

Method- and species-specific detection probabilities of fish occupancy in Arctic lakes: implications for design and management

Trevor B. Haynes, Amanda E. Rosenberger, Mark S. Lindberg, Matthew Whitman, and Joel A. Schmutz

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 multimethod 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.

Résumé : Les études sur l'occurrence des espèces ne tiennent souvent pas compte des fausses absences dans l'échantillonnage sur le terrain. Nous nous sommes penchés sur les probabilités de détection associées à cinq types d'engins pour six espèces de poissons dans un échantillon de lacs de la North Slope, en Alaska. Nous avons utilisé une approche de modélisation de l'occupation pour obtenir des estimations des probabilités de détection pour chaque méthode. Les variations de la probabilité de détection selon l'engin et l'espèce étaient considérables. Par exemple, les probabilités de détection pour le verveux allaient de 0,82 (ET = 0,05) pour le cisco sardinelle (*Coregonus sardinella*) à 0,04 (ET = 0,01) pour le chabot visqueux (*Cottus cognatus*). Des variables propres au site avaient également une incidence sur la probabilité de détection, dont la profondeur du lac, l'année, le jour d'échantillonnage et la connexion du lac à un cours d'eau. À l'exception de l'épuisette et de la nasse à vairons placée sur la rive, chaque type d'engins offrait la probabilité de détection la plus élevée pour au moins une espèce. Ces résultats suggèrent que le recours à plusieurs méthodes pourrait être l'approche la plus efficace pour l'échantillonnage de la communauté entière de poissons d'un lac arctique. Les estimations de la probabilité de détection seront utiles à l'élaboration de protocoles optimaux d'échantillonnage et de surveillance des poissons dans les lacs arctiques. [Traduit par la Rédaction]

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 (J. Martin et al. 2009).

Recent advances in occupancy estimation (MacKenzie et al. 2002, 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.

Received 13 December 2012. Accepted 5 May 2013.

Paper handled by Associate Editor Joseph Michael Jech.

T.B. Haynes. School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.

A.E. Rosenberger. US Geological Survey, Missouri Cooperative Fish and Wildlife Research Unit, University of Missouri, Columbia, MO 65211, USA.

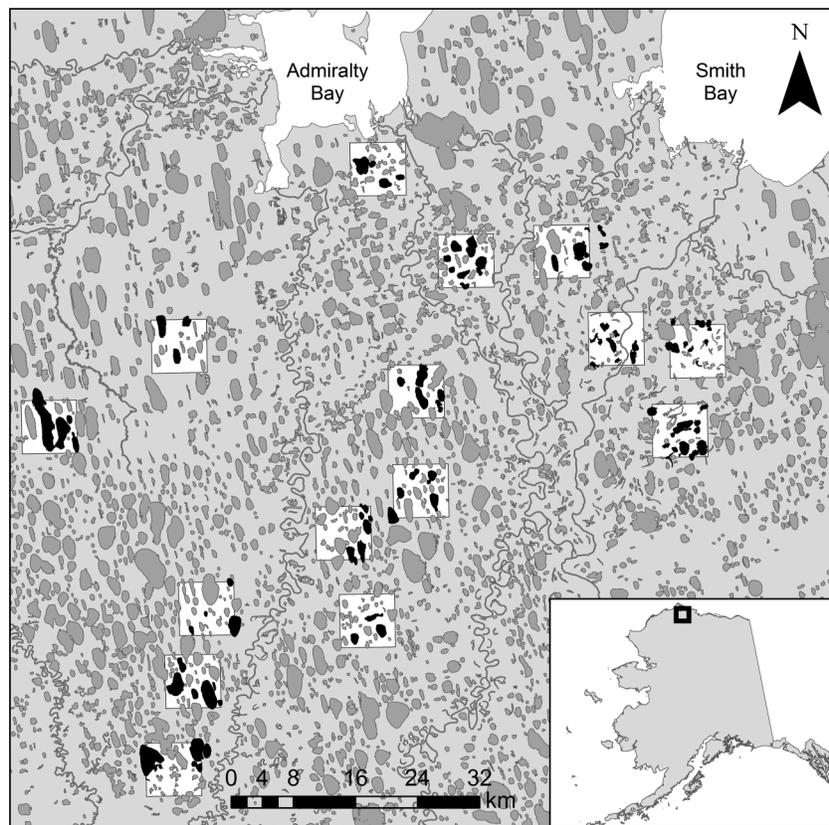
M.S. Lindberg. Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.

M. Whitman. Bureau of Land Management, Fairbanks District Office, Fairbanks, AK 99709, USA.

J.A. Schmutz. US Geological Survey, Alaska Science Center, Anchorage, AK 99508, USA.

Corresponding author: Trevor B. Haynes (e-mail: t.haynes@alaska.edu).

Fig. 1. Study area on the North Slope of Alaska. Sample plots are shown as white boxes, and sampled lakes are shaded in black.



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 are 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, 2008b). 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 (1 foot = 30.48 cm)) 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 km²) 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 (*Coregonus nasus*), and Arctic grayling (*Thymallus arcticus*). Specifically, we (i) compare detection probabilities of different gear types and (ii) 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 km × 7 km plots that were randomly distributed across the study area (Fig. 1). Within a plot, we randomly chose lakes with the following caveats: (i) 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 (ii) 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 (two nets, three temporal replicates), minnow trap (eight traps, two temporal replicates), fyke net (two nets, two temporal replicates), dip net (eight spatial replicates), and beach seine (two 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 m × 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 2–3 h 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 the 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 stretched mesh and had a frame opening of 1.1 m × 1.1 m, followed by five sequential hoop frames spaced 0.8 m apart and measuring 0.6 m × 0.6 m in size. Attached to the hoop net were two 15.2 m × 1.2 m wings and a 30.5 m × 1.2 m centerline with 0.6 cm stretched mesh. Wings and centerline had float lines and weighted lead lines. The hoop net had three net throats within the frame measuring 15 cm × 23 cm at the middle of each throat. We set nets either in the morning (0800–1200) or the evening (2000–2400) 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 cm × 38 cm × 20 cm and 41 cm × 41 cm × 41 cm) on the lakeshore. We swept nets along the lake bottom adjacent to shore for three 8 min 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.

Multimethod analysis

We used the multimethod 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 multimethod ap-

proach 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 dataset 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 2012). 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, percentage of the lake deeper than 2 m (Grunblatt and Atwood 2012), day from the beginning of sampling for each season (4 July in 2009 and 23 June 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 two-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.

Table 1. Model ranking for the multimethod 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).

Model ^a	AIC_c	ΔAIC_c	AIC weight	Likelihood	K
$p(\text{LakeDepth} + \text{LakeArea} + \text{Day} + \text{Year} + \text{Species} \times \text{Method})$	4613.90	0.00	1.00	1.00	41
$p(\text{LakeDepth} + \text{LakeArea} + \text{Species} \times \text{Method})$	4665.46	51.56	0.00	0.00	31
$p(\text{Day} + \text{Year} + \text{Species} \times \text{Method})$	4666.21	52.31	0.00	0.00	31
$p(\text{LakeDepth} + \text{LakeArea} + \text{Day} + \text{Year} + \text{Species} \times \text{Method}), \text{No Method} \times \text{Covar}$	4691.17	77.27	0.00	0.00	25
$p(\text{Species} \times \text{Method})$	4727.76	113.86	0.00	0.00	21
$p(\text{LakeDepth} + \text{LakeArea} + \text{Day} + \text{Year} + \text{Species} \times \text{Method}), \text{DMT} = \text{SMT}$	4884.54	270.64	0.00	0.00	34
$p(\text{LakeDepth} + \text{LakeArea} + \text{Day} + \text{Year} + \text{Species} + \text{Method})$	4969.04	355.14	0.00	0.00	31

Note: Fish were sampled in lakes on the Arctic Coastal Plain, Alaska.

^aAll 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 \times Covar). Detection probabilities of deep (DMT) and shore minnow traps (SMT) were estimated separately unless otherwise indicated (DMT = SMT).

Table 2. Model ranking for the multimethod analysis for large-bodied 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).

Model ^a	AIC_c	ΔAIC_c	AIC weight	Likelihood	K
$p(\text{Species} \times \text{Method} + \text{LakeArea} + \text{LakeDepth} + \text{Year} + \text{Day})$	1081.27	0.00	0.97	1.00	23
$p(\text{Species} \times \text{Method} + \text{LakeArea} + \text{LakeDepth})$	1089.39	8.12	0.02	0.02	17
$p(\text{Species} \times \text{Method} + \text{LakeArea} + \text{LakeDepth} + \text{Year} + \text{Day}), \text{No Method} \times \text{Covar}$	1091.15	9.88	0.01	0.01	15
$p(\text{Species} \times \text{Method} + \text{Year} + \text{Day})$	1092.08	10.81	0.00	0.00	17
$p(\text{Species} \times \text{Method})$	1092.46	11.19	0.00	0.00	11
$p(\text{Species} \times \text{Method} + \text{LakeArea} + \text{LakeDepth} + \text{Year} + \text{Day}), \text{BGN} \neq \text{PGN}$	1092.98	11.71	0.00	0.00	29
$p(\text{LakeArea} + \text{LakeDepth} + \text{Year} + \text{Day})$	1119.13	37.86	0.00	0.00	20

Note: Fish were sampled in lakes on the Arctic Coastal Plain, Alaska.

^aAll 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 \times Covar). Detection probabilities of benthic (BGN) and pelagic gill nets (PGN) were estimated as equal unless indicated otherwise (BGN \neq PGN).

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 (T. 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 \pm standard error unless otherwise specified.

Results

Multimethod analysis

Goodness-of-fit tests on the multimethod datasets suggested that there was no lack of fit for either small- (mean $\hat{c} \pm SD = 1.045 \pm 0.213$) or large-bodied fish analyses (mean $\hat{c} \pm SD = 0.592 \pm 0.248$); 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 1 and 2). For small-bodied species, the detection probabilities of deep and shore min-

now 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 3 and 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 5). Lake depth generally had a positive influence on detection, except in the case of sampling large-bodied species with the fyke net (logit $\beta = -0.65 \pm 0.18$). Lake area generally had a negative effect on detection, but most effects were weak with the exception of fyke net (small-bodied, logit $\beta = -0.44 \pm 0.13$), shore minnow traps (logit $\beta = -0.23 \pm 0.08$), and gill net, for which there was a positive effect (logit $\beta = 0.43 \pm 0.20$). 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 species (logit $\beta = 0.93 \pm 0.24$) and a positive but weaker effect for small-bodied species (logit $\beta = 0.15 \pm 0.11$).

Table 3. Detection probability estimates (with standard errors) of small-bodied fish species for each gear type.

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)

Note: 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.

Table 4. Detection probability estimates (with standard errors) of large-bodied fish species for each gear type.

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)

Note: 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.

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 three deep minnow traps total. Top models for both the fyke net and deep minnow trap analyses included only species effects, and model ranking suggested only limited support for sample covariates in both cases (Tables 6 and 7). Setting a fyke net near a stream connection had little effect on detection probability (logit $\beta = -0.05 \pm 0.19$; third model ($p(\text{Species} + \text{Stream})$); Table 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 $\beta = -0.11 \pm 0.17$; second model ($p(\text{Species} + \text{Time})$); Table 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 \times Species model $\Delta\text{QAIC}_c = 11.11$, Stream \times Species model $\Delta\text{QAIC}_c = 11.92$). 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 $\beta = 0.13 \pm 0.09$; second model ($p(\text{Species} + \text{MTDepth})$); Table 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

Table 5. Logit-scale regression coefficients of site covariates for the top models for small- and large-bodied fish species.

Covariate	Method	Large-bodied		Small-bodied	
		Estimate	SE	Estimate	SE
Day ^a	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 ^b	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 ^c	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		

Note: Fish were sampled in lakes on the Arctic Coastal Plain, Alaska.

^aMeasured as day from beginning of the sampling season, with the first day = 0.

^bMean \pm SD = 146.3 ± 192.8 ha, range = 15.0–1489.3 ha.

^cMean \pm SD = 92.8 ± 141.7 ha, range = 0–1109.2 ha.

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 that the use of 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 multimethod 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 invest-

Table 6. Model ranking based on Akaike's information criterion adjusted for sample size and overdispersion (QAIC_c), differences in QAIC_c (Δ 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.

Model	QAIC _c	Δ QAIC _c	QAIC _c weight	Likelihood	<i>K</i>
<i>p</i> (Species)	549.73	0.00	0.55	1.00	9
<i>p</i> (Species + Time)	551.77	2.04	0.20	0.36	10
<i>p</i> (Species + Stream)	551.92	2.19	0.18	0.33	10
<i>p</i> (Species + Stream + Time)	553.98	4.25	0.07	0.12	11
<i>p</i> (Species + Time + Time \times Species)	560.84	11.11	0.00	0.00	15
<i>p</i> (Species + Stream + Stream \times Species)	561.65	11.92	0.00	0.00	15
<i>p</i> (.)	568.77	19.04	0.00	0.00	4

Note: 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. Fish were sampled in lakes on the Arctic Coastal Plain, Alaska.

ment 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-Aroita 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 (Fig. 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-Aroita 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 streamlined sampling, which often

Table 7. Model ranking based on Akaike's information criterion adjusted for sample size and overdispersion (QAIC_c), differences in QAIC_c (Δ QAIC_c), model weight, model likelihood, and number of parameters (*K*) for the single-season model of deep minnow trap detection probability analysis for small-bodied fish species.

Model	QAIC _c	Δ QAIC _c	QAIC _c weight	Likelihood	<i>K</i>
<i>p</i> (Species)	486.24	0.00	0.34	1.00	5
<i>p</i> (Species + MTDepth)	486.89	0.65	0.25	0.72	6
<i>p</i> (Species + MTDepth + Species \times MTDepth)	486.90	0.66	0.25	0.72	7
<i>p</i> (.)	488.89	2.65	0.09	0.27	4
<i>p</i> (MTDepth)	489.35	3.11	0.07	0.21	5

Note: Model set included models with the depth of the deep 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. Fish were sampled in lakes on the Arctic Coastal Plain, Alaska.

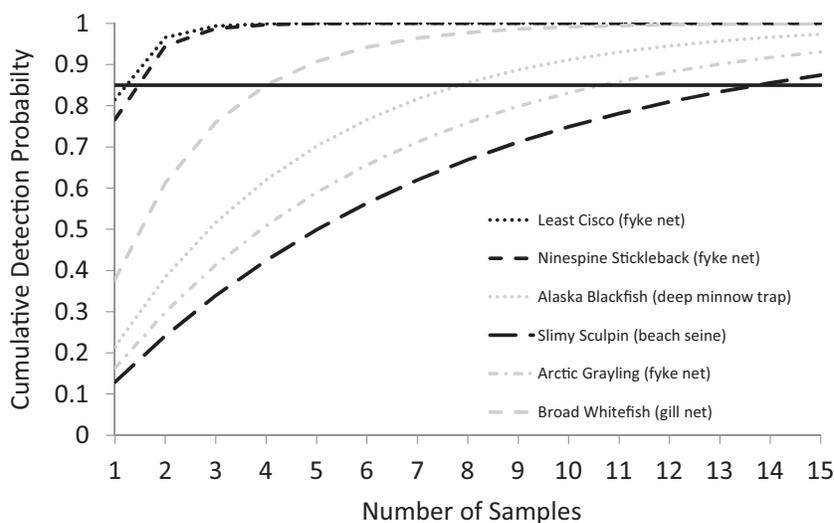
leads to less mortality. Regardless of species or method, our results suggest that multiple samples are required to detect species with the high degree of confidence necessary to avoid bias (i.e., detection probability ≥ 0.9 ; McKann et al. 2012).

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 >2 m in depth), suggesting that most gear types are more effective at capturing target species in lakes that have a higher percentage of their area >2 m 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 because of 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

Fig. 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.



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; Mookerji et al. 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 that 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 fu-

ture. 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 prone to have the strongest impact in Arctic regions (P. Martin et al. 2009), and there is anticipated to be major changes in the function of freshwater ecosystems in the North Slope (Wrona et al. 2006; Reist 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.

Acknowledgements

The authors thank contributors, including Mary Rabe, Kim Titus, and the Wildlife Diversity Program at Alaska Department of Fish & Game; Jeff Adams, Bill Carter, and the Fisheries Division at US Fish and Wildlife Service – Fairbanks; and Debbie Nigro and Bureau of Land Management – Fairbanks. John Pearce and two anonymous reviewers made helpful suggestions on earlier drafts of this manuscript. Data collection would not have been possible without the indispensable help of the field assistants and pilots who aided in the fieldwork. This project was funded by a State Wildlife Grant awarded through Alaska Department of Fish & Game. TBH was funded by a Natural Sciences and Engineering Research Council of Canada postgraduate scholarship.

References

Bailey, L.L., Hines, J.E., Nichols, J.D., and MacKenzie, D.I. 2007. Sampling design trade-offs in occupancy studies with imperfect detection: examples and soft-

- ware. *Ecol. Appl.* **17**(1): 281–290. doi:10.1890/1051-0761(2007)017[0281:SDTIOS]2.0.CO;2. PMID:17479851.
- Bohl, E. 1979. Diel pattern of pelagic distribution and feeding in planktivorous fish. *Oecologia*, **44**(3): 368–375. doi:10.1007/BF00545241.
- Bonar, S.A., Hubert, W.A., and Willis, D.W. 2009. Standard methods for sampling North American freshwater fishes. American Fisheries Society, Bethesda, Maryland.
- Burnham, K.P., and Anderson, D.S. 2002. Model selection and multi-model inference. Springer-Verlag, New York.
- Cott, P.A., Sibley, P.K., Gordon, A.M., Bodaly, R.A., Mills, K.H., Somers, W.M., and Fillatre, G.A. 2008a. Effects of water withdrawal from ice-covered lakes on oxygen, temperature, and fish. *JAWRA J. Am. Water Resour. Assoc.* **44**(2): 328–342. doi:10.1111/j.1752-1688.2007.00165.x.
- Cott, P.A., Sibley, P.K., Somers, W.M., Lilly, M.R., and Gordon, A.M. 2008b. A review of water level fluctuations on aquatic biota with an emphasis on fishes in ice-covered lakes. *JAWRA J. Am. Water Resour. Assoc.* **44**(2): 343–359. doi:10.1111/j.1752-1688.2007.00166.x.
- Donovan, T.M., and Hines, J. 2006. Exercises in occupancy modeling and estimation [online]. Available from <http://www.uvm.edu/envnr/vtcfwru/spreadsheets/occupancy.htm> [accessed 6 March 2012].
- Elton, C.S. 1927. Animal ecology. Meuthen, London.
- Grunblatt, J., and Atwood, D. 2012. Habitat inventory: mapping lakes on the North Slope Coastal Plain of Alaska using Synthetic Aperture Radar (SAR). Unpublished Report.
- Guillera-Arroita, G., and Lahoz-Monfort, J.J. 2012. Designing studies to detect differences in species occupancy: power analysis under imperfect detection. *Method. Ecol. Evol.* **3**(5): 860–869. doi:10.1111/j.2041-210X.2012.00225.x.
- Guillera-Arroita, G., Ridout, M.S., and Morgan, B.J.T. 2010. Design of occupancy studies with imperfect detection. *Method. Ecol. Evol.* **1**(2): 131–139. doi:10.1111/j.2041-210X.2010.00017.x.
- Guisan, A., and Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. *Ecol. Model.* **135**(2): 147–186. doi:10.1016/S0304-3800(00)00354-9.
- Hershey, A.E., Gettel, G.M., McDonald, M.E., Miller, M.C., Mooers, H., O'Brien, W.J., Pastor, J., Richards, C., and Schuldt, J.A. 1999. A geomorphic-trophic model for landscape control of Arctic lake food webs. *Bioscience*, **49**(11): 887–897. doi:10.2307/1313648.
- Hershey, A.E., Beaty, S., Fortino, K., Keyse, M., Mou, P.P., O'Brien, W.J., Ulseth, A.J., Gettel, G.A., Lienesch, P.W., Luecke, C., McDonald, M.E., Mayer, C.H., Miller, M.C., Richards, C., Schuldt, J.A., and Whalen, S.C. 2006. Effect of landscape factors on fish distribution in arctic Alaskan lakes. *Freshw. Biol.* **51**(1): 39–55. doi:10.1111/j.1365-2427.2005.01474.x.
- Hines, J.E. 2006. PRESENCE2 — software to estimate patch occupancy and related parameters [online]. USGS-PWRC. Available from <http://www.mbr-pwrc.usgs.gov/software/presence.html>.
- Kahilainen, K., Malinen, T., Tuomala, A., and Lehtonen, H. 2004. Diel and seasonal habitat and food segregation of three sympatric *Coregonus lavaretus* forms in a subarctic lake. *J. Fish Biol.* **64**(2): 418–434. doi:10.1111/j.0022-1112.2004.00307.x.
- Kendall, W.L., and White, G.C. 2009. A cautionary note on substituting spatial subunits for repeated temporal sampling in studies of site occupancy. *J. Appl. Ecol.* **46**(6): 1182–1188. doi:10.1111/j.1365-2664.2009.01732.x.
- Krebs, C.J. 1978. The experimental analysis of distribution and abundance. Harper & Row, New York.
- Levy, D.A. 1990. Reciprocal diel vertical migration behavior in planktivores and zooplankton in British Columbia lakes. *Can. J. Fish. Aquat. Sci.* **47**(9): 1755–1764. doi:10.1139/f90-199.
- Long, R.A., Donovan, T.M., MacKay, P., Zielinski, W.J., and Buzas, J.S. 2011. Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. *Landsc. Ecol.* **26**(3): 327–340. doi:10.1007/s10980-010-9547-1.
- MacKenzie, D.I., and Bailey, L.L. 2004. Assessing the fit of site-occupancy models. *J. Agric. Biol. Environ. Stat.* **9**(3): 300–318. doi:10.1198/108571104X3361.
- Mackenzie, D.I., and Royle, J.A. 2005. Designing occupancy studies: general advice and allocating survey effort. *J. Appl. Ecol.* **42**(6): 1105–1114. doi:10.1111/j.1365-2664.2005.01098.x.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, A.J., and Langtimm, C.A. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**(8): 2248–2255. doi:10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2.
- MacKenzie, D.I., Nichols, J.D., Sutton, N., Kawanishi, K., and Bailey, L.L. 2005. Improving inferences in population studies of rare species that are detected imperfectly. *Ecology*, **86**(5): 1101–1113. doi:10.1890/04-1060.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., and Hines, J.E. 2006. Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence. Elsevier Academic Press, Burlington, Massachusetts.
- MacKenzie, D.I., Seamans, M.E., Gutiérrez, R.J., and Nichols, J.D. 2012. Investigating the population dynamics of California spotted owls without marked individuals. *J. Ornithol.* **152**(S2): 597–604. doi:10.1007/s10336-010-0544-6.
- Martin, J., Runge, M.C., Nichols, J.D., Lubow, B.C., and Kendall, W.L. 2009. Structured decision making as a conceptual framework to identify thresholds for conservation and management. *Ecol. Appl.* **19**(5): 1079–1090. doi:10.1890/08-0255.1. PMID:19688917.
- Martin, P.D., Jenkins, J.L., Adams, F.J., Jorgenson, M.T., Matz, A.C., Payer, D.C., Reynolds, P.E., Tidwell, A.C., and Zelenak, J.R. 2009. Wildlife Response to Environmental Arctic Change: Predicting Future Habitats of Arctic Alaska. Report of the Wildlife Response to Environmental Arctic Change (WildREACH): Predicting Future Habitats of Arctic Alaska Workshop, 17–18 November 2008, US Fish and Wildlife Service, Fairbanks, Alaska.
- Mattfeldt, S.D., and Grant, E. 2007. Are two methods better than one? Area constrained transects and leaf litterbags for sampling stream salamanders. *Herpetol. Rev.* **38**(1): 43–45.
- McKann, P.C., Gray, B.R., and Thogmartin, W.E. 2012. Small sample bias in dynamic occupancy models. *J. Wildl. Manage.* **77**(1): 172–180. doi:10.1002/jwmg.433.
- MJM Research. 2001. Fish utilization of lakes in Eastern NPR-A: 1999–2001. Report prepared for ConocoPhillips Alaska, Inc., Anchorage, Alaska.
- MJM Research. 2007. Survey of lakes in support of CPAI exploration prospects — 2007. Report prepared for ConocoPhillips Alaska, Inc., Anchorage, Alaska, and Anadarko Petroleum Corporation, The Woodlands, Texas.
- Moilanen, A. 2002. Implications of empirical data quality to metapopulation model parameter estimation and application. *Oikos*, **96**(3): 516–530. doi:10.1034/j.1600-0706.2002.960313.x.
- Mookerji, N., Heller, C., Meng, H.J., Bürgi, H.R., and Müller, R. 1998. Diel and seasonal patterns of food intake and prey selection by *Coregonus* sp. in re-oligotrophic Lake Lucerne, Switzerland. *J. Fish Biol.* **52**(3): 443–457. doi:10.1111/j.1095-8649.1998.tb02009.x.
- Natsumeda, T. 1998. Home range of the Japanese fluvial sculpin, *Cottus pollux*, in relation to nocturnal activity patterns. *Environ. Biol. Fishes*, **53**(3): 295–301. doi:10.1023/A:1007410519726.
- Nichols, J.D., Bailey, L.L., O'Connell, A.F., Jr., Talancy, N.W., Campbell Grant, E.H., Gilbert, A.T., Annand, E.M., Husband, T.P., and Hines, J.E. 2008. Multi-scale occupancy estimation and modelling using multiple detection methods. *J. Appl. Ecol.* **45**(5): 1321–1329. doi:10.1111/j.1365-2664.2008.01509.x.
- Nielsen, L.A., and Johnson, D.L. 1983. Fisheries techniques. American Fisheries Society, Blacksburg, Virginia.
- Pavlacky, D.C., Blakesley, J.A., White, G.C., Hanni, D.J., and Lukacs, P.M. 2012. Hierarchical multi-scale occupancy estimation for monitoring wildlife populations. *J. Wildl. Manage.* **76**(1): 154–162. doi:10.1002/jwmg.245.
- Reist, J.D., Wrona, F.J., Prowse, T.D., Power, M., Dempson, J.B., King, J.R., and Beamish, R.J. 2006. An overview of effects of climate change on selected Arctic freshwater and anadromous fishes. *AMBIO*, **35**(7): 381–387. doi:10.1579/0044-7447(2006)35[381:A00EOC]2.0.CO;2. PMID:17256642.
- Royle, J.A., and Nichols, J.D. 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology*, **84**(3): 777–790. doi:10.1890/0012-9658(2003)084[0777:EAFRPA]2.0.CO;2.
- Smith, L.C., Sheng, Y., and MacDonald, G.M. 2007. A first pan-Arctic assessment of the influence of glaciation, permafrost, topography and peatlands on northern hemisphere lake distribution. *Permafrost Periglac.* **18**(2): 201–208. doi:10.1002/ppp.581.
- Tyre, A.J., Possingham, H.P., and Lindenmayer, D.B. 2001. Inferring process from pattern: can territory occupancy provide information about life history parameters? *Ecol. Appl.* **11**(6): 1722–1737. doi:10.1890/1051-0761(2001)011[1722:IPFPCT]2.0.CO;2.
- Wrona, F.J., Prowse, T.D., Reist, J.D., Hobbie, J.E., Lévesque, L.M., and Vincent, W.F. 2006. Climate change effects on aquatic biota, ecosystem structure and function. *AMBIO*, **35**(7): 359–369. doi:10.1579/0044-7447(2006)35[359:CCEOAB]2.0.CO;2. PMID:17256640.