

Trophic dynamics of shrinking Subarctic lakes: naturally eutrophic waters impart resilience to rising nutrient and major ion concentrations

Tyler L. Lewis^{1,3} · Patricia J. Heglund² · Mark S. Lindberg¹ · Joel A. Schmutz³ · Joshua H. Schmidt⁴ · Adam J. Dubour¹ · Jennifer Rover⁵ · Mark R. Bertram⁶

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Abstract Shrinking lakes were recently observed for several Arctic and Subarctic regions due to increased evaporation and permafrost degradation. Along with lake drawdown, these processes often boost aquatic chemical concentrations, potentially impacting trophic dynamics. In particular, elevated chemical levels may impact primary productivity, which may in turn influence populations of primary and secondary consumers. We examined trophic dynamics of 18 shrinking lakes of the Yukon Flats, Alaska, that had experienced pronounced increases in nutrient (>200 % total nitrogen, >100 % total phosphorus) and ion concentrations (>100 % for four major ions combined) from 1985–1989 to 2010–2012, versus 37 stable lakes with relatively little chemical change over the same period. We found that phytoplankton stocks, as indexed by

chlorophyll concentrations, remained unchanged in both shrinking and stable lakes from the 1980s to 2010s. Moving up the trophic ladder, we found significant changes in invertebrate abundance across decades, including decreased abundance of five of six groups examined. However, these decadal losses in invertebrate abundance were not limited to shrinking lakes, occurring in lakes with stable surface areas as well. At the top of the food web, we observed that probabilities of lake occupancy for ten waterbird species, including adults and chicks, remained unchanged from the period 1985–1989 to 2010–2012. Overall, our study lakes displayed a high degree of resilience to multi-trophic cascades caused by rising chemical concentrations. This resilience was likely due to their naturally high fertility, such that further nutrient inputs had little impact on waters already near peak production.

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✉ Tyler L. Lewis
tlewis@usgs.gov

¹ Department of Biology and Wildlife and Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA

² US Fish and Wildlife Service, 2630 Fanta Reed Road, La Crosse, WI 54603, USA

³ US Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, USA

⁴ US National Park Service, Central Alaska Network, 4175 Geist Road, Fairbanks, AK 99709, USA

⁵ US Geological Survey, Earth Resources Observation and Science (EROS) Center, 47914 252nd Street, Sioux Falls, SD 57198, USA

⁶ US Fish and Wildlife Service, Yukon Flats National Wildlife Refuge, 101 12th Avenue, Room 264, Fairbanks, AK 99701, USA

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Introduction

The highest global concentration of lakes occurs at Arctic and Subarctic latitudes (Verpoorter et al. 2014), providing important habitat for a diversity of wildlife species. The regions' abundant lakes are largely a byproduct of its cold climate, in which short ice-free seasons limit evapotranspiration and widespread permafrost inhibits soil permeability (Ford and Bedford 1987). In recent decades, however, Arctic and Subarctic areas have experienced a period of unprecedented warming (New et al. 2011), potentially stressing the region's long-term water balance. In particular, warmer temperatures may lead to longer ice-free seasons and increased evaporative water loss (Magnuson et al.

2000; Smol and Douglas 2007a, b), while simultaneously increasing drainage of lake water via degradation of extant permafrost (Jorgenson et al. 2001; Jepsen et al. 2013a, b). To date, net losses in lake surface area have been documented for certain Arctic and Subarctic regions of Alaska (Riordan et al. 2006; Rover et al. 2012), Canada (Smol and Douglas 2007a, b; Carroll et al. 2011), and Siberia (Smith et al. 2005).

Two of the major processes causing losses in lake surface area—increased evaporation and permafrost thaw—may simultaneously generate pronounced changes in water chemistry (Lewis et al. 2015a). Increased evaporation, if not balanced by concurrent increases to water inputs, concentrates solutes into smaller water volumes. Lakes that lose water in this manner tend to exhibit greater increases in nutrient and ion concentrations than those that lose water via surface outflow or subsurface infiltration (Fritz 1996). At the same time, thawing permafrost, by exposing previously frozen organic matter to decomposition and flushing, may increase nutrient and ion concentrations in nearby lakes (Petrone et al. 2006; Wrona et al. 2006). Overall, recent research has indicated that shrinking lakes, relative to their stable counterparts, have higher specific conductivities (Roach et al. 2011), indicative of higher ion loads, and higher nitrogen and phosphorus concentrations (Corcoran et al. 2009; Lewis et al. 2015a).

Despite these compelling trends for shrinking lakes, little is known about how such chemical changes may impact ecosystem processes. In general, nitrogen and phosphorus, rather than light or carbon, limit productivity in shallow Arctic and Subarctic lakes (Ogbebo et al. 2009). Accordingly, as nitrogen and phosphorus levels increase, shrinking lakes may experience elevated productivity, in which the added nutrients stimulate primary production and thereby add more overall energy to the lake ecosystem (Dodson et al. 2000). Increased primary productivity at the base of the food web may then transfer upward to primary consumers, thereby driving increases in their abundance and biomass (Peterson et al. 1993; Slavik et al. 2004). In northern lakes, primary consumer communities are typically dominated by aquatic invertebrates, whose populations may quickly track changes in primary productivity because of their low generation times and high fecundity (Greig et al. 2012). For example, artificial fertilization of a shallow Arctic lake caused increased benthic and planktonic primary production, which in turn supported a three- to fivefold increase in snail densities (Hershey 1992; Hobbie et al. 1999). However, chironomid densities in this same Arctic lake were unaffected by nutrient additions, demonstrating that the response of invertebrates to fertilization varies widely by taxa. In addition to nutrients, abundance of aquatic invertebrates also varies in response to salinity, although this is based more on physiology than on trophic

energy flow (Pinder et al. 2005). As ions concentrate in shrinking lakes (Lewis et al. 2015a), raising salinity levels, invertebrates with low salt tolerances may become osmotically stressed, causing reduced growth or death (James et al. 2003). Hence, simultaneous increases of nutrients and ions in shrinking lakes may have varying effects on invertebrate abundance, favoring some taxa while harming others.

Aquatic invertebrates constitute the primary prey base for a variety of predators in Arctic and Subarctic lakes, including fish and waterbirds (Lewis et al. 2015b). Accordingly, changes in invertebrate abundance may transfer upward to the highest trophic levels, thereby influencing distributions and abundance of several animals that hold significant anthropogenic and economic value. In this manner, rising nutrient concentrations in shrinking lakes may ultimately cascade across multiple trophic levels, from primary producers to aquatic invertebrates to predators (Carpenter et al. 1985). Such multi-trophic cascades have been experimentally demonstrated in freshwater systems through the use of artificial fertilization; long-term additions of phosphorus to an Arctic stream caused a positive response at all trophic levels, including increases in algal stocks, grazing invertebrate densities, and fish growth rates (Slavik et al. 2004). In addition to multi-trophic impacts caused by nutrient additions, pronounced changes in salinity may also impact top-level predators by causing osmotic stress, especially for fishes, while having little impact on waterbirds and other semi-aquatic species (James et al. 2003).

Our study was situated on lakes of the Yukon Flats, Alaska, which are characterized by their shallow depth, colored water, and high fertility, with over 70 % classified as eutrophic or hypereutrophic on the basis of their nutrient loads (Heglund and Jones 2003). In recent decades, high evaporation rates (Anderson et al. 2013), decreased snowfall (Jepsen et al. 2013b), and thawing permafrost (Jepsen et al. 2013a) have contributed to net losses in lake surface area across this Subarctic region. These losses in lake area caused substantial chemical changes; of 55 lakes originally sampled for water chemistry during the period 1985–1989, eighteen shrank over the intervening 25 years, leading to mean solute concentrations that had, by 2010–2012, increased by 237 % for total nitrogen, 131 % for total phosphorus, 49 % for calcium, 510 % for chloride, 66 % for magnesium, and 118 % for sodium (Lewis et al. 2015a). In particular, the more than doubling of nitrogen and phosphorus concentrations occurred despite many of these lakes being eutrophic since the 1980s. Conversely, of the remaining 37 lakes with stable surface areas, mean chemical concentrations changed much less over the same time period: +76 % for total nitrogen, –50 % for total phosphorus, +10 % for calcium, +118 % for chloride, +49 % for magnesium, and –2 % for sodium (see Table 1 for water chemistry values). These same 55 lakes were simultaneously sampled for abundance of common autotrophic and heterotrophic organisms, providing us a

Table 1 Mean (\pm SE) aquatic concentrations (mg/l) of nutrients (total nitrogen, total phosphorus) and major ions (calcium, chloride, magnesium, sodium) for shrinking ($n = 18$) and stable lakes ($n = 37$) of the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012

	Shrinking lakes		Stable lakes	
	1985–1989	2010–2012	1985–1989	2010–2012
Total nitrogen	1.55 \pm 0.49	5.24 \pm 0.49	1.10 \pm 0.35	1.93 \pm 0.34
Total phosphorus	0.38 \pm 0.15	0.87 \pm 0.16	0.13 \pm 0.10	0.06 \pm 0.11
Calcium	22.65 \pm 3.93	33.85 \pm 3.97	24.51 \pm 2.75	27.00 \pm 2.76
Chloride	11.84 \pm 16.54	72.24 \pm 16.25	3.56 \pm 11.68	7.76 \pm 11.28
Magnesium	30.89 \pm 8.31	51.31 \pm 8.33	16.05 \pm 5.80	23.99 \pm 5.80
Sodium	200.64 \pm 140.75	437.38 \pm 142.81	22.92 \pm 98.97	22.49 \pm 99.25

unique opportunity to examine impacts of chemical changes on trophic dynamics of shrinking lakes. Specifically, we examined changes in abundance and distributions of several lacustrine organisms in shrinking versus stable lakes of the Yukon Flats from the period 1985–1989 to 2010–2012, focusing on three broad trophic levels: (a) phytoplankton, indexed by chlorophyll concentration; (b) aquatic invertebrates; and (c) waterbirds, which served as top predators in the absence of fish. Moreover, our study design, though non-manipulative, offered a before-after-control-impact (BACI) framework, with control (stable lakes) and experimental (shrinking lakes) units measured both pre- (1985–1989) and post-impact (2010–2012). BACI designs, which are rarely available for naturally occurring impacts such as ours, avoid the primary pitfall of many environmental impact studies, in which differences between experimental and control sites may be unrelated to the impact, having existed beforehand.

Overall, the goals of our study were twofold, assuming aspects of both exploratory and confirmatory research:

- Exploratory—we provide an initial examination of how ecosystems of Subarctic lakes, particularly those with naturally high nutrient levels, responded to enduring losses in surface area, thereby gaining novel insights that inform future research and conservation efforts.
- Confirmatory—using a bottom-up trophic framework, we predicted that increased nutrient concentrations in shrinking lakes would stimulate phytoplankton production, which would then support increased abundance of aquatic invertebrates, including primary and secondary consumers. More abundant invertebrate populations would subsequently influence waterbird distributions, evident via increased waterbird occupancy rates on shrinking lakes during the most recent decade.

Materials and methods

Study area

The Yukon Flats is a large basin in interior Alaska bisected by the Yukon River and encompassed by the 34,800-km²

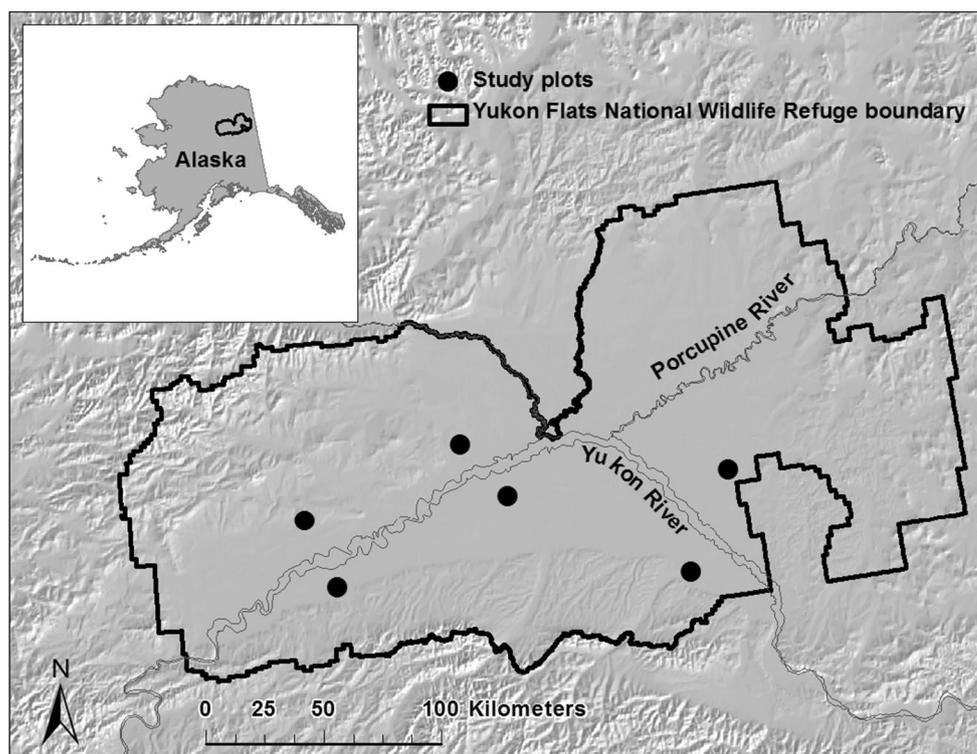
Yukon Flats National Wildlife Refuge (Fig. 1). The refuge contains >40,000 lakes and wetlands and is largely pristine natural habitat. Of >15,000 lakes examined in the region, 9–16 % decreased in surface area extent from 1979 to 2009 (Rover et al. 2012). The area has a continental Subarctic climate, characterized by low precipitation (17 cm year⁻¹) and seasonal temperature extremes (summer average, 15 °C; winter average, -27 °C), and is underlain by continuous and discontinuous permafrost (Pastick et al. 2013). Mixed boreal forest covers much of the Yukon Flats and is dominated by black (*Picea mariana*) and white (*Picea glauca*) spruce, Alaska birch (*Betula neolaskana*), quaking aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and willow (*Salix* spp.).

Our research was conducted on six randomly selected plots located throughout the Yukon Flats National Wildlife Refuge (Fig. 1). These plots, which were originally used for limnological and avian research in the 1980s (Heglund and Jones 2003), measured 10.36 km² and contained from seven to 17 lakes, for a total of 77 study lakes. Of these study lakes, 55 were large enough (>1 ha) to be reliably classified as shrinking versus stable using remotely sensed imagery (see “Lake surface area” below), ranging in size from 1.2 to 283.2 ha with a mean of 15.77 ha. Our study lakes were uniformly shallow (mean depth = 0.94 m), rarely measuring deeper than 2 m, and were generally located within closed basins that had few well-defined inlets or outlets. This combination of shallow depth and lack of surface outlets precluded fish in all our study lakes.

Chlorophyll samples

During the period 1985–1989, we sampled total chlorophyll concentration of each lake one to two times per month (June–September) in 2 of 5 years, with the exception of 15 lakes sampled in ≥ 3 years. We re-sampled these same lakes ($n = 55$) for chlorophyll concentration from 2010 to 2012, sampling each lake once per month (June–August) in 2 of 3 years, with the exception of 17 lakes sampled all 3 years. Our chlorophyll samples were collected from the water column and we used identical field methods in each decade. First, we collected 8 l of water from near the lake’s

Fig. 1 Map of the study area in the Yukon Flats National Wildlife Refuge, Alaska, showing the location of the six study plots



midpoint and 25 cm below the surface. We then filtered measured volumes of lake water through Gelman A/E glass fiber filters (Pall, Port Washington, NY) until a visually noticeable algal stain developed, collecting two filters per sample event. Following their use, we immediately placed filters in protective sleeves, desiccated them with silica gel beads, and kept them in dark, cool storage until transported to freezers. In the laboratory, we extracted chlorophyll with 90 % ethanol and used fluorometric methods to measure its concentration (Knowlton 1984), using this same procedure and laboratory (Jones Limnology Lab, University of Missouri, Columbia, MO) in each decade. Our final chlorophyll values were averaged from the two filters collected per sample event and were corrected for the volume of water passed through each filter.

Aquatic invertebrate samples

Our study lakes were initially sampled for aquatic invertebrates from 1985 to 1989. Because intra-annual sample dates from this period were missing, we were unable to assess number of sample events per lake per month; however, most lakes were sampled in 2 of 5 years, thus including sources of inter-annual variation. We re-sampled these same lakes ($n = 55$) for aquatic invertebrates from 2010 to 2012, sampling each lake once per month (June–July) in 2 of 3 years, with the exception of 17 lakes sampled all 3 years. We collected aquatic invertebrates along

transects located at random locations along lake perimeters and oriented perpendicular to shore. We scaled number of transects to lake area, with a minimum of two and maximum of 21 transects per lake. Along each transect we collected one invertebrate sample per vegetative zone, and a typical transect contained two samples. Vegetative zones included emergent and submergent vegetation, with the most common plants being cattail (*Typha latifolia*), pondweed (*Potamogeton* spp.), sedge (*Carex* spp.), and hornwort (*Ceratophyllum demersum*). In the event that we encountered one or no vegetative zone, we collected an extra sample in the open water zone. We used a standardized D-frame sweep net (0.5-mm mesh) to collect invertebrates from the water column, pulling it horizontally for 1 m just below the surface and through the vegetation. We placed invertebrates in ethanol and transported them to the laboratory, where we identified them to minimal taxonomic groupings, typically family, and enumerated number of individuals per group. We replicated our field and laboratory methods for invertebrate collections across decades, including the number and location of transects at each lake.

Waterbird surveys

We surveyed each lake from 1985 to 1989 for waterbirds 1–3 times per month in 2 of 5 years, with the exception of 18 lakes that we surveyed in each of 4 years. We re-surveyed these same lakes ($n = 77$) from 2010 to 2012,

surveying each lake one or two times per month (June–August) in 2 of 3 years (2010–2012), except for 17 lakes that we surveyed all 3 years. We timed our surveys to cover the breeding cycle, from nesting (June) through brood-rearing (July–August). We surveyed waterbirds from shore on small lakes and from canoes on large lakes. We recorded species, sex, and age (adult vs. chick) of each individual observed on the lake. Our survey methods were replicated across decades, with the exception that our 2010–2012 surveys consisted of two independent counts conducted over a 1- to 2-day period to allow for estimation of detection probability (see “Analyses”). See Lewis et al. (2015b) for a complete description of our repeat survey methods.

Lake surface area

We used linear trends in lake surface area from 1979 to 2011, following methods described in Rover et al. (2012), to categorize each of our study lakes ($n = 55$) as shrinking ($>20\%$ decrease; median = 34% decrease, range = 21 – 94% decrease) or stable ($<20\%$ decrease; median = 4% decrease, range = 19% decrease to 34% increase). We derived lake surface areas across the 32-year period from Landsat data with a supervised decision tree classification model to differentiate water from terrestrial surfaces. We selected Landsat data for 22 unique acquisition dates that provided minimal cloud obstruction across a wide geographic area. These 22 dates covered 16 of the 32 years and the bulk of the ice-free season (8 May–16 September), thus including sources of both intra- and inter-annual variation. We used a conservative cut-off of $>20\%$ loss in surface area to classify lakes as shrinking, rather than a continuous description, to account for the coarse resolution (30 m pixel) of Landsat imagery and the high degree of inter-annual variation in surface area. Further, we restricted this classification to lakes with a surface area >1 ha ($n = 55$) because lakes smaller than this size could not be reliably classified using Landsat imagery.

Chlorophyll and invertebrate analyses

Our first analysis examined changes in chlorophyll levels from the period 1985–1989 to 2010–2012 in shrinking versus stable lakes. We used log chlorophyll concentration (micrograms per liter) as our response variable for a series of general linear mixed models, applying the log transformation to account for otherwise heteroscedastic residuals. Our model set consisted of five a priori models containing combinations of the following covariates: ordinal date (intra-annual date on a scale of 1–366), decade (defined categorically as 1980s vs. 2010s), extent (defined categorically as shrinking vs. stable), and an interaction between decade and extent. The interaction term provided important

insight into long-term impacts of chemical changes on shrinking lakes; under a BACI study design, a significant effect of the ecological impact appears via the interaction between site (stable vs. shrinking lake) and time (1985–1989 vs. 2010–2012). We included ordinal date in every model to control for intra-annual differences in chlorophyll levels, which was not our primary interest, but could confound our interpretation. We also included lake identity and year as random effects in all models to account for pseudoreplication and explain added uncertainty incurred by sampling a particular population of lakes. This analysis was restricted to lakes with a surface area >1 ha ($n = 55$), from which we analyzed 869 chlorophyll samples collected across the two decadal periods.

We next examined changes in abundance of aquatic invertebrates from the period 1985–1989 to 2010–2012 in shrinking versus stable lakes, focusing on six taxonomic groups that were both abundant and important prey of waterbirds: Amphipoda, Chironomidae, Coleoptera, Corixidae, Gastropoda, and Odonata. These six taxa together accounted for 65% of total invertebrates in our samples. For each taxonomic group we fit a series of generalized linear mixed models using raw invertebrate counts (no. per sample) as our response variable. Such count data are often fit with Poisson models; however, our variance was degrees of magnitude larger than the mean, suggesting Poisson models were inappropriate. Hence, we fit our most parameterized model with Poisson, negative binomial, and zero-inflated Poisson and negative binomial distributions, and then compared the model fit with Akaike’s information criterion (AIC). Our model selection indicated that a negative binomial provided the best fit for our count data, and all further models were fit using this distribution. As further confirmation, we compared distributions of our raw count data to post hoc predictions based on our mixed models to ensure that the negative binomial distribution properly fit our data. Our model set was identical to that used for our chlorophyll analysis, except that ordinal date, being unavailable for our 1980s data, was not included in any model. We included lake identity as a random effect in all models and restricted this analysis to lakes with a surface area >1 ha ($n = 55$). Our analysis consisted of 4881 invertebrate samples with a combined count of 336,178 individuals.

Chlorophyll and invertebrate models were fit using the nlme (Pinheiro et al. 2013) and lme4 (Bates et al. 2014) packages in program R, respectively. We used an information-theoretic approach to model selection (Burnham and Anderson 2002), in which model fit was compared using AIC and AIC weights (w_i). We based inference of fixed effects on model selection metrics (Δ AIC, w_i) and precision of parameter estimates (β). When 95% confidence intervals (CIs) overlapped 0, the parameter was deemed

uninformative. In our results, we present all parameter estimates as $\beta \pm 95\%$ CI.

Waterbird analyses

We examined decadal changes in distributions of waterbirds on lakes of the Yukon Flats by fitting a hierarchical Bayes' single-season occupancy model to our waterbird survey data (MacKenzie et al. 2002). These models simultaneously estimated probability of lake occupancy (ψ) and probability that a waterbird was detected given presence (p). Such models were appropriate for our data because of the low detection probabilities observed for many waterbird species, especially during the breeding season when broods and hens are highly secretive (Walker et al. 2013; Lewis et al. 2015b). We converted counts of each species per lake per survey to presence (one or more individuals detected) or absence (not detected).

Occupancy models require temporally replicated presence/absence data to simultaneously estimate ψ and p (MacKenzie et al. 2002). To accommodate this data structure, surveys are designed in a nested fashion whereby a primary survey consists of $k \geq 2$ secondary surveys. Moreover, occupancy models assume that the occurrence state of a site does not change over the duration of a primary survey. For waterbirds, which are highly mobile, this assumption is typically met by conducting all secondary surveys either simultaneously, or within a narrow time frame (e.g., <24 h). Our 1980s surveys, however, did not incorporate temporally replicated secondary surveys (i.e., $k = 1$). Rather, while we surveyed each lake multiple times per year in the 1980s, days to weeks elapsed between each survey. Accordingly, to create the nested data structure needed for occupancy models, we treated each survey per lake per year as a secondary survey, with the whole of these secondary surveys combining to create the primary survey unit. Thus, each primary survey contained 1 year of survey data per lake. This design violates the closure assumption because waterbirds may have emigrated from a lake during our primary survey unit. Violation of this assumption, however, is not always that problematic because temporary absence of a species from a site will be incorporated as one component of imperfect detection (Kéry and Schaub 2011). Consequently, for our study, ψ is defined as the proportion of lakes occupied at least once during the decadal study period, rather than the proportion of lakes that were permanently occupied, as would be the case had the closure assumption been met (Mordecai et al. 2011; Kéry and Schaub 2011).

Our 2010–2012 survey design differed from that of the 1980s in that each waterbird survey consisted of $k = 2$ secondary surveys, each being completed within a 24-h window (Lewis et al. 2015a, b). Accordingly, to create

consistency between our decadal datasets for occupancy modeling, we combined each of these original secondary surveys from 2010 to 2012 into one presence/absence record. Next, we treated each survey from 2010 to 2012 as a secondary survey, thereby matching our 1980s data structure in which secondary surveys were separated by days to weeks. Under this updated data structure, we conducted 189 primary surveys that contained, on average, $k = 3.66$ secondary surveys during the period 1985–1989, versus 169 primary surveys containing an average of $k = 3.45$ secondary surveys during the period 2010–2012.

We fit one occupancy model for each of the ten most common waterbird species observed during our surveys, which together accounted for >95% of individuals counted: American wigeon (*Anas americana*), canvasback (*Aythya valisineria*), green-winged teal (*Anas crecca*), horned grebe (*Podiceps auritus*), mallard (*Anas platyrhynchos*), northern pintail (*Anas acuta*), northern shoveler (*Anas clypeata*), ring-necked duck (*Aythya collaris*), lesser scaup (*Aythya affinis*), and white-winged scoter (*Melanitta fusca*). We fit separate models for adults and chicks of each species, for a total of 20 occupancy models (i.e., 10 species \times 2 age groups). We modeled p in relation to two covariates that may affect detection: ordinal date, which controlled for time-dependent changes in waterbird growth and behavior, and decade (1980s vs. 2010s), which accounted for decadal differences in survey design. Specifically, we expected that p would be higher during the period 2010–2012 because surveys conducted then consisted of two replicated counts, as explained above. We modeled ψ in relation to one covariate, decade, to assess changes in distributions of waterbirds from the period 1985–1989 to 2010–2012. We did not include extent (stable vs. shrinking lake) as a covariate, nor the decade \times extent interaction, because our occupancy models generally failed to converge upon parsing of our survey data into further categories. Moreover, this allowed us to include data from 22 lakes that were too small (<1 ha) for accurate lake extent categorization, raising our sample size from 55 to 77 lakes. Finally, we modeled p and ψ using the logit-link function and included lake identity as a random effect in all occupancy models.

We performed Bayesian analysis of occupancy models using R2WinBUGS in program R (Sturtz et al. 2005), which called on WinBUGS version 1.4 (Lunn et al. 2000) to run a Markov chain Monte Carlo algorithm. We used an uninformative normal prior with a logit-scale mean of 0 and SD of 0.01. We normalized continuous covariates to a mean of 0 and assessed convergence using the R-hat statistic (Gelman and Hill 2007). We based our inference regarding effect sizes of covariates on posterior means and 95% Bayesian credible intervals (BCI). When 95% BCI overlapped 0, we deemed the covariate uninformative. Likewise, for each waterbird species, we deemed broadly

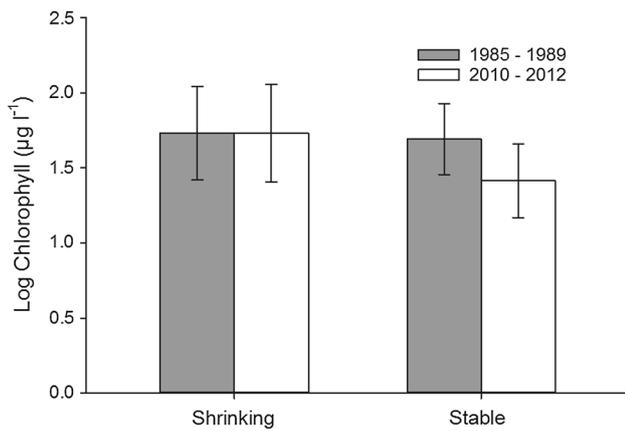


Fig. 2 Aquatic concentration of chlorophyll (µg/l) for shrinking ($n = 18$) and stable lakes ($n = 37$) of the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012. Data are restricted to lakes with surface areas >1 ha. Mean concentrations \pm 95 % confidence intervals (CI) are based on parameter estimates from the global model

Table 2 Model selection results from linear mixed models describing variation in log chlorophyll concentration (µg/l) in shrinking and stable lakes of the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012

Model ^a	Δ AIC	k	w_i
Ordinal + extent	0	6	0.44
Ordinal + decade + extent	0.58	7	0.33
Ordinal + decade + extent + decade \times extent	1.34	8	0.23
Ordinal	763.09	5	0
Ordinal + decade	764.55	6	0

Models are listed in order of Δ Akaike information criterion (AIC) and we also present number of parameters (k) and model weights (w_i). Data are restricted to lakes with surface areas >1 ha ($n = 55$). Covariates include Ordinal (intra-annual date), Decade (1980 vs. 2010s), Extent (shrinking vs. stable), and a Decade \times Extent interaction

^a All models included random effects of lake and year

overlapping 95 % BCI across decades to indicate a lack of difference in ψ from the period 1985–1989 to 2010–2012.

Results

Chlorophyll

Losses in lake surface area had no discernible impact on chlorophyll concentrations of Yukon Flats lakes. Chlorophyll levels in stable ($n = 37$) and shrinking lakes ($n = 18$) remained relatively unchanged from 1985–1989 to 2010–2012 (Fig. 2). The decade \times extent interaction,

Table 3 Parameter estimates (*Est.*), unconditional SEs, and lower (LCI) and upper 95 % confidence intervals (UCI) from linear mixed models describing variation in log chlorophyll concentration (µg/l) in shrinking and stable lakes of the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012

Covariate	Est.	SE	LCI	UCI
Intercept	1.66	0.22	1.23	2.09
Ordinal	0.01	0.01	−0.01	0.03
Decade ^a	−0.19	0.16	−0.50	0.12
Extent ^a	−0.18	0.13	−0.43	0.07
Decade \times extent ^a	−0.28	0.25	−0.77	0.21

Parameter estimates and associated SE and CI are derived from the top model in which the parameter occurred. Data are restricted to lakes with surface areas >1 ha ($n = 55$). Covariates include Ordinal (intra-annual date), Decade (1980 vs. 2010s), Extent (shrinking vs. stable), and a Decade \times Extent interaction

^a Reference values: Decade—2010s; Extent—Stable; Decade \times Extent—2010s \times Stable

which tested for unequal decadal changes in chlorophyll levels in stable versus shrinking lakes, received low support ($w_i = 0.23$; Table 2) and had a parameter estimate with a 95 % CI that broadly overlapped 0 ($\beta = -0.28 \pm 0.49$; Table 3). The best-fitting model ($w_i = 0.44$) contained ordinal date and extent as covariates (Table 2), indicating that chlorophyll levels were nominally higher in shrinking versus stable lakes. However, the parameter estimate for extent was poorly estimated ($\beta = -0.18 \pm 0.25$; Table 3) and there was considerable overlap of 95 % CIs between stable and shrinking lakes (Fig. 2). Finally, the model with decade and extent received moderate support ($w_i = 0.33$), but both covariates (decade, $\beta = -0.19 \pm 0.31$) had 95 % CI that widely overlapped 0 (Table 3).

Aquatic invertebrates

Abundance of five invertebrate groups—Amphipoda, Coleoptera, Corixidae, Gastropoda, and Odonata—decreased from 1985–1989 to 2010–2012, while that of Chironimidae increased over the same period. However, with the exception of Amphipoda and Corixidae, these decadal changes in abundance were largely independent of losses in lake area, having similar magnitude and direction of change for both shrinking ($n = 18$) and stable ($n = 37$) lakes (Fig. 3). For Gastropoda and Odonata, the best-supported-model contained the covariate of decade (Table 4) and indicated that their abundances decreased by 78 and 50 % from the period 1980–1989 to the period 2010–2012, respectively. Moreover, the decade covariate was precisely estimated for both Gastropoda ($\beta = -1.51 \pm 0.16$) and Odonata ($\beta = -0.69 \pm 0.18$), in sharp contrast to decade \times extent which had 95 % CIs that widely overlapped 0 (Gastropoda $\beta = -0.26 \pm 0.37$; Odonata $\beta = 0.12 \pm 0.41$).

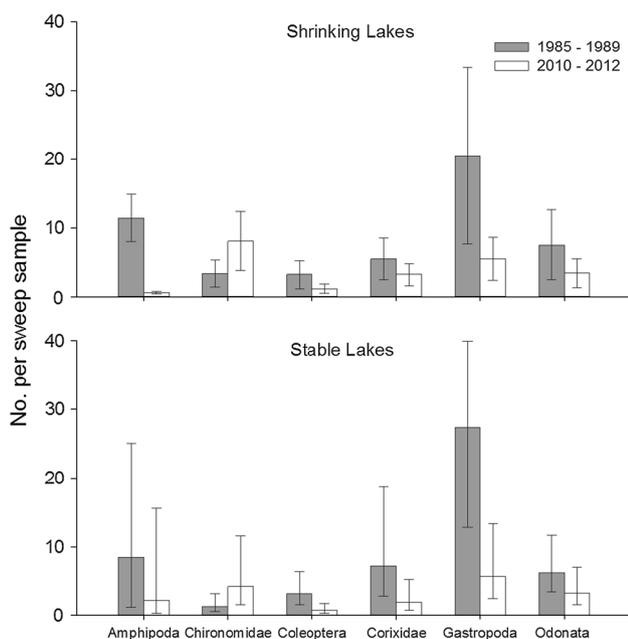


Fig. 3 Abundance (no./sweep sample) of six groups of aquatic invertebrates in shrinking ($n = 18$) and stable lakes ($n = 37$) of the Yukon Flats, Alaska, across two time periods: 1985–1989 vs. 2010–2012. Data are restricted to lakes with surface areas >1 ha. Mean abundance $\pm 95\%$ CIs are based on parameter estimates from the global model

For Coleoptera and Chironomidae, the best-supported model contained decade \times extent (Table 4), suggesting distinct decadal changes in abundance in shrinking versus stable lakes. However, decade \times extent was poorly estimated with a 95% CI that overlapped zero for Coleoptera ($\beta = -0.42 \pm 0.43$) and Chironomidae ($\beta = 0.31 \pm 0.51$), versus the decade covariate which was well estimated with a large effect size (Coleoptera $\beta = -1.34 \pm 0.20$; Chironomidae $\beta = 1.08 \pm 0.24$; Table 5). Predicted model values indicate that Coleoptera abundance decreased by 74% from the 1980s to 2010s, while that of Chironomidae increased by 194% over the same period. Overall, of all covariates considered, decade had the largest effect size and most precise estimate for all six invertebrate groups (Table 5).

For Amphipoda and Corixidae, decadal losses in abundance differed for shrinking ($n = 18$) versus stable lakes ($n = 18$), with Amphipoda declining by 95% in shrinking versus 74% in stable lakes and Corixidae declining by 42% in shrinking versus 73% in stable lakes. Model selection results for both taxa were unequivocal, providing no support for models lacking decade \times extent ($w_i = 0$; Table 4). Moreover, decade \times extent parameter estimates were large, negative, and well-estimated for both Amphipoda and Corixidae (Table 5).

Waterbirds

Probability of lake occupancy ($n = 77$ lakes) for adults of ten waterbird species did not differ from the period 1985–1989 to 2010–2012 (Fig. 4). For all ten species, 95% BCI from 1985 to 1989 broadly overlapped those from 2010 to 2012. Moreover, overlapping credible intervals were not driven by poor precision, as nine of ten species had 95% BCI with a range of ≤ 0.28 for each decade. Likewise, with the exception of ring-necked ducks, point estimates of occupancy probability were remarkably steady across decades, differing by <0.10 from the period 1985–1989 to 2010–2012. For adult ring-necked ducks, the point estimate of occupancy probability in the period 1985–1989 ($\psi = 0.21$) was markedly lower than that observed in the period 2010–2012 ($\psi = 0.47$). However, 95% BCI from the 1980s for this species were imprecise (95% BCI = 0.02, 0.71) and widely overlapped those of the 2010s (95% BCI = 0.47, 0.56), primarily due to poor detection probability ($p = 0.10$) during the 1980s (Table 6).

Similar to adults, probability of lake occupancy for chicks of the ten species did not differ from the period 1985–1989 to 2010–2012 (Fig. 4). The 95% BCI from the period 1985–1989 overlapped those from the period 2010 to 2012 for all ten species. However, 95% BCI were generally less precise than for adults, especially for mallards, northern shovellers, and ring-necked ducks. Likewise, for all ten waterbird species, probabilities of detection for chicks (Table 6) were considerably lower than those of adults.

Discussion

Using an exceptional historic database that benchmarked past lake conditions, we found that lakes with substantial losses in surface area did not exhibit unique changes, relative to stable lakes, in chlorophyll concentrations, aquatic invertebrate abundance, or waterbird distributions. These results, which spanned at least three trophic levels, suggest that long-term chemical changes in shrinking lakes of the Subarctic did not trophically propagate through lake ecosystems. Moreover, our results occurred despite the pronounced magnitude of chemical changes in shrinking lakes, including increased concentrations of $>200\%$ for total nitrogen, $>100\%$ for total phosphorus, $>40\%$ for calcium, $>500\%$ for chloride, $>50\%$ for magnesium, and $>100\%$ for sodium (Lewis et al. 2015a). While our findings depict two snapshots of lake environments in the 1980 and 2010s, each decadal sampling period consisted of at least 3 years of data from 55 lakes, suggesting a prevailing ecological pattern that overrides lake-to-lake and

Table 4 Model selection results from generalized linear mixed models describing variation in abundance (no./sweep sample) of six groups of aquatic invertebrates in shrinking and stable lakes of the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012

Invertebrate	Model ^a	Δ AIC	k	w_i
Amphipoda	Decade + extent + decade \times extent	0	6	1.00
	Decade	43.82	4	0
	Decade + extent	44.66	5	0
	Null	397.86	3	0
	extent	399.50	4	0
Chironomidae	Decade + extent + decade \times extent	0	6	0.50
	Decade + extent	0.32	5	0.42
	Decade	3.67	4	0.08
	Extent	117.39	4	0
	Null	120.51	3	0
Coleoptera	Decade + extent + decade \times extent	0	6	0.73
	Decade + extent	3.31	5	0.14
	Decade	3.47	4	0.13
	Extent	332.48	4	0
	Null	333.00	3	0
Corixidae	Decade + extent + decade \times extent	0	6	1.00
	Decade	18.79	4	0
	Decade + extent	19.59	5	0
	Null	307.78	3	0
	Extent	309.13	4	0
Gastropoda	Decade	0	4	0.55
	Decade + extent + decade \times extent	1.62	6	0.24
	Decade + extent	1.90	5	0.21
	Null	501.93	3	0
	Extent	503.81	4	0
Odonata	Decade	0	4	0.63
	Decade + extent	1.79	5	0.26
	Decade + extent + decade \times extent	3.31	6	0.12
	Null	83.14	3	0
	Extent	84.88	4	0

Models are listed in order of Δ AIC and we also present k and w_i . Data are restricted to lakes with surface areas >1 ha ($n = 55$). Covariates include decade (1980 vs. 2010s), extent (shrinking vs. stable), and a decade \times extent interaction. For abbreviations, see Table 2

^a All models included random effect of lake

year-to-year variation. Furthermore, our BACI study design provides a high level of inference strength, being based on shrinking and stable lakes that were measured both before and after reductions in lake surface area.

Under a bottom-up trophic framework, the minimal influence of rising chemical concentrations on trophic dynamics starts at the base of the food web, where we observed no decadal changes in chlorophyll levels. This result was unexpected given the large magnitude of nutrient enrichment in shrinking lakes, along with previous studies that observed increased algal production following fertilization of high-latitude lakes and streams (Slavik et al. 2004; O'Brien et al. 2005). Most of these studies, however, occurred in oligo- or mesotrophic waterbodies characterized by strong nutrient limitations and clear waters (e.g.,

Hobbie et al. 1999; Schindler et al. 2008). Conversely, in eutrophic lakes, planktonic chlorophyll production may reach some upper limit after which water transparency becomes so low that light is limiting, regardless of nutrient conditions (Schindler 1978). Our study lakes have some of the highest documented nutrient levels for Subarctic regions and generally qualify as eutrophic or hypereutrophic, even before the recent nutrient increases (Heglund and Jones 2003; Lewis et al. 2015a). Accordingly, planktonic chlorophyll production in our study lakes may have neared its upper limits dating back to the 1980s, such that recent nutrient increases had little impact. Moreover, these upper limits may be relatively low for our study lakes due to their pronounced discoloration and high loads of suspended solids, both of which exacerbate light attenuation

Table 5 Model-averaged parameter estimates (*Est.*) and SEs from generalized linear mixed model describing variation in abundance (no./sweep) of six groups of aquatic invertebrates in shrinking and

stable lakes of the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012

Covariate	Amphipoda		Chironomidae		Coleoptera		Corixidae		Gastropoda		Odonata	
	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE
Intercept	2.38 ^b	0.76	1.19 ^b	0.37	1.15 ^b	0.29	1.69 ^b	0.35	3.21 ^b	0.15	1.87 ^b	0.14
Decade ^a	-1.74 ^b	0.10	1.08 ^b	0.12	-1.34 ^b	0.10	-1.15 ^b	0.08	-1.51 ^b	0.08	-0.69 ^b	0.09
Extent ^a	0.79	0.91	-0.68	0.39	-0.36	0.32	-0.38	0.40	0.29	0.33	-0.09	0.24
Decade × Extent ^a	1.60 ^b	0.24	0.31	0.26	-0.42	0.22	-0.79 ^b	0.19 [†]	-0.26	0.19	0.12	0.21

Parameter estimates and associated SEs for each covariate are derived from the following models: Intercept—top model as ranked by AIC; Decade and Extent—top model as ranked by AIC, with the exception of the interaction model; Decade × Extent—the interaction model. Data presented in this table are restricted to lakes with surface areas >1 ha ($n = 55$). Covariates include Decade (1980, 2010s), Extent (shrinking, stable, expanding), and a Decade × Extent interaction

^a Reference values for categorical parameters: Decade—2010s; Extent—stable; Decade × Extent—2010s × stable

^b Parameter estimates with 95 % CI that did not include zero

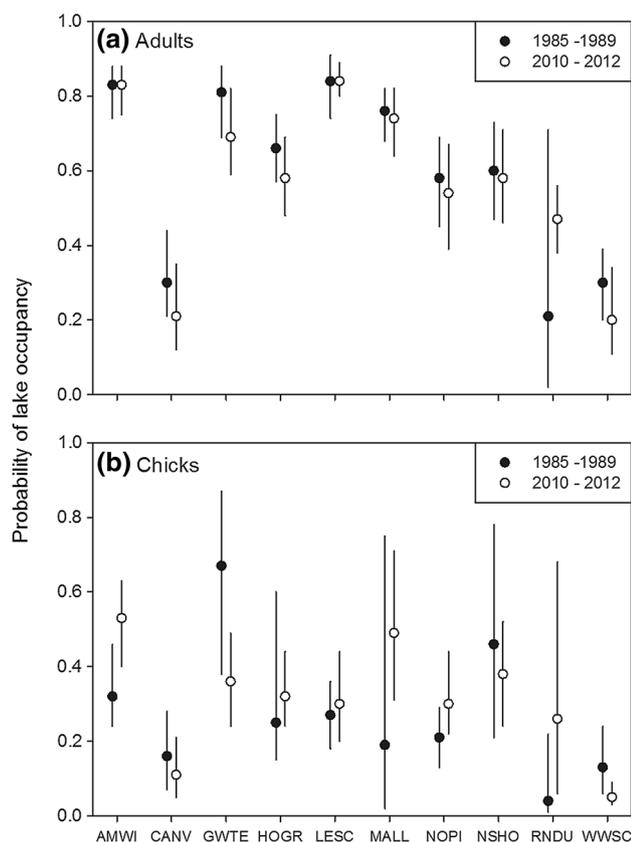


Fig. 4 Mean probability of lake occupancy \pm 95 % Bayesian credible intervals for **a** adults and **b** chicks of ten species of waterbirds in the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012. Data were included for 77 study lakes, irrespective of surface area. Waterbird species include American wigeon (*AMWI*), Canvasback (*CANV*), green-winged teal (*GWTE*), horned grebe (*HOGGR*), lesser scaup (*LESC*), mallard (*MALL*), northern pintail (*NOPI*), northern shoveler (*NSHO*), ring-necked duck (*RNDU*), and white-winged scoter (*WWSC*)

(Heglund and Jones 2003). As a whole, we suggest that this combination of lake qualities—a long-established eutrophic state and high light attenuation—uniquely positioned our shrinking lakes to be relatively resilient to nutrient enrichment, thereby maintaining stable levels of chlorophyll production.

In addition to this built-in resilience, various other factors may have contributed to our observed lack of chlorophyll change in shrinking lakes. First, our nutrients were measured as total nitrogen and total phosphorus, which include all chemical forms irrespective of their bioavailability (Lewis et al. 2015a). As a result, some portion of the nutrient gains in our shrinking lakes were likely recalcitrant and unavailable to phytoplankton, thereby limiting shifts in chlorophyll levels. This contrasts sharply with artificial fertilization studies, in which added nutrients are readily bioavailable and quickly incorporated into aquatic food webs (e.g., Peterson et al. 1993; Slavik et al. 2004). Second, our chlorophyll samples were obtained on a monthly or bimonthly basis, providing periodic snapshots of standing phytoplankton stocks. In shallow, eutrophic lakes such as ours, grazing zooplankton can filter the entire water column daily, depressing standing stocks of phytoplankton even though their rates of production may be high (Hanson and Butler 1994). Thus, phytoplankton production in our shrinking lakes may have increased in response to nutrient enrichment, yet remained unapparent in our samples due to rapid phytoplankton turnover by zooplankton grazers. Likewise, our snapshots of chlorophyll levels may not detect nutrient-driven increases to overall annual production, especially if such increases are spread over what is now a longer ice-free season (Smol and Douglas 2007b, Surdu et al. 2014). Finally, nutrient enrichment in shrinking

Table 6 Probability of detection (p) and lower (LBCI) and upper 95 % Bayesian credible intervals (UBCI) for ten species of waterbird adults and chicks on lakes of the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012

Waterbird species	1985–1989			2010–2012		
	p	LBCI	UBCI	p	LBCI	UBCI
Adults						
American wigeon	0.64	0.60	0.68	0.64	0.58	0.69
Canvasback	0.42	0.35	0.47	0.49	0.39	0.58
Green-winged teal	0.54	0.48	0.58	0.59	0.54	0.65
Horned grebe	0.57	0.53	0.62	0.70	0.65	0.75
Lesser scaup	0.65	0.61	0.69	0.66	0.62	0.71
Mallard	0.51	0.46	0.57	0.63	0.57	0.68
Northern pintail	0.59	0.55	0.64	0.53	0.47	0.60
Northern shoveler	0.57	0.52	0.62	0.60	0.54	0.65
Ring-necked duck	0.10	0.02	0.22	0.58	0.52	0.65
White-winged scoter	0.54	0.48	0.60	0.51	0.44	0.61
Chicks						
American wigeon	0.31	0.25	0.39	0.45	0.37	0.55
Canvasback	0.26	0.18	0.35	0.45	0.36	0.59
Green-winged teal	0.12	0.08	0.18	0.35	0.23	0.45
Horned grebe	0.21	0.09	0.33	0.65	0.51	0.93
Lesser scaup	0.29	0.23	0.37	0.69	0.57	0.79
Mallard	0.06	0	0.19	0.35	0.25	0.42
Northern pintail	0.18	0.13	0.23	0.37	0.28	0.44
Northern shoveler	0.10	0.05	0.16	0.24	0.18	0.32
Ring-necked duck	0.44	0	0.95	0.58	0.13	1
White-winged scoter	0.22	0.14	0.34	0.68	0.48	0.93

Data include all study lakes, irrespective of surface area, for a total of $n = 77$ lakes

lakes may have positively impacted primary producers that our study did not monitor, especially macrophytes and periphyton which commonly dominate productivity in shallow high-latitude lakes (Rautio et al. 2011). For example, research from Arctic Alaska found that the emergent macrophytes *Carex aquatilis* and *Arctophila fulva*, both of which are common in the Yukon Flats, dominated in-lake primary production relative to phytoplankton (Lougheed et al. 2011).

Further up the trophic chain, we found large changes in invertebrate abundance from the period 1985–1989 to 2010–2012, including decreased abundance of five of the six groups we examined: Amphipoda, Coleoptera, Corixidae, Gastropoda, and Odonata. These decadal changes, however, co-occurred in shrinking and stable lakes, suggesting that losses in invertebrate abundance were systematic and largely unrelated to changes in surface area and water chemistry. Instead, such widespread invertebrate declines suggest a more pervasive cause, especially given the large spatial scale (~900,000 ha) from which our study lakes were located. Foremost, summer temperatures at northern latitudes have increased by at least twice the global average (New et al. 2011), including significant increases in the Yukon Flats over recent decades (Anderson et al. 2013;

Jepsen et al. 2013a). Warmer air temperatures have likely driven concurrent increases in lake temperatures, including higher summer maxima (Lougheed et al. 2011). Such aquatic warming may be especially pronounced in our shallow study lakes because of their high surface to volume ratios, closed basins, and nearly 24-h solar incidence during summer. Additionally, summer air temperatures in the Yukon Flats are higher than for any other comparable latitude in North America, occasionally exceeding 37 °C. For aquatic invertebrates, lake temperatures may exceed their physiological tolerances more frequently than during previously cooler decades, potentially causing losses in abundance over time (Wrona et al. 2006). In particular, warm water holds less dissolved oxygen, thereby causing oxygen stress that can be directly lethal for invertebrates, or increase their susceptibility to other environmental stressors (Sprague 1963; Wrona et al. 2006). Moreover, our study lakes are inherently prone to deoxygenation due to their stagnant waters and high loads of rotting vegetation. In addition to the physiologic challenges, warmer water temperatures may also influence aquatic invertebrates via phenological changes. In particular, longer ice-free seasons and earlier algal production may negatively impact aquatic invertebrates by creating phenologic mismatches between

resource availability and important life cycle stages such as breeding and larval development (Wrona et al. 2006).

While five of six invertebrate groups declined in abundance over time, Chironomidae larvae increased in abundance by approximately 190 % from the period 1985–1989 to 2010–2012. Chironomidae are among the most tolerant of aquatic invertebrates to temperature and oxygen extremes, commonly serving as bioindicators of water quality (Saether 1979; Ferrington 2008). Much of this tolerance stems from their remarkable diversity, which often exceeds 80 species/site in the Nearctic (Ferrington 2008). As lakes undergo state transitions, for example shifting towards high temperature or low oxygen conditions, the high diversity of Chironomidae increases the likelihood that a species will be present that can thrive in the new conditions. In the Yukon Flats, significantly higher summer air temperatures, as discussed above, have likely caused concurrent increases to lake temperatures, with potential for episodic hypoxia of lake waters. These changes to lake environments, while negatively impacting most invertebrate groups, may have favored certain species of Chironomidae tolerant to such conditions, leading to our observed increase in Chironomidae abundance over time. Indeed, such patterns have been documented in the paleolimnological records of several Arctic lakes, where large increases in Chironomidae abundance, particularly for “warm-water” taxa, occurred simultaneous with rising lake water temperatures (Quinlan et al. 2005).

As opposed to biological responses, the observed differences in invertebrate abundance may have, in part, resulted from unknown differences in sampling protocols across decades. We attempted to exactly replicate invertebrate collection methods from the period 1985–1989 to 2010–2012. However, decadal differences in our sampling procedures, such as removal of invertebrates from the net, sweep length, and sweep depth, may have unknowingly occurred. Such hypothetical sampling differences, if consistent across decades, would ultimately manifest via our estimates of invertebrate abundance, including increased distance between 1980s versus 2010s estimates. As well, some covariates from our 1980s invertebrate database were lost over time, including intra-annual sample date and vegetation type. Again, if these covariates unknowingly differed across decades, then their omission from our analyses may have influenced our decadal estimates of invertebrate abundance. Overall, however, the sheer magnitude of changes, including losses in abundance of >70 % for Gastropoda, Coleoptera, and Amphipoda, suggests a real temporal shift in invertebrate abundance that cannot be solely attributed to differences in sampling methods.

At the top of the food web, we observed that lake occupancy of waterbirds, including adults and chicks, remained unchanged from 1985–1989 to 2010–2012. While our

waterbird data did not allow us to analytically separate stable versus shrinking lakes, the remarkable stability of our occupancy estimates across decades suggests that losses in surface area had, at most, minimal impact on waterbird distributions. Moreover, this decadal stability in occupancy probability was notably consistent, spanning ten species of waterbirds. Viewed from an ecosystem perspective, our waterbird results fit our overall observation that chemical changes in shrinking lakes did not initiate a series of trophic cascades. Nonetheless, the decadal stability in waterbird occupancy was unforeseen given the wide-ranging losses in invertebrate abundance. In the absence of fish, waterbirds are the top predators on our study lakes during summer, feeding primarily on aquatic invertebrates (Lewis et al. 2015b). Thus, we expected that losses in invertebrate abundance would lead to lower occupancy levels during the most recent decade, as waterbirds abandoned lakes with too few invertebrates. Comparisons with other Subarctic boreal regions, however, indicate that invertebrate abundance in our study lakes remained relatively favorable despite recent decadal losses (e.g., Haszard and Clark 2007; Gurney 2011). For example, our mean densities of Amphipoda, Gastropoda, and Odonata each exceeded 100 m^{-3} during 2010–2012 (Lewis et al. 2015b), providing ample prey for waterbirds. Accordingly, we suggest that losses of invertebrate abundance, while substantial, had a minimal impact on waterbirds to date, being of insufficient magnitude to impact waterbird occupancy.

Our inference on waterbird populations and their response to habitat changes was based on estimates of occupancy probability, as opposed to abundance. For large populations, occupancy can, at times, be unresponsive to changing habitats, mainly because large numerical changes may have little impact on presence/absence (MacKenzie et al. 2006). Our study lakes, however, were generally small, with a mean surface area of 15 ha, and supported likewise small waterbird populations; e.g., for eight of ten species, counts averaged fewer than seven adults and one chick per lake. Such small lakes and low counts allow occupancy to rapidly change in accordance with shifting lake habitats, as opposed to large lakes that harbor large waterbird numbers. Moreover, previous research from our study area indicated that waterbird occupancy was sensitive to invertebrate abundance (Lewis et al. 2015b). Finally, it was difficult to view all the waterbirds from one shore-based location during our surveys, thus requiring observers to move around the lake via canoe. These movements caused birds to redistribute across the lake, making our surveys prone to double-counting. Under such circumstances, occupancy is less prone to over-estimation bias than is abundance (MacKenzie et al. 2006), thereby providing a better fit for our survey design.

In summary, we observed that ecosystems of Yukon Flats lakes were largely resilient to rising chemical concentrations associated with long-term losses in surface area. While decadal changes to ecosystems were observed, most notably for aquatic invertebrates, these changes were not exclusive to shrinking lakes, following similar paths in lakes with stable surface areas and little long-term chemical change. Much of this resilience was likely due to our study lakes' historically high nutrient levels, such that further increases in nitrogen and phosphorus had little impact on waters already near peak production. For shrinking lakes of other northern regions, our results suggest that those with naturally eutrophic waters are well positioned to withstand ecosystem-wide impacts caused by chemical changes. This apparent resilience, however, cannot be extended to oligotrophic lake systems, which often respond differently to nutrient enrichment (Schindler et al. 2008), nor into the future, primarily owing to sustained climatic warming that may further impact surface area and water chemistry of northern lakes. Often, lake ecosystems exhibit a high degree of resilience up to some threshold, after which they undergo abrupt changes to alternative states (Carpenter 2003). For our study lakes, and lakes of similar Arctic and Subarctic regions, this hypothetical threshold may be quickly approaching given the high magnitude of chemical changes and losses in surface area that have already occurred.

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