

Multi-trophic resilience of boreal lake ecosystems to forest fires

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Abstract. Fires are the major natural disturbance in the boreal forest, and their frequency and intensity will likely increase as the climate warms. Terrestrial nutrients released by fires may be transported to boreal lakes, stimulating increased primary productivity, which may radiate through multiple trophic levels. Using a before-after-control-impact (BACI) design, with pre- and postfire data from burned and unburned areas, we examined effects of a natural fire across several trophic levels of boreal lakes, from nutrient and chlorophyll levels, to macroinvertebrates, to waterbirds. Concentrations of total nitrogen and phosphorus were not affected by the fire. Chlorophyll *a* levels were also unaffected, likely reflecting the stable nutrient concentrations. For aquatic invertebrates, we found that densities of three functional feeding groups did not respond to the fire (filterers, gatherers, scrapers), while two groups increased (shredders, predators). Amphipods accounted for 98% of shredder numbers, and we hypothesize that fire-mediated habitat changes may have favored their generalist feeding and habitat ecology. This increase in amphipods may, in turn, have driven increased predator densities, as amphipods were the most numerous invertebrate in our lakes and are commonly taken as prey. Finally, abundance of waterbird young, which feed primarily on aquatic invertebrates, was not affected by the fire. Overall, ecosystems of our study lakes were largely resilient to forest fires, likely due to their high initial nutrient concentrations and small catchment sizes. Moreover, this resilience spanned multiple trophic levels, a significant result for ecologically similar boreal regions, especially given the high potential for increased fires with future climate change.

Key words: aquatic invertebrates; boreal forest; ecological subsidy; forest fire; freshwater food web; resilience; trophic ecology; waterbirds.

INTRODUCTION

Fires are one of the most widespread and severe disturbances in many ecosystems, and thereby play an important role in regulating ecosystem structure and function. Although a terrestrial disturbance in origin, the effects of fires extend to aquatic ecosystems via cross-habitat transfers of energy and nutrients (Bisson et al. 2003). Fires release nutrients and organic matter locked in terrestrial resources such as soils and vegetation, making them available for transport to aquatic ecosystems. Yields of nitrogen and phosphorus, the two most commonly limiting nutrients for vegetative growth, frequently increase in aquatic systems following fires (Carignan et al. 2000, McEachern et al. 2000). Depending on fire and catchment characteristics, nutrient increases can be quite dramatic; following a forest fire in a pristine catchment, aquatic nitrate increased ninefold, total nitrogen twofold, and total phosphorus fourfold (Kelly et al. 2006). Importantly, this flux of energy and nutrients from terrestrial to aquatic habitats,

known as an ecological subsidy (Polis et al. 2004), may be a significant driver of aquatic productivity across several trophic levels.

At the outset, elevated aquatic nutrients often stimulate primary productivity, typically evident via increased phytoplanktonic and benthic chlorophyll *a* (Scrimgeour et al. 2001, Kelly et al. 2006). Increased primary production may, in turn, drive increases in secondary production of aquatic herbivores, which are often dominated by invertebrates in freshwater systems (Malison and Baxter 2010a). Aquatic invertebrates in Canadian lakes had greater biomass in burned vs. unburned areas, and this persisted 15–20 years postfire (Scrimgeour et al. 2001). However, changes in secondary consumer communities following fires are difficult to generalize, and are typically related to the stochastic nature of fire disturbance, as well as the ecology of the impacted invertebrates (Minshall 2003). For example, shredders in streams may decline postfire due to the loss of allochthonous leaf detritus, while scrapers may thrive in response to increased periphyton growth (Minshall 2003, Mellon et al. 2008). Finally, consumers specializing on aquatic invertebrates may also benefit from forest fires, as the pulse of aquatic productivity travels up trophic levels. Fish growth rates were 12–30% greater following a forest fire, presumably in response to

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increased abundance of invertebrate food sources (Kelly et al. 2006).

In the boreal forest, fires are the major natural disturbance, and their long-term frequency and intensity are predicted to increase as the climate warms (Chapin et al. 2008). The area burned in the North American boreal forest tripled from the 1960s to 1990s, mainly because of an increased frequency of extreme fire years (Kasischke and Turetsky 2006). During the 1990s and 2000s alone, >25% of Alaska's boreal forest burned (Kasischke et al. 2010). Because much of the boreal forest lies in the permafrost zone, effects of boreal fires on aquatic ecosystems may be especially pronounced. Permafrost stores large amounts of organic carbon and nutrients that are largely removed from active biogeochemical cycling; however, by removing the vegetative layers that insulate the ground, fires may accelerate thawing of permafrost and subsequent activation of its stored organic matter (O'Donnell et al. 2011). Thus, in addition to aboveground biomass released during the fire, boreal fires may also increase the release and transport of permafrost-associated nutrients, some of which may ultimately enrich aquatic ecosystems.

Boreal wetlands and lakes account for ~50% of global lake surface area (Schindler 1998), and are internationally important bird areas, annually supporting >15 million breeding waterbirds in North America. Nonetheless, little is known of fire impacts on boreal lakes, especially those impacts on aquatic food webs. Boreal lakes often support complex food webs that span multiple trophic levels. Many of these lakes are shallow and, because of the harsh winter climate, freeze to or near the benthos, effectively excluding fish populations (Bayley et al. 2007). Fishless lakes support more abundant and complex populations of aquatic invertebrates due to the relaxation of piscine predation (Bendell and McNicol 1987). These lakes are especially important for breeding waterbirds because aquatic invertebrates are the primary food source for rapidly growing waterbird chicks (DesGranges and Gagnon 1994).

In this study, we ask: Does a natural forest fire release sufficient nutrients to stimulate eutrophication of boreal lakes, and if so, does this enrichment transfer across trophic levels such that each level experiences increased productivity? To answer this question, we studied the effects of a natural wildfire on lakes of the Yukon Flats, a pristine boreal forest basin in Alaska that annually supports >1 million breeding waterbirds. The Yukon Flats is one of the most flammable boreal regions in North America, and charcoal records indicate the area has shifted into a new regime of unprecedented fire activity, with fire frequency from the most recent decades far surpassing that of the past 10 000 years (Kelly et al. 2013). Of our 14 study lakes on the Yukon Flats, 7 were largely surrounded by burned forest, while 7 were not, fortuitously creating a robust study design in which lakes in unburned areas served as in-site controls. Further, all lakes were sampled the summer preceding

the fire, allowing us to use a before-after-control-impact (BACI) study design where prefire data serves as the baseline at each lake (Morrison et al. 2008). By employing prefire data, the BACI design avoids the inference threat common to most wildfire studies, in which differences between burned and unburned sites may be unrelated to the fire, having existed beforehand. Under this design, which is rarely available for naturally occurring fire events such as ours, we provide the first known data describing multitrophic effects of a forest fire on boreal lake ecosystems. Specifically, we tested four successive predictions: (1) total nitrogen and phosphorus will increase more in burned vs. unburned areas following the fire; (2) chlorophyll concentrations in burn-affected lakes will be stimulated by increased nutrient levels; (3) aquatic invertebrate abundance in burn-affected lakes will positively respond to heightened nutrient and chlorophyll levels; and (4) abundance of waterbird chicks will respond to increased invertebrate abundance, being greater on lakes in burned areas.

MATERIALS AND METHODS

Study site

The Yukon Flats is a large basin (~30 000 km²) in interior Alaska that contains >40 000 lakes and wetlands and is largely pristine natural habitat. The area is underlain by discontinuous permafrost, has low landscape relief, and supports a mixed boreal forest dominated by black spruce (*Picea mariana*), white spruce (*P. glauca*), Alaska birch (*Betula neoalaskana*), quaking aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and willow (*Salix* spp.). Our study site (66.4° N, 148.3° W) contained 14 study lakes spread across 16 km² (Appendix A). Lakes varied in size from 5000 to 600 000 m², but were uniformly shallow, never measuring deeper than 2 m. All study lakes functioned largely as closed basins, with no well-defined surface inlets or outlets. This combination of shallow depth and lack of outlets precluded fish populations in all lakes. In September 2010, a lightning-ignited fire burned a large portion of the study site. Satellite data from Monitoring Trends in Burn Severity was available for approximately half our study area and classified the burn severity as 55% moderate, 19% high, 18% low, and 8% unburned.⁵ The fire removed most standing vegetation in the burned areas, and in some instances, the peat and upper organic soil layers were also consumed, leaving behind bare mineral soils. See Appendix A for map and images of burned and unburned boreal habitats in the study area.

Lake classification

We classified each lake as either burned or unburned, and hereafter use this terminology throughout. We were unable to categorize lakes based on extent of spatial

⁵ www.mtbs.gov

overlap between their catchments and the fire; lake catchments were unknown because of the extremely low relief of the study area (<10 m) and the lack of defined inlets draining into lakes. In its place, we digitally added a 200-m buffer around the perimeter of each lake and then estimated spatial overlap between buffers and the fire to classify lakes as burned (>55% of buffer was burned; seven lakes) or unburned (<25% of buffer was burned; seven lakes). Geospatial borders for lakes and fires were acquired from the National Hydrography Dataset and Alaska Interagency Coordination Center, respectively. The 200-m buffer was used because it was the maximum size at which buffers did not grossly extend into the surface area, and thereby catchments, of neighboring lakes. Also, because buffers conformed to lake perimeters, the total area encompassed by each buffer was approximately scaled to lake size. Mean percentage (\pm SD) of buffers within burned forest were $89\% \pm 19\%$ and $13\% \pm 12\%$ for burned and unburned lakes, respectively.

Water chemistry

We sampled water chemistry of each lake once per month (June–August) per year (2010–2012), with the exception of August 2012. We collected 8 L of water from near the lake's center point and 25 cm below the surface as per prior water sampling protocol developed for the Yukon Flats (Heglund 1992). Our study lakes, because of their shallow depth, are frequently mixed and thermal stratification is ephemeral (Heglund and Jones 2003); thus, the lake's center point provided a relevant location from which to gauge its general water chemistry status, including inputs from terrestrial sources. Water samples were used to measure total nitrogen (TN), total phosphorus (TP), and chlorophyll *a* (CHL). Three 5-mL aliquots of lake water were acidified on site with sulfuric acid and stored at cold temperatures for determination of TN. Three unacidified 5-mL aliquots of lake water, also kept at cool temperatures, were used for TP. For CHL, we filtered measured volumes of lake water on site through Gelman A/E glass fiber filters (Gelman Filters, Pall Corporation, Port Washington, New York, USA) until a noticeable algal stain developed on the filter. We collected two filters per sample event, and filters were immediately placed in protective sleeves, desiccated with silica gel beads, and kept in dark, cool storage until transported to laboratory freezers.

In the laboratory, TP concentration was determined by colorimetric measurement of orthophosphate following persulfate oxidation (method 4500-PE [APHA 1995]). TN concentration was measured by second-derivative spectroscopic analysis of persulfate-oxidized samples (Crumpton et al. 1992). CHL was extracted with 90% ethanol and concentrations were determined with fluorometric methods (Knowlton 1984). Final TN and TP values are averages of the three aliquots collected per sample event. Final CHL values are

averaged from the two filters collected and are corrected for the volume of water passed through each filter. All laboratory analyses were conducted by the Jones Limnology Laboratory, University of Missouri, Columbia, Missouri, USA.

Aquatic invertebrates

Aquatic invertebrates were collected from each lake once per month (June–July) per year (2010–2012). Sampling transects were established at random locations along the perimeter of each lake and oriented perpendicular to shore. The number of transects was scaled to lake area, and each lake had a minimum of 2 and a maximum of 13 transects. Abundance and type of aquatic invertebrates are related to aquatic vegetation (Gregg and Rose 1985). Thus, along each transect, we collected one invertebrate sample per unique vegetative zone, and a typical transect contained 2–3 samples. Vegetative zones included both 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 ≤ 1 vegetative zones were encountered, an extra sample was collected in the open water zone. Samples were collected from the water column with a D-frame sweep net (0.5-mm mesh) by pulling it horizontally for 1 m just below the water surface and through the vegetation. The contents of each sweep sample were placed in ethanol and transported to the laboratory for further processing. Invertebrates were identified to minimum taxonomic levels, typically family, and enumerated. Counts were then converted to volumetric densities (individuals per cubic meter) based on net-frame dimensions and length of sweep.

Waterbird surveys

We surveyed each lake for waterbirds (ducks and grebes) 1–2 times per month (June–August) for each year (2010–2012), with the exception of August 2012. Surveys were timed to cover the breeding cycle, from nesting (early June) through brood rearing (late June–August). Observers recorded species and age (adult vs. chick) of each waterbird observed on the lake. We employed repeat sampling, in which each survey consisted of two independent counts conducted over 1–2 days, allowing us to estimate detection probability (see *Statistical analyses*; also Royle 2004). For small lakes that could be surveyed from one viewing location, repeat counts were conducted back-to-back by unique observers. Larger lakes, however, required the observer to move among multiple survey points by canoe, and these movements potentially affected waterbird detection on subsequent counts. Thus, under the assumption that observer effects decrease with time since the survey, we separated repeat counts on large lakes by 24 hours to establish independence between counts.

Statistical analyses

The primary goal of our analyses was to determine effects of forest fires on three aspects of aquatic ecology: (1) water chemistry, (2) aquatic invertebrates, and (3) abundance of waterbird chicks. We first analyzed water chemistry data, using three response variables: TN, TP, and CHL. For each response variable, we fit an a priori set of general linear mixed models using the ‘nlme’ package in program R (Pinheiro et al. 2013). Our model set was composed of six models, one of which was a null intercept-only model. Three models examined temporal patterns in the data without including fire effects, and included a model with Year (2010, 2011, 2012), a model with Date (intra-annual date), and a model with Year \times Date interaction. In BACI study designs, a significant effect of the ecological impact appears via the interaction between site (control vs. impact) and time (pre- vs. postimpact). Thus we tested for an effect of fire on water chemistry by including the interaction between Fire (burned vs. unburned) and Period (pre- vs. postfire) in our final two models. Specifically, one model included the Fire \times Period interaction and its main effects, while the other included the interaction term, its main effects, and Date. Finally, all models included the random effects of study lake ($n = 14$) and sample event ($n = 8$).

For analyses of aquatic invertebrates, we first classified each family by their functional feeding group (filterer, gatherer, predator, scraper, shredder) to improve the ecological interpretation of results. We used raw invertebrate counts (individuals per sample) as response variables in our model sets, which is typically fit with Poisson distribution models. However, our variance was degrees of magnitude larger than the mean, raising doubts as to the appropriateness of Poisson models. Accordingly, we fit our most parameterized model with negative binomial, Poisson, and zero-inflated negative binomial and Poisson distributions, and then compared model fit with AIC. Results indicated that our count data followed a negative binomial distribution and were not zero-inflated. For each functional feeding group, we fit a candidate set of negative binomial generalized linear mixed models using the ‘glmmADMB’ package in program R (Skaug et al. 2012). Candidate model sets were identical to those used for our analysis of water chemistry (see *Water chemistry*) and included lake as a random effect.

We used N-mixture models (Royle 2004), a type of hierarchical generalized linear model, to determine effects of fires on waterbird abundance (chicks per lake). Analyses were restricted to chicks because, as opposed to adults, they feed primarily on invertebrates, making them more sensitive to changes in invertebrate densities. Our hierarchical models are composed of two components: (1) the detection model (p), which estimates detection probability given imperfect detection, and (2) the abundance model (λ), which describes how variation in ecological processes affects abundance. These models are appropriate for our data because the

small size and secretive nature of waterbird chicks leads to low probabilities (<0.5) of detection, which, if unaccounted for, yield biased and unreliable estimates of abundance (Walker et al. 2013). For abundance, we used an a priori set of candidate models identical to that used for water chemistry and invertebrates, with the exception that Lake area was included in each model and itself constituted a one-variable model, for a total of seven models. These abundance models were paired with counterpart models describing detection: null abundance and detection models occurred together, while the other six abundance models were paired with identical detection models that included the variable of Observer. Observer categorically classifies surveyors as experienced or inexperienced. All N-mixture models were fit using maximum likelihood estimation in R package ‘unmarked’ (Fiske and Chandler 2011). To determine the appropriate distribution of our abundance data, we first fit our most parameterized model with negative binomial, Poisson, and zero-inflated Poisson distributions. Results indicated that the negative binomial distribution provided the best fit and hence was used in all models of waterbird abundance.

We used an information-theoretic approach to model selection, in which the relative fit of models within a candidate set were compared with Akaike’s Information Criterion (AIC) and AIC weights (w_i). Inference of fixed effects was based on model selection and precision of parameter estimates. When large standard errors (SE) indicated imprecise parameter estimates, the variable was deemed uninformative. We used model-averaged parameter estimates and unconditional SEs when candidate model sets displayed selection uncertainty, with multiple models being supported by the data. Otherwise, when a clear top model emerged, we used parameter estimates and SEs from the highest-ranked model.

RESULTS

Water chemistry

We collected 112 water samples from 14 lakes during 2010–2012, and concentrations of TN, TP, and CHL ranged from 1500 to 3500 $\mu\text{g/L}$, 30–120 $\mu\text{g/L}$, and 1–25 $\mu\text{g/L}$, respectively. TN, TP, and CHL were all unaffected by the forest fire, as their postfire values remained largely similar to those from the prefire period on both burned and unburned lakes (Fig. 1). For all three water chemistry variables, models incorporating fire parameters (fire, period, fire \times period) received little support ($w_i \leq 0.09$; Appendix B: Table B1) and had imprecise parameter estimates with large standard errors (Appendix C: Table C1). The best-fitting model ($w_i = 0.69$) to explain variation in TN contained only date as an explanatory variable; TN increased over the summer, from June to August, then receded back to lower values by the onset of the following summer (Fig. 1). The model containing date \times year received moderate support ($\Delta\text{AIC}_c = 2.19$), although imprecise parameter estimates

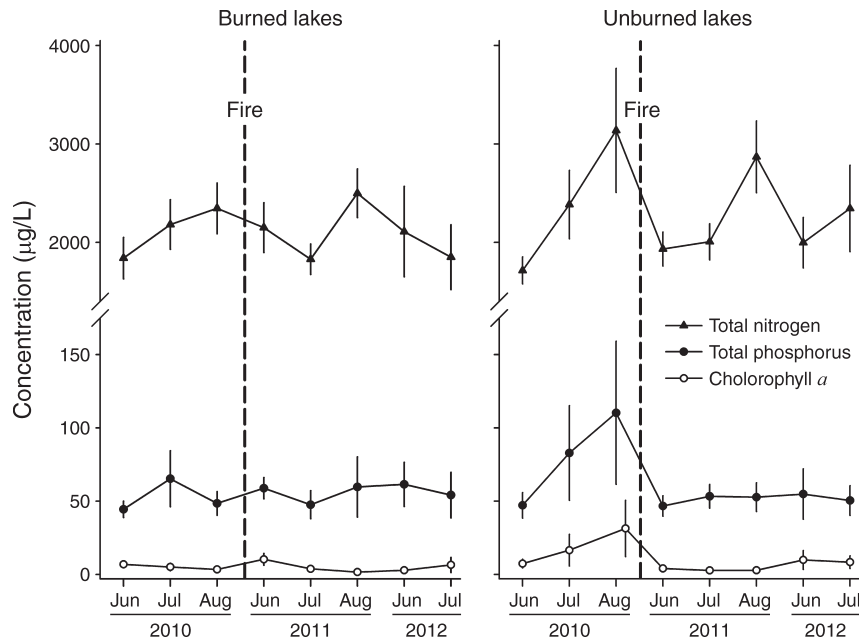


FIG. 1. Concentrations ($\mu\text{g/L}$) of total nitrogen, total phosphorus, and chlorophyll *a* from burned and unburned lakes over three consecutive summers (2010–2012). The timing of the forest fire is indicated by the dashed vertical line. Concentration values are monthly means \pm SE. Note the break in the scaling of the y-axis.

for year indicate this support was driven mainly by date (Appendix C: Table C1). Similarly, date was the only variable receiving support from the CHL model set, although its model weight ($w_i = 0.48$) indicated a lower level of support than for TN models. CHL concentrations were negatively related to date and generally decreased over the summer period (Fig. 1). Finally, TP concentrations were not well described by any of the explanatory variables used in our models set. The best-supported model ($w_i = 0.49$) for describing variation in TP was the null model, which fit an intercept only.

Aquatic invertebrates

We collected 1035 invertebrate samples from 2010–2012, containing a total of 78 394 individuals from 55 families. The most common taxa for each functional feeding group, listed in order of abundance, were as follows: filterers, Conchostraca, Ostracoda, Sphaeriidae; gatherers, Chironomidae, Collembola, Baetidae; scrapers, Physidae, Planorbidae, Lymnaeidae; shredders, Amphipoda, Phryganeidae, Leptoceridae; predators, Coenagrionidae, Hirudinea, Dytiscidae.

The fire had little to no effect on densities of filterers, gatherers, and scrapers. For each of these groups, pre- and postfire densities generally followed similar trajectories across burned and unburned lakes, indicating that changes in densities were not driven by fires (Fig. 2). For gatherers and scrapers, models with fire parameters received almost no support ($w_i \leq 0.06$). For filterers, the model with fire parameters and date received some support ($w_i = 0.20$), but parameter

estimates for fire and fire \times period were imprecise (Appendix C: Table C2). Rather, for all three groups, the best-supported model ($w_i \geq 0.78$) contained date, year, and date \times year. This model indicates that densities of filterers, gatherers, and scrapers are subject to intra- and interannual fluctuations, with year 2011 generally supporting higher densities of all three groups (Fig. 2).

The fire had a positive effect on densities of shredders and predators. Shredder densities were similar on burned vs. unburned lakes prior to the fire. Following the fire, however, shredder densities increased on burned lakes while remaining steady on unburned lakes (Fig. 2). For predators, densities were generally higher post- vs. prefire on both burned and unburned lakes. However, increases were almost two times more pronounced on burned lakes, as well as more recurrent from month to month (Fig. 2). For both shredders and predators, the best-supported model ($w_i \geq 0.76$) describing variation in density contained fire parameters (fire, period, fire \times period) and date (Appendix B: Table B2). Both shredder and predator densities were positively related to date, indicating that densities increased over the summer from June to July (Fig. 2). Finally, predator densities were moderately influenced by year, with the model containing date \times year receiving a small level of support ($\Delta\text{AIC} = 2.3$). However, because year is confounded with fire, year effects cannot be interpreted without first considering the effects of fire; in this instance, effects of fire appear to supersede those of year.

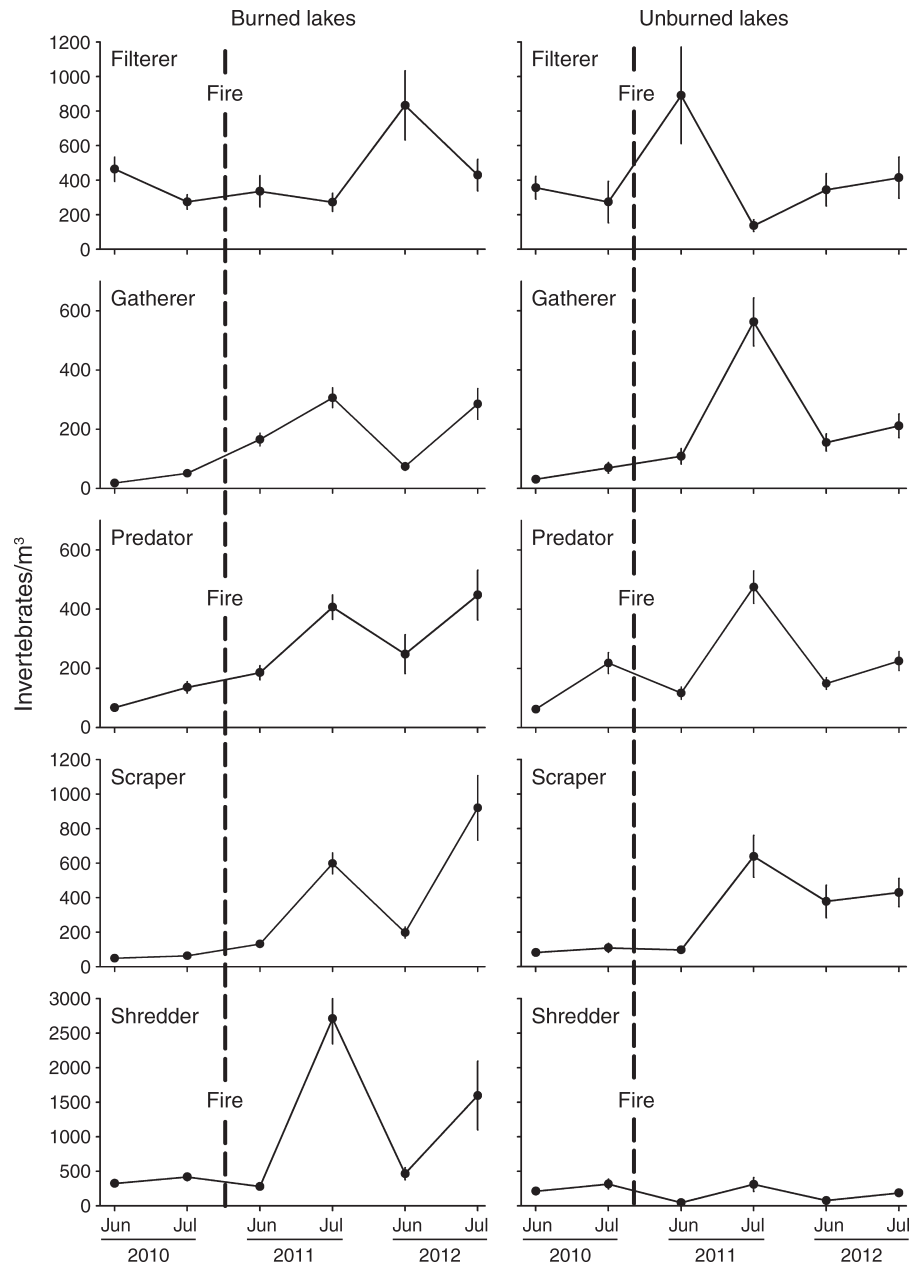


FIG. 2. Densities (individuals/m³) of aquatic invertebrates, organized into functional feeding groups, from burned and unburned lakes over three consecutive summers (2010–2012). The timing of the forest fire is indicated by the dashed vertical line. Density values are monthly means \pm SE. Note the different scales of the y-axes among functional feeding groups.

Waterbird abundance

We conducted 140 surveys from 2010 to 2012, counting 4070 waterbird chicks from 13 species. Lesser Scaup (*Aythya affinis*) and American Wigeon (*Anas americana*) were the most numerous species, accounting for 33% and 18% of total chicks, respectively, followed by Mallard (*Anas platyrhynchos*; 9%), Canvasback (*Aythya valisineria*; 9%), Horned Grebe (*Podiceps auritus*; 8%), and White-winged Scoter (*Melanitta fusca*; 7%). The top model ($w_i = 0.94$) describing variation in

chick abundance contained fire parameters (fire, period, fire \times period) and date (Appendix B: Table B3). Support for this model, however, was driven by the main effects of fire and period, and not their interaction. This is because the interaction fire \times period had a parameter estimate near zero with a standard error more than three times as large as the estimate (-0.21 ± 0.73). Viewed without the interaction, the main effect of fire indicates unburned lakes had more chicks than burned lakes, while that of period indicates higher chick abundances

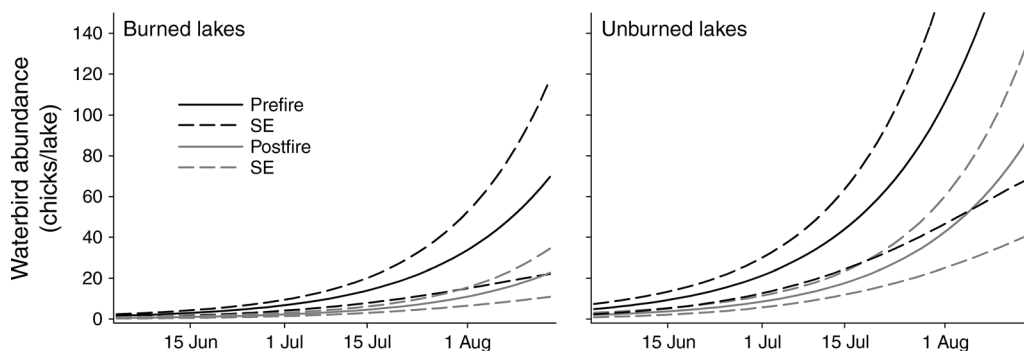


FIG. 3. N-mixture model results showing the detection-probability corrected relationship between waterbird abundance (chicks/lake) and date. Relationships are categorized by burn category (burned vs. unburned) and period (pre- vs. postfire).

pre- vs. postfire (Appendix C: Table C3). However, when we account for the nonsignificant interaction between fire and period, we observe that (1) higher chick abundances on unburned lakes existed both pre- and postfire, and (2) higher prefire abundances existed on both burned and unburned lakes (Fig. 3). Accordingly, without a significant interaction term, we conclude that the fire had no discernible impact on chick abundance.

Date appeared in all models with a $w_i > 0$ and indicated that chick abundance increased over the summer, which is expected given that a higher proportion of nests have hatched at later dates. Lake area was positively related to chick abundance, with higher abundances on larger lakes. Year received moderate support, largely due to lower chick abundances during summer 2012. Finally, detection probability differed little between experienced and inexperienced observers, averaging 0.54 ± 0.02 . Parameter estimates are presented in Appendix C: Table C3.

DISCUSSION

Water chemistry

Contrary to our predicted increase, we found that a large boreal forest fire had minimal effects on aquatic nutrient concentrations in the two years immediately following the fire. Likewise, we detected no fire-mediated increase in chlorophyll *a* concentration. This result was expected in view of our observation that TN and TP were not affected by the fire; P, and to a lesser degree N, commonly limit primary productivity in lakes, such that detectable changes in chlorophyll require concomitant changes in P or N (Schindler 1977). However, while chlorophyll concentrations can be contextually explained, the lack of postfire change in TN and TP concentrations requires further exploration.

In general, lakes of the Yukon Flats are nutrient rich, with high biological productivity; of 129 lakes sampled from 1985 to 1989, Heglund (1992) categorized $>75\%$ as eutrophic or hypereutrophic based on their nutrient composition. Similarly, lakes in our study area were naturally eutrophic with elevated levels of TN ($\bar{x} = 2199 \mu\text{g/L}$) and TP ($\bar{x} = 59 \mu\text{g/L}$). Accordingly, inputs of fire-

derived nutrients must be quite large to produce a detectable and biologically significant increase in lake nutrients. Such inputs will go undetected if they do not exceed background levels of intra- and interannual variation, which is sizeable in our study lakes because of the sheer magnitude of their nutrient values. This situation differs from other boreal regions for which fire effects have been previously described. For example, boreal lakes of the Mackenzie River Delta, although located in a similar subarctic habitat, averaged $\sim 1000 \mu\text{g/L}$ of TN and $17 \mu\text{g/L}$ of TP, both values being less than half our nutrient concentrations (Haszard and Clark 2007). In the Boreal Shield region of Canada, lakes are characteristically poor in nutrients because they are underlain by granitic rock, which is resistant to dissolution (Carignan et al. 2000). Following a forest fire in this region, TP increased $10 \mu\text{g/L}$ in lakes, representing a two- to threefold increase above prefire levels (Carignan et al. 2000); in our study lakes, a two- to threefold increase would require TP inputs of $60\text{--}120 \mu\text{g/L}$.

While high prefire nutrient values tend to dampen the effect of fire-mediated inputs, these values must be considered in combination with the morphology of the surrounding landscape. Notably, our study area has low landscape relief ($<10 \text{ m}$) and few, if any, permanent drainage networks on the surface. Lakes in areas of such low relief typically have small catchments, reducing the effective area over which terrestrial nutrients are collected by inflowing waters (Magnuson et al. 2006). Similarly, catchments of our study lakes, although undefined, are presumably quite small. Supporting this view is the high surface water ($15\text{--}20\%$ of study area) and lake density ($>1.5 \text{ lakes/km}^2$) of our study area, necessitating small catchments, and the generally poor patterns of surface drainage, in which rain and meltwater often form pools in localized depressions rather than draining to lakes. Importantly, these small, flat catchments likely restricted erosion and transport of fire-derived nutrients to our lakes, thereby reducing the impact of the fire. In areas with greater topography or larger catchments, effects of fires on lake water

chemistry may be more pronounced. For example, a boreal forest fire in mountainous terrain caused 1.5- and 2-fold increases in lake TN and TP, respectively (McEachern et al. 2000). These lakes, because of the variable topography, had clearly defined catchments, which were, on average, 21 times greater in area than the actual lakes, a situation clearly different from that of our study area. Indeed, given that nearly 20% of our study area is water, catchments can be, at most, four times larger than lake areas (i.e., 80% land/20% water = 4:1 ratio).

While the restricted flow of small catchments is evident on the surface of our study area, we are unsure of the amount or extent of subsurface flow. If subsurface flow is common, then catchments may be larger than they appear from the surface. Subsurface flow in the Yukon Flats is patchy because of its discontinuous permafrost distribution, being greatest in permafrost-free areas with sand and gravel substrates, and reduced or absent in areas with continuous permafrost (Walvoord et al. 2012). Our study area displays a number of landscape features typical of continuous permafrost, including laterally expanding thermokarst lakes, thick deposits of peat on the forest floor, and numerous poorly drained black spruce bogs (Jorgenson and Osterkamp 2005). Additionally, soils in our study area are dominated by fluvial silts with low hydrologic permeability, further impeding subsurface flow (Williams 1962). Taken together, these characteristics suggest that subsurface flow is spatially restricted in our study area, if not absent altogether. Thus, as for surface catchments, subsurface catchments are likely small and localized, restricting the spatial extent over which fire-derived nutrients were exported to our lakes.

All of the reasons discussed above, high prefire nutrient levels, small catchments, low topography, and permafrost, likely acted in concert to minimize the short-term impact of the fire on water chemistry. Other reasons, although not discussed in detail, may also be important. Fire-derived nutrients may be taken up by soils or vegetation before reaching our lakes. This was documented in Minnesota, in which a large forest fire caused increased phosphorus levels in runoff water, but much of this phosphorus was immobilized in the soil before reaching nearby lakes (McColl and Grigal 1975). Also of importance is the relative magnitude of alternative sources of nutrient inputs, such as snowmelt and precipitation. Bayley et al. (1992) found that postfire inputs of nitrogen, although elevated, were a minor contributor to lake nutrient budgets in comparison to inputs from precipitation. For our study lakes, precipitation may be an important nutrient input because significant amounts fall directly onto lake surfaces, given that nearly 20% of the study area is water. Finally, TP and TN are coarse measurements of a complex nutrient system; other nutrient states, such as dissolved and organic forms, may have been affected by the fire, but masked by our coarse measurements.

Aquatic invertebrates

Densities of shredders and predators increased in response to the fire, while those of filterers, gatherers, and scrapers did not. We predicted that postfire increases in invertebrate densities would be driven by fire-mediated nutrient pulses, under the premise that elevated nutrients would stimulate primary productivity, which in turn would increase secondary production of invertebrates. Because the fire did not increase nutrient levels, other fire-related causes must be responsible for increased shredder and predator densities. While these density increases may not be fire related, we find this unlikely given the strong inference of the BACI study design.

Amphipods accounted for 98% of shredder numbers and were the most numerous invertebrate in our lakes. Scrimgeour et al. (2001) similarly documented increased amphipod numbers in burned lakes, although this was attributed to elevated nutrient levels. Amphipods have high rates of growth and reproduction, often producing five or more broods per year, and relatively short life spans of ± 1 year (Welton and Clarke 1980). Such high rates of reproduction and turnover allow for rapid numerical responses to changing conditions from disturbances such as fires. Rapid density increases were also evident intra-annually, as the year's first bouts of brood production (May–June) led to marked spikes in amphipod densities during our July sampling.

While generally considered shredders, amphipods have a generalist diet that is hard to categorize, including allochthonous and autochthonous plant material and detritus, as well as occasional bouts as predators (MacNeil et al. 1997, Kelly et al. 2002). Generalists often succeed following disturbances such as fires because of their ability to quickly adapt to newly created conditions or habitats. Following a large fire in Yellowstone, trophic generalists were the most abundant invertebrates in streams because of their tolerance of altered physical conditions and resources (Mihuc and Minshall 1995). Similar results were obtained from burnt forests in Idaho, where postfire streams had greater biomass of *r*-strategist, generalist invertebrates relative to unburned streams (Malison and Baxter 2010b). For our lakes, fire disturbances included a loss of shade from lakeside canopy cover, loss of shoreline and emergent vegetation, and unidentified changes to water chemistry and resource inputs. These changes, while not quantified, may have favored amphipods and their generalist ecology. Further, our measurement of chlorophyll *a* from the water column does not account for alternate channels of primary production that may have been affected by the fire, including epibenthic and macrophyte productivity. Macrophytes, in particular, have the potential to influence amphipods because they commonly provide them with both food and refugia from predators (Thiébaud and Gierlinski 2008).

Numbers of predatory aquatic invertebrates also increased in response to the wildfire, the most common

of which included Odonata larvae, leeches, and Coleoptera larvae (family Dytiscidae). All of these predators are known to consume amphipods (Merritt et al. 2008). Accordingly, the simplest explanation for their postfire increase is that the rise in amphipod numbers provided an abundant prey base from which predators could build their populations. This explanation seems plausible when considering the sheer numbers of amphipods in our lakes; amphipods comprised 45% of total invertebrates, and their postfire densities on burned lakes averaged >1000 individuals/m³. Malison and Baxter (2010b) observed similar predator increases in burnt streams, attributing this to an increased prey base of generalist invertebrates that thrived in fire-disturbed habitats. In addition, the absence of fish in our lakes reduces predatory pressure on invertebrate predators, potentially allowing their numbers to respond to prey abundance more strongly than in lakes with fish (Bendell and McNicol 1987).

In contrast to shredders and predators, densities of filterers, gatherers, and scrapers were unaffected by the fire. Aquatic invertebrate densities are notoriously variable and, while previous studies have documented fire-mediated changes in their densities, a similar number have found no effect (Rinne 1996, Minshall et al. 1997). The high variability in invertebrate numbers is often ascribed to factors such as season, location, and time, with such factors overriding any potential response to fire (Hochkirch and Adorf 2007). This was the case for filterers, gatherers, and scrapers in our study lakes, as densities of all three groups varied considerably both within and across years. Moreover, their lack of a fire response was reasonably expected given that nutrient and chlorophyll levels were not affected by the fire. This is especially relevant for filterers and scrapers, which feed directly on the primary production of phytoplankton and epibenthic algae, respectively. Importantly, no negative effects of the fire were detected for any of the five functional feeding groups; densities either increased or did not change in response to the fire.

Waterbird abundance

Abundance of waterbird young decreased from the pre- to postfire period, although this decrease was evident on both burned and unburned lakes, suggesting two mutually exclusive interpretations: (1) from the perspective of waterfowl, the fire adversely impacted the entire study area, including burned and unburned lakes, or (2) decreases in chick abundance were independent of the fire and occurred at a spatial scale larger than our study area; thus the concomitant decrease at burned and unburned lakes. Under interpretation 1, a likely mechanism is that fire reduced the amount and quality of nesting habitat in the study site. Waterfowl nest in dense understory vegetation near wetlands (Kantrud 1990), some of which was consumed during the fire. While the loss of these habitats was more severe near burned lakes, waterfowl may choose nesting habitats at

scales larger than that of the individual lake, thereby deeming much of the study area as unsuitable following the burn. Indeed, waterfowl often move broods considerable distances from nest to water body, suggesting that nesting habitat is chosen at a different scale than that of brood-rearing habitat. Alternatively, interpretation 2 is probable when considering factors that operate on chick abundance at spatial scales large enough to easily encompass our entire study area. Factors include, but are not limited to, temperature, precipitation, predator density, and female breeding propensity. For example, precipitation during the early brood period lowers chick survival (Krapu et al. 2000). Precipitation occurs at a scale much larger than our study area, such that severe precipitation events would adversely affect chick survival on both burned and unburned lakes, lowering abundance in the process.

Ultimately, while the postfire decrease in waterbird young may be suggestive of a negative fire impact, we have no definitive evidence of this without a significant interaction between fire and period. This also highlights the strength of the BACI study design. Had we conducted solely a postimpact study, as is common in fire research, we would have been unaware that the lower abundance of chicks on burned lakes had existed prefire, leading us to falsely conclude that the fire negatively impacted chick abundance. It should also be noted that estimation of abundance for upper trophic level predators such as waterbirds is inherently difficult due to their small populations and advanced mobility. As such, the high variability associated with our estimate of fire \times period may partly reflect this difficulty. Nonetheless, given the high precision of estimates for the remaining parameters in our waterbird models, we think our data set was sufficient for estimating fire effects, or the lack thereof, on waterbird abundance.

Last, amphipods are a major prey item of multiple waterbird species, including Lesser Scaup, which was the most abundant species in our study area (Anteau and Afton 2008). Further, occupancy of lakes by scaup broods is positively related to amphipod density throughout the Yukon Flats (T. L. Lewis, *unpublished data*). Nonetheless, the number of waterbird young decreased concurrently with an increase in amphipods on burned lakes. Moreover, chick abundance decreased on unburned lakes as well, even though these lakes experienced no change in amphipod densities. Taken together, these results suggest that chick numbers are responding to other ecological factors operating at large spatial scales, as discussed previously, and that smaller-scale shifts in amphipod densities are not the primary drivers of chick abundance.

Fire resilience of boreal lakes

The fire in our study area was fairly severe, with 74% of the burn classified as moderate to high severity. Further, because the fire occurred in late summer when permafrost soils were maximally thawed, the burn

penetrated deep into the ground and frequently exposed bare mineral soils. Yet despite this extensive burn, TN and TP did not change in impacted lakes. This stability largely escalated through the trophic structure of our study lakes, as the fire caused little impact in the succeeding trophic levels of primary producers, aquatic invertebrates, and waterbirds. The only exception to this postfire stability was a positive impact of fire on shredder and predator invertebrates, an observation that warrants further research. For ecologically similar regions of the boreal forest, namely, high aquatic nutrient concentrations and small catchments, these results indicate that, in the short term, ecosystems of boreal lakes are largely resilient to forest fires. Given the sheer size of the boreal forest in North America (0.4×10^9 hectares [1.5×10^9 acres]) and the number of lakes within its bounds (>2 million), such ecologically similar regions are likely common. The region in which our study occurred, the Yukon Flats, alone has $>40,000$ lakes and wetlands, many of which are ecologically similar to our study lakes (Heglund 1992). Moreover, our results are especially significant in view of recent changes to fire regimes in the boreal forest. During the 2000s, the annual area of boreal forest burned in Alaska was 50% higher than in any decade since 1940, due to an increased number of years with extensive fires (Kasischke et al. 2010). This increase in fire extent and severity has been linked to climate change in northern latitudes, and climate models indicate a further increase in fire pressure (Chapin et al. 2008). Finally, our results support the belief, put forward by Minshall (2003), that forest fires in general are not detrimental to the sustained maintenance of diverse and productive aquatic ecosystems.

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SUPPLEMENTAL MATERIAL

Appendix A

Supplementary map and images of burned and unburned boreal habitats from our study area ([Ecological Archives E095-107-A1](#)).

Appendix B

Model selection results, listed in order of ΔAIC_c , from models evaluating effects of forest fires on water chemistry, aquatic invertebrates, and abundance of waterbird chicks on boreal lakes ([Ecological Archives E095-107-A2](#)).

Appendix C

Parameter estimates and standard errors from models evaluating effects of forest fires on water chemistry, aquatic invertebrates, and abundance of waterbird chicks on boreal lakes ([Ecological Archives E095-107-A3](#)).