they need to better manage aquatic resources on the ACP, despite the general lack of sampling. The conceptual model provides a broader understanding of the factors governing fish populations on the ACP. Lake connectivity and overwintering habitat (i.e., water deeper that about 2 m) are key influences on the distribution of Arctic fishes. Preventing impasses to fish passage or limiting water withdrawal that eliminates deep water refuges are useful management goals for maintaining existing fish community structure. The conceptual model also provides a basis for future scientific investigation. The model can generate testable hypotheses about fish movements, distributions and occupancy dynamics such as local extinction and colonization. Future refinement to this conceptual model will increase our understanding of Arctic fish ecology and improve management practices on the ACP.

The diet of breeding yellow-billed loons represents a major information gap. Results from Chapter 4 suggest that Alaska blackfish are an important diet item early in the breeding season. The early season importance of blackfish is likely due to their widespread distribution after spring break-up, before other species, such as opportunistic colonizers (e.g., ninespine stickleback), or migratory species (e.g., least cisco) can reach maximum mid-summer occupancy in lakes. Models suggested that three-spined stickleback and broad whitefish were also major prey items. However, these species were likely consumed by loons in staging areas, given that three-spined stickleback are not widespread in interior ACP lakes and broad whitefish have relatively low occupancy probabilities (Haynes et al. 2014). Chapter 4 takes an important first step in understanding the diet of yellow-billed loons; however, future work on yellow-billed loon diet should focus on mid- to late-breeding season to contrast with early season results.

Findings from Chapter 5 suggest that breeding yellow-billed loons may be saturating quality habitat (i.e., large, deep lakes), and the presence of least cisco affects occupancy dynamics (probability of colonization). Although I examined other fish occupancy variables as covariates, they were not supported as important to loon occupancy dynamics. Lake area and depth may be serving proximate measures of prey availability because large, deep lakes are also most likely to have fish (Haynes et al. 2013). Over the study period, occupancy of nesting loons increased while chick occupancy (i.e., chick production) decreased. The negative relationship between loon densities and breeding success is the case for common loons (Hammond et al. 2012) and for loons on the ACP (Schmutz and Uher-Koch, unpublished data). Although the reasons for an increase in nesting occupancy are unknown, the large "floater" population – the population of non-breeding yellow-billed loons (Earnst et al. 2005) indicates that breeding opportunities are limited, likely due to limited high quality territories (Hunt 1998). The propensity of floaters to defer breeding involves trade-offs between producing a chick in the current year and future reproductive output. Rejection of vacant lakes by floaters suggests that nesting attempts on these lakes will not increase their lifetime reproductive fitness. Rather, floaters, although able to breed, may avoid the risks of breeding in the current year by deferring breeding until a high quality lake can be successfully defended from conspecifics and other loons species (Piper et al. 2006). Multiple factors influence whether floaters defer breeding, including cues from breeders and current environmental conditions (Zack and Stutchbury 1992). The increase in nesting occupancy over the study period suggests that cues reflected a trend in favorable conditions for floaters to recruit to the breeding population. Further information on the floater population would be necessary to assess these dynamics; however, less information on the floater population is available because non-breeding yellow-billed loons are more difficult to study. Floaters may be buffering changes in the breeding population (Hunt 1998), stabilizing occupancy of breeding yellow-billed loons on the ACP while simultaneously negatively impacting chick production through conspecific mortality of chicks during prospecting (Piper et al. 2006, Evers 2010). Thus, it is possible that the floater population was shrinking without any corresponding negative trend in the breeding population if the floater population is being reduced through increased recruitment to the breeding population (Franklin 1992). The increase in breeding loons appears to negatively affect chick survival, and thus, could further reduce recruitment to the floater population (Penteriani et al. 2011). Given the likely importance of the floaters to yellow-billed loon population and breeding dynamics, future efforts should include assessment of the reproductively mature floater population (e.g., floater to breeder ratio, Hunt 1998) to allow for a more comprehensive assessment of loon population dynamics.

Arctic ecosystems will continue to be a challenge to manage due to increased development pressures and the impacts of climate change. Arctic ecosystems, including the freshwater environments, have already experienced substantial change (Post et al. 2009). The paucity of ecological information exacerbates this challenge, as managers will be required to act without the scientific information necessary for informed management. This dissertation provides valuable findings that are directly relevant to current management practices and conservation concerns and also provides a basis for future research on Arctic fishes and loons. Although results from this study fill in important information gaps, the extensive gaps in the understanding of Arctic ecosystems will necessitate innovative research and management practices that are adaptive and move beyond a focus on single resource.

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