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PRIMARY RESEARCH PAPER

Long-term change in limnology and invertebrates in Alaskan boreal wetlands

Robin M. Corcoran · James R. Lovvorn · Patricia J. Heglund

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Abstract Climate change is more pronounced at high northern latitudes, and may be affecting the physical, chemical, and biological attributes of the abundant wetlands in boreal forests. On the Yukon Flats, located in the boreal forest of northeast Alaska, wetlands originally sampled during 1985–1989 were re-sampled for water chemistry and macroinvertebrates in summer 2001–2003. Wetlands sampled lost on average 19% surface water area between these periods. Total nitrogen and most metal cations (Na, Mg, and Ca, but not K) increased between these periods, whereas total phosphorus and chlorophyll *a* (Chl *a*) declined. These changes were greater in wetlands that had experienced more drying (decreased surface area). Compared with 1985–1989, densities of cladocerans, copepods, and ostracods in both June and August were much higher in 2002–2003, whereas densities of amphipods, gastropods, and chironomid larvae were generally lower. In comparisons among wetlands in 2002–2003 only, amphipod biomass was lower in wetlands with lower Chl *a*, which might help explain the decline of amphipods since the late 1980s when Chl *a* was higher. The decline in Chl *a* corresponded to greatly increased zooplankton density in June, suggesting a shift in carbon flow from scrapers and deposit-feeders to water-column grazers. Declines in benthic and epibenthic deposit-feeding invertebrates suggest important food web effects of climate change in otherwise pristine wetlands of the boreal forest.

Keywords Climate change · Drying of wetlands · Invertebrate communities · Limnological change · Wetland food webs

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R. M. Corcoran · J. R. Lovvorn
Department of Zoology, University of Wyoming, Laramie, WY 82071, USA

J. R. Lovvorn
e-mail: lovvorn@uwyo.edu

R. M. Corcoran (✉)
US Fish and Wildlife Service, Sonny Bono Salton Sea National Wildlife Refuge, 906 West Sinclair Road, Calipatria, CA 92233-9744, USA
e-mail: robin_corcoran@fws.gov

P. J. Heglund
US Geological Survey, Upper Midwest Environmental Science Center, 2630 Fanta Reed Road, La Crosse, WI 54603, USA
e-mail: pheglund@usgs.gov

P. J. Heglund
US Fish and Wildlife Service, Region 3, National Wildlife Refuge System, 2630 Fanta Reed Road, LaCrosse, WI 54603, USA
e-mail: patricia_heglund@fws.gov

Introduction

Winter temperatures in the boreal forest of Alaska have increased by as much as 3–4°C over the past 60 years (Hansen & Lebedeff, 1987; Weller et al., 1999), and by the end of the 21st century this region is expected to warm by more than twice the global average (Arctic Climate Impact Assessment, 2004). Numerous lakes cover about 10% of the boreal area (Schindler, 1998), and climate warming of the magnitude already seen in the boreal forest of Alaska is likely to have significant impacts on ecosystem structure and function of wetlands (Rouse et al., 1997; Carvalho & Kirika, 2003; Wrona et al., 2006). In this paper, we examine trends in limnology and macroinvertebrate communities over a period of 19 years in boreal wetlands of northwestern North America.

The few available studies suggest that increased warming has already caused major changes in the physical, chemical, and biological characteristics of boreal lakes (Schindler, 1997). The northwest boreal zone of North America receives relatively little precipitation (often <30 cm year^{-1}), and the abundant wetlands result largely from: (1) cool, short summers with low evapotranspiration, and (2) an impermeable permafrost, layer which prevents infiltration and impedes drainage of the upper unfrozen layer (Ford & Bedford, 1987). Widespread melting of permafrost, which has already been documented (Osterkamp & Romanovsky, 1999; Jorgenson et al., 2001), and increased evapotranspiration will result in fewer, more nutrient-rich wetlands (Rouse et al., 1997; Moser et al., 2002; Yoshikawa & Hinzman, 2003; Smith et al., 2005). Nutrients will be concentrated as wetlands dry; and as permafrost underlying wetlands and adjacent uplands melts, rates of nutrient mineralization and leaching into surface waters will increase (van Breemen et al., 1998; Jones et al., 2005). Resulting changes in trophy may cause major shifts in community structure (Bayley & Prather, 2003).

Climate also affects the timing of important life-history events. In a review of phenological shifts, 62% of 677 species showed trends in life cycles toward spring advancement (Parmesan & Yohe, 2003). If different species show unique responses to changing temperature, their interactions with other species may be altered (Winder & Schindler, 2004). An example is the temporal mismatch that has developed between peak food demands of nestling songbirds and peak insect availability, due to earlier leaf flush resulting from warmer springs in Europe (Thomas et al., 2001).

Such changes have already occurred in aquatic food webs. A longer ice-free season in boreal lakes of Ontario has resulted in higher total nitrogen concentration and cations, and increased populations and diversity of phytoplankton despite overall declines in chlorophyll (Schindler et al., 1996). Over a period of three to four decades in some north-temperate lakes, peak densities of herbivorous rotifers and some *Daphnia* spp. have advanced by up to 3 weeks in response to earlier algal blooms due to warming (Carvalho & Kirika, 2003; Winder & Schindler, 2004). In Alaskan arctic tundra, 16 years of physical, chemical, and biological data indicated negative impacts of climate warming on lake trout (*Salvelinus namaycush*), the keystone predator in many arctic and boreal lakes (McDonald et al., 1996). In polar tundra of Spitsbergen, chironomid emergence was normally spread evenly across the summer, but higher temperatures caused a large early emergence (Hodkinson et al., 1998). As a result, very high biomass early in the growing season became exhausted toward the end of the season, with potentially severe consequences for seasonally breeding predators of invertebrates such as birds (Thomas et al., 2001).

On the Yukon Flats in eastern interior Alaska, surface water area decreased by about 18% between 1952 and 2000 (Riordan et al., 2006); remaining lakes are likely more eutrophic. Wetlands with higher nutrient levels often differ in abundance and community structure of invertebrates (Jorgenson et al., 1992; Hart & Lovvorn, 2005). Thus, it becomes important to know how climate warming might be affecting relations between water chemistry and macroinvertebrates. On the Yukon Flats, existing data from the 1980s (Heglund, 1988, 1992; Heglund & Jones, 2003) provided a unique opportunity to assess long-term limnological changes in response to climate warming.

In this research, we determined whether changes in water chemistry and macroinvertebrate communities occurred between 1985–1989 and 2001–2003 in wetlands of the Yukon Flats. Because there are few published studies on invertebrates in the northwest boreal forest (cf. Swadling et al., 2000; Scrimgeour et al., 2001; Walker et al., 2003), we also examined specific relations between water chemistry and macroinvertebrate communities in 2001–2003.

Materials and methods

Study area and sampling plots

The Yukon Flats are a vast basin bisected by the Yukon River in interior Alaska (65.7–67.5°N, 142.5–150.0°W, Fig. 1). The basin is underlain by discontinuous permafrost, and includes over 20,000 wetlands scattered over 35,000 km^2 of mostly undeveloped wilderness. Shoreline and surrounding vegetation is variable, including floating peat, emergent plants, sedge meadow, and spruce forest. Summer temperatures can exceed 38°C and are warmer than at any other area with similar latitude in North America; however, winter temperatures may reach −60°C. Most lakes in the area have maximum depth <2 m and freeze to the sediments each winter; the resulting lack of permanent fish communities allows invertebrates to reach high densities. Yukon Flats wetlands are rich in nutrients: over 70% of 129 lakes studied in the mid-1980s were classified as eutrophic or hypereutrophic (Heglund & Jones, 2003). These high nutrient levels result from the wetlands' geological setting in carbonate alluvium, high mixing rates, and shallow depths. See Heglund & Jones (2003) for a detailed description of study plots which were re-sampled in this study.

In this area of discontinuous permafrost, patterns of unfrozen soil through which ground water can flow are complicated and varied, especially when those patterns are changing with warming climate. Intensive investigations in the Chena River floodplain of interior Alaska (Lawson et al., 1996) found the distribution of ground water above, below, and within discontinuous permafrost to be very complex. We have no information from the Yukon Flats generally, or around our study ponds in particular, on varying permafrost depth, distribution, or continuity. However, we presume that groundwater movement is limited mostly to the active zone of annual freezing and thawing, and to localized unfrozen regions of soil ("taliks", Riordan, 2004). Moreover, the annual precipitation of only 18–28 cm is within the range of semiarid to desert conditions, suggesting that such numerous areas of surface water persist mostly because frozen soils prevent water loss by seepage, while annual evaporation rates have historically been low. As only closed-basin wetlands (with no surface-water outlet) were included in our study, the main modes of water loss appeared to be evapotranspiration and local drainage due to thawing of permafrost (Riordan et al., 2006).

On the Yukon Flats National Wildlife Refuge (NWR), we measured water chemistry and macroinvertebrates, in wetlands on three study plots (Fig. 1) that were randomly selected in a study of waterbird–wetland characteristics from 1985–1989 (Heglund, 1988, 1992). To assess water chemistry changes since the 1980s, we re-sampled nine wetlands: two wetlands on Plot C, two wetlands on Plot H, and five wetlands on Plot M. To examine current relations between water chemistry and macroinvertebrate biomass, we added four wetlands adjacent to Plot M that were not studied in the 1980s, increasing our sample size to 13 wetlands.

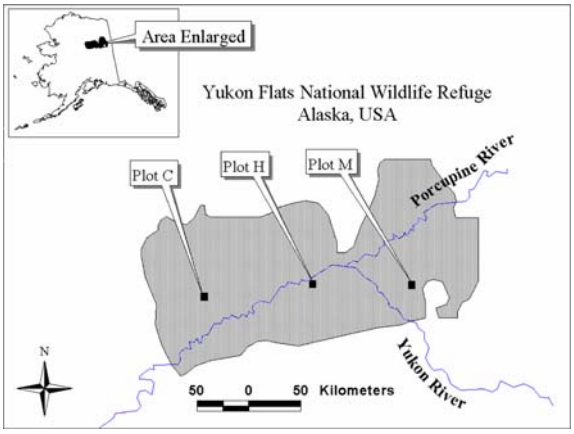

Fig. 1 Location of study plots C, H, and M on the Yukon Flats National Wildlife Refuge (NWR), Alaska, USA

Changes in wetland area

Aerial photographs taken in June 1952 were compared with (1) high-resolution color-infrared aerial photographs taken in June 1978, and (2) the panchromatic band of a Landsat Enhanced Thematic Mapper + satellite image (spatial resolution 15 m) taken on 24 June 2000. All three images were imported into a geographic information system (ArcView 3.4; ESRI, Inc., Redlands, CA) after georectification with ERDAS IMAGINE 8.6 (Leica Geosystems, Heerbrugg, Switzerland). For georectification we used a minimum of 30 control points for each image, and maintained a Maximum Root Mean Squared Error of <30 m. The 13 wetlands included in this study were digitized for each time period, the area of open surface

water (excluding emergent vegetation) was then calculated in ArcView, and percent area lost for each wetland between the years of these images was determined.

Limnological sampling

To document changes in water chemistry between the first (1985–1989) and second (2001–2003) periods, sampling was repeated according to the protocols of Heglund (1992). Monthly (June, July, August) water samples were collected from nine wetlands, and analyzed for total nitrogen (TN), total phosphorus (TP), sodium (Na), magnesium (Mg), calcium (Ca), potassium (K), alkalinity, Chl *a*, total suspended solids (TSS), and total volatile solids (TVS). One 4-l plastic container was filled with water from just below the water surface near the center of each wetland. TN, TP, and alkalinity were analyzed from samples frozen shortly after collection; TN and TP were determined by continuous-flow colorimetric assay after persulfate oxidation (Stable Isotope/Soil Biology Laboratory, University of Georgia Institute of Ecology, Athens, GA), and alkalinity by titrating with 0.02 N H_2SO_4 after adding a color indicator. Concentrations of major cations (Na, Mg, Ca, K) were determined by flame atomic absorption spectrophotometry on samples preserved upon collection with nitric acid.

For analyses of Chl *a*, TSS, and TVS, measured volumes of water were filtered on site; filters were immediately sealed in aluminum foil and frozen. Chl *a* samples were collected on 0.45-μm glass-fiber filters, and concentrations were measured fluorometrically after extraction in buffered ethanol. TSS and TVS were sampled by pre-filtering water through a 500-μm filter (in 2001–2003 but not 1985–1989), and then collecting the remaining suspended solids on 1.5-μm Whatman filters that had been pre-ashed and pre-weighed. To estimate TSS (mg l^{-1}), filters were dried at 105°C for 2 h and weighed. The filters were then ashed at 500°C for 1 h and weighed again to yield TVS.

To test for differences between decades (1980s vs. 2000s), we used repeated-measures multivariate analysis of variance (MANOVA) which accounts for correlation due to repeated measurements on the same wetlands in different months and years, and which analyzes the response of several correlated dependent variables. Nine wetlands were sampled once each month for three months over five years in the 1980s and over three years in the 2000s; however, individual wetlands were sampled in only two or three of those years in either decade, preventing some comparisons. We did not test for differences over time in TSS or TVS due to differences in sampling methods between the 1980s and 2000s.

Decade (1980s vs. 2000s) was the within-subjects factor for repeated-measures MANOVA. To test for relations between wetland area loss and changes in water chemistry, we divided wetlands into two categories based on area loss; category 1 if there was <20% area lost between 1952 and 2000, and category 2 if there was >20% area lost between 1952 and 2000. We chose 20% as the cutoff because there was a clear break in the data, with wetlands gaining or losing only slightly in surface area (−1 to +5%) or losing >20% (21–49%). Wetland area loss was the between-subjects factor in the MANOVA. To compensate for low power inherent in MANOVA, we set $\alpha = 0.10$ for all analyses.

Temporal changes in macroinvertebrates

To determine if biomasses of major macroinvertebrate groups had changed between the 1980s and 2000s, invertebrates were collected according to Heglund's protocols in the earlier study. Nine wetlands sampled in both the 1980s and 2000s were resampled twice each year in June and August. In 2002 and 2003, invertebrates in the water column were sampled with a sweep net (0.5-mm mesh, rectangular frame 20 × 45 cm) at 10 sites along a single transect in each wetland during each sampling period. The transects ran perpendicular to shoreline, and the average water depth at all sites during 2002–2003 was 1.08 m ($n = 390$, SE = 0.02). From a randomly selected starting point along the shoreline, sampling was conducted at 20-m intervals beginning 10 m toward open water from the edge between emergent vegetation and open water. During June sampling, there were no visible submersed macrophytes (owing to freezing of the water column during winter), and in August the occurrence of macrophytes varied among samples (*Potamogeton* spp. dominated at 46% of sites, *Ceratophyllum demersum* at 33% of sites). In the 1980s, stratified random sampling was used to establish transects perpendicular to shoreline that

spanned the most common vegetation types of the wetland. One sweep-net sample per vegetation zone per wetland in each month, and an additional sample from unvegetated deeper water along each transect, were collected. The number of transects depended on wetland size, with a minimum of two transects per wetland.

At each station, the sweep net was pulled horizontally for a distance of 1 m just below the water surface. Sweep-net data were converted to volumetric densities (number l^{-1}) based on the net frame dimensions and length of sweep. In 2002–2003, the number of samples collected from each wetland was the same ($n = 10$) for each sampling period (June and August). In the 1980s, the number of samples collected from each wetland depended on wetland size and variation in habitat type, and ranged from 1 to 10 (mean = 3).

For each wetland in 2002–2003, we determined the dry mass (DM) and ash-free dry mass (AFDM) of a subsample of each taxon for June and August separately. Dry biomass was calculated for each taxon as AFDM × numerical density for sweep-net samples (yielding mg l^{-1}). Lacking AFDM for samples collected in the 1980s, we used wetland- and season-specific AFDM from 2002–2003 to convert these data from abundance (number l^{-1}) to biomass (mg l^{-1}).

Changes in macroinvertebrate biomass between decades were evaluated with paired *t*-tests on log-transformed means for each wetland. Taxa compared accounted for an average 92% of total biomass in all wetlands sampled in 2002–2003. Given the typically high variability in invertebrate data, we set $\alpha = 0.10$ for all analyses, and a Dunn-Sidak correction was used to adjust the α level for multiple comparisons.

Macroinvertebrate biomass vs. water chemistry

To examine relations between macroinvertebrate biomass and water chemistry in the 2000s, we used the invertebrate sampling methods of Murkin & Kadlec (1986). We sampled the nine wetlands used for long-term studies, and added four other wetlands adjacent to Plot M that had not been sampled in the 1980s. Nine wetlands were sampled in both 2002 and 2003, and four were sampled only in 2003.

At each of the 10 stations sampled by the methods of Heglund (see above), a second sweep-net sample was collected by protocols of Murkin & Kadlec (1986). A rectangular net (20 × 45 cm, 0.5-mm mesh) was swept vertically from the bottom to the water surface. Sweep-net data were converted to volumetric densities (number l^{-1}) based on the net frame dimensions and water depth at the sampling site. For benthic invertebrates (collected only in 2003), a sediment core sample (5 cm diameter, 5 cm depth) was taken at each of the 10 stations during both June and August, and washed through a 0.5-mm sieve.

To analyze relations between invertebrate biomass and water chemistry, we calculated biomass for each taxon as AFDM × numerical density for both sweep-net samples (yielding g l^{-1}) and core samples (yielding g cm^{-3}) during June and August separately. We compared the biomass between sweep-net and sediment core samples by converting data from both sample types to grams AFDM per square meter. Thus, we compared the macroinvertebrate biomass for the entire water column per square meter of bottom to the biomass in the top 5 cm of sediments below the same square meter of bottom.

In addition to the nine wetlands used for long-term comparisons, monthly samples of water chemistry were also collected from four wetlands adjacent to Plot M where invertebrates were sampled. This effort increased the sample size for relating macroinvertebrate communities to water chemistry, but did not contribute data on changes in wetlands between the 1980s and 2000s.

Because many of the limnological measures covaried, and because we were interested in the overall relations between limnology and invertebrate biomass, principal component analysis (PCA) was used to reduce the dimensionality of the water chemistry data. Relations between limnological measures (TN, TP, metal cations, alkalinity, Chl *a*, TVS) were summarized by PCA with varimax rotation, using the means from each wetland. PCA scores were then used as independent variables in multiple regressions, with the mean biomasses of different invertebrate taxa from each wetland as dependent variables. All invertebrate groups making up over 5% of total biomass in both sweep-net and core samples during those sampling periods ($n = 8$ taxa) were used as response variables. All invertebrate biomass data were $\log_{10}(x + 1)$ transformed, which normalized residuals and increased homogeneity of variance.

Results

Changes in wetland area: 1950s to 2000s

The availability of images determined which years (1952, 1978, 2000) could be compared for evaluating wetland surface area. Given the few years of available images, between-year variations in precipitation might confound detection of long-term trends. To check this possibility, we examined precipitation data for the summer and previous winter from the three weather stations closest to Yukon Flats NWR having reliable records between 1950 and 2004 (Fig 2). The stations were (1) Bettles FAA Airport, located 100 km west of Yukon Flats NWR; (2) College Observatory north of Fairbanks, 100 km south of the refuge, and (3) the town of Eagle, 150 km southeast of the refuge. For each station, mean annual precipitation was calculated for 1951–2004. In 1952, annual precipitation was above average at two stations, but below average at another. In 1978, precipitation at all sites was below average, whereas in 2000 precipitation at all sites was above average. Thus, while 1978 was anomalously dry, 2000 was among the wettest years on record. If images from these years reflected only year-to-year variation and not long-term change, we would expect the June 2000 image to have surface water area at least as high as in June 1952. Thus, any declines in wetland surface area that were detected between 1952 and 2000 should reflect long-term trends rather than annual variation.

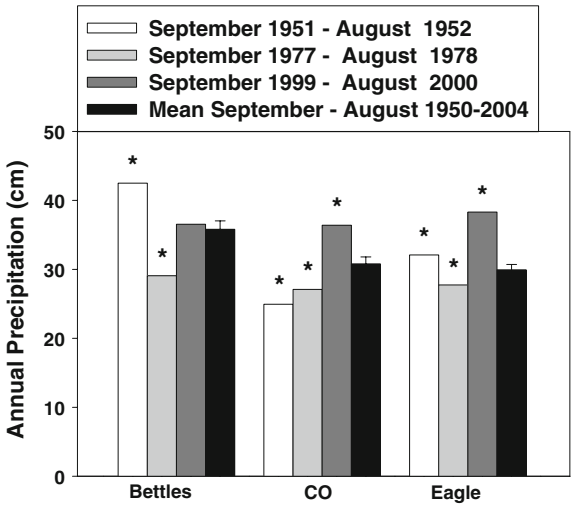

Fig. 2 Annual precipitation (cm) from 1 September to 31 August measured at three weather stations adjacent to Yukon Flats National Wildlife Refuge (YFNWR), Alaska: (1) Bettles FAA Airport, 100 km west of YFNWR, (2) College Observatory (CO), Fairbanks, Alaska, 100 km south of YFNWR, and (3) Eagle, Alaska, 150 km southeast of YFNWR. Mean annual precipitation (from 1 September to 31 August) for 1951 to 2004 was based on all years that did not include months with >1 day of missing data ($n = 49$ years for Bettles, $n = 52$ years for CO, and $n = 36$ years for Eagle). Error Bars = 1 SE. Asterisks indicate significant differences between individual years vs. the mean for 1951–2004 (t-test, $P < 0.05$)

The two wetlands studied on Plot C (Fig. 1) did not lose surface water area during either of the time periods (1952–1978 or 1978–2000); in fact, wetland C722 had a net gain in area of about 33% between 1952 and 1978 (percent change = [(final − initial)/initial] × 100, Table 1). Wetland area loss was high for the two wetlands on Plot H, with losses of 24% (1952–1978) and 23% (1978–2000) during the two time periods for cumulative losses (1952–2000) of 37 to 45%. Wetland area loss on Plot M was variable (mean of 26% for 1952–2000), with the smallest wetlands showing the highest losses. Ninety-three percent of wetland loss on Plot M, and 93% of loss for all wetlands combined, occurred during the more recent time period, 1978–2000. The mean of absolute area loss for all nine wetlands between 1952 and 2000 was 19%, similar to the 18% loss calculated for 1,370 wetlands on the Yukon Flats over the same period (Riordan et al., 2006).

Changes in water chemistry and macroinvertebrates: 1980s to 2000s

In the nine wetlands studied, TN increased by 141% between the 1980s and 2000s, whereas TP declined by 17% and Chl *a* declined by 52% (percent change = [(final − initial)/initial] × 100). All metal cations that were studied except K increased by 33 to 34%, whereas alkalinity was unchanged (Table 2). In an overall test (MANOVA), the slopes of change in water chemistry between decades differed between wetlands with low (<20%) vs. high (>20%) area loss (Wilks' Lambda, $F_{8,34} = 2.81$, $P < 0.02$). Changes in TN, Mg, Ca, K, and Chl *a* were greater in wetlands losing >20% of surface area, whereas changes in Na were very similar in wetlands with low and high area loss (Table 3). In contrast, changes in TP and alkalinity were greater in wetlands losing <20% of area; the direction of change differed according to

Table 1 Areas (ha) of nine wetlands located on three study plots (C, H, and M, Fig. 1) on the Yukon Flats, Alaska. Alphanumeric codes for different wetlands begin with the letter for the plot that contained the wetland. Area of wetlands includes open surface water excluding emergent vegetation

Wetland	Area (ha)			Change in area (%)		
	1952	1978	2000	1952–1978	1978–2000	1952–2000
C718	48.5	49.0	50.9	+1.1	+3.8	+4.9
C722	6.8	9.0	9.3	+33.4	+3.4	+37.9
H111	26.2	19.2	14.3	−26.6	−25.4	−45.3
H116	301.8	238.8	189.0	−20.9	−20.9	−37.4
M620	70.6	72.3	71.5	+2.4	−1.1	+1.3
M625	7.6	7.7	6.0	+0.5	−20.9	−20.5
M628	14.5	13.6	14.2	−6.7	+4.7	−2.2
M630	3.9	3.4	1.7	−13.5	−51.3	−57.9
M634	3.4	3.4	1.7	−2.1	−49.3	−50.4

Table 2 Means (±1 SE) of water chemistry variables in 1985–1989 vs. 2001–2003 for nine wetlands on the Yukon Flats, Alaska, and results of repeated-measures MANOVA tests of differences between decades (including Dunn-Sidak correction for multiple comparisons between decades)

Measure	1980s	2000s	Difference (%)	*P*
TN (mg l^{-1})	1.93 ± 0.17	4.65 ± 0.32	+141	<0.01
TP (mg l^{-1})	0.45 ± 0.08	0.37 ± 0.07	−17	0.04
Na (mg l^{-1})	63.71 ± 9.58	85.54 ± 9.95	+34	<0.01
Mg (mg l^{-1})	48.28 ± 6.25	64.59 ± 6.44	+34	<0.01
Ca (mg l^{-1})	27.80 ± 1.89	36.93 ± 2.86	+33	<0.01
K (mg l^{-1})	14.91 ± 1.76	15.68 ± 1.88	+5	0.56
Alkalinity (meq l^{-1})	8.92 ± 1.02	8.63 ± 0.84	−3	0.33
Chl *a* (μg l^{-1})	23.22 ± 3.63	11.13 ± 2.62	−52	<0.01

TN total nitrogen, *TP* total phosphorus, *Chl* a chlorophyll *a*

Table 3 Mean percent change in water chemistry variables between decades (1985–1989 vs. 2001–2003) in wetlands with low (<20%, $n = 4$) vs. high (>20%, $n = 5$) loss of surface area over the same period on the Yukon Flats, Alaska

Measure	Difference (%)		*P*
	<20% area loss	>20% area loss	
TN (mg l^{-1})	+118	+163	0.38
TP (mg l^{-1})	−28	+5	0.02
Na (mg l^{-1})	+39	+32	0.53
Mg (mg l^{-1})	+11	+56	<0.01
Ca (mg l^{-1})	+14	+53	0.09
K (mg l^{-1})	−8	+19	0.05
Alkalinity (meq l^{-1})	−23	+14	<0.01
Chl *a* (μg l^{-1})	−44	−62	0.84

The *P*-values are for the interaction between decade and wetland area loss in repeated-measures MANOVA. The Dunn-Sidak α-level correction for multiple comparisons between decades yields $\alpha = 0.013$ for individual tests

TN total nitrogen, *TP* total phosphorus, *Chl* a chlorophyll *a*

area loss, with declines in wetlands with low area loss but increases in wetlands with high area loss (Table 3). In testing for the interaction between decade and wetland area loss, the Dunn-Sidak α-level correction for multiple comparisons yielded $\alpha = 0.013$ for individual tests, indicating that the interaction was significant for both Mg (Wilks' Lambda, $F_{1,41} = 8.97$, $P < 0.01$) and alkalinity (Wilks' Lambda, $F_{1,41} = 11.03$, $P < 0.01$).

In horizontal sweep-net samples collected near the water surface (protocol of Heglund, 1992), only copepod biomass in June (mg l^{-1}) changed significantly, increasing 31-fold (from 0.014 to 0.427 mg l^{-1}) between decades (paired *t*-test, $P < 0.02$, Fig. 3). Small sample size (nine wetlands) and the typically high variability in aquatic invertebrate populations contributed to lack of statistical significance between decades. Consequently, we inspected the data for trends in invertebrate taxa that

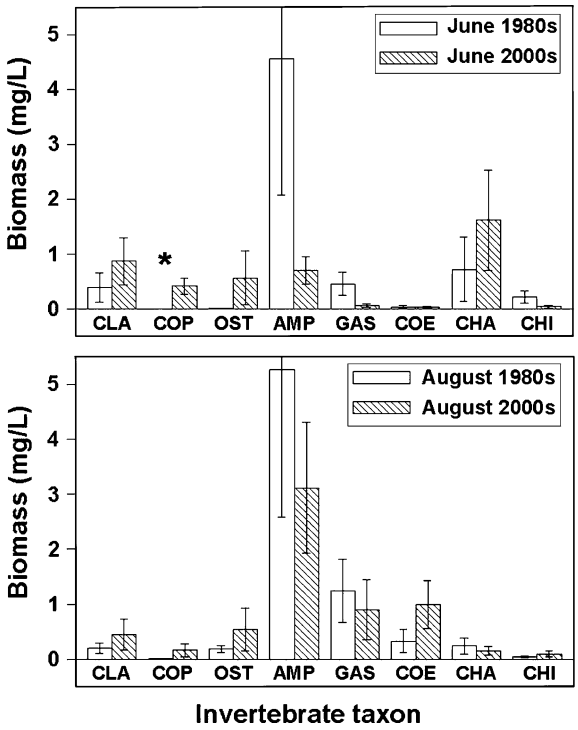

Fig. 3 Mean biomass (AFDM, mg l^{-1}) of different invertebrate taxa in horizontal sweep-net samples (protocol of Heglund, 1992) in 1985–1989 vs. 2002–2003 for nine wetlands on the Yukon Flats, Alaska. Error bars = ±1 SE. CLA = cladoceran, COP = copepod, OST = ostracod, AMP = amphipod, GAS = gastropod, COE = coenagrionid (damselfly) larvae, CHA = chaoborid (phantom midge) larvae, CHI = chironomid larvae. The *asterisk* indicates significant change between decades for copepods in June (paired *t*-test, $n = 8$, $P = 0.016$)

would be predicted given the significant differences in water chemistry between decades (see preceding section). In general, declines between decades occurred in deposit-feeding invertebrates: amphipods, gastropods, and chironomid larvae (Fig. 3). Because of several thousand-fold changes in the biomass of some invertebrates, we used relative percent difference (RPD = [(final − initial)/0.5 (final + initial)] × 100) rather than percent difference to express changes between decades. Relative mean biomass of amphipods declined between decades by 146% in June and 51% in August (RPD). The results were similar for gastropods with declines in biomass of 150% and 32% in June and August respectively. Chironomid biomass declined by 129% in June but increased by 77% in August. In contrast, June and August biomasses of the two major zooplankton taxa increased (RPD) by 75% and 79% (cladocerans) and 193% and 192% (copepods), whereas the biomass of chaoborid (phantom midge) larvae that prey on zooplankton increased by 76% in June between the two decades.

Water chemistry and macroinvertebrate biomass: 2002–2003

Nutrient concentrations in the 13 wetlands sampled during 2001–2003 were highly variable, but indicated that most wetlands were eutrophic to hypereutrophic based on Nürnberg's (1996) criteria for TN and TP. Relative to TN and TP, Chl *a* concentrations (Table 2) were a third to half those expected based on typical nutrient–chlorophyll relations in lakes (Prairie et al., 1989). The only significant seasonal trend was in TP, which increased between June (mean ± 1 SE = 0.399 ± 0.127 mg l^{-1}) and August (0.550 ± 0.165 mg l^{-1}) (paired *t*-test, $P = 0.004$). These values suggest that in 2001–2003, standing stocks of phytoplankton (Chl *a*) were depressed relative to actual production, probably because of heavy grazing by zooplankton.

To examine relations between invertebrate biomass and water chemistry, we used PCA on nine limnological variables (Table 4). The first axis (PC1) explained 48% of the total variation in water

Table 4 Loadings of water chemistry variables on the first 3 principal components (PC1, PC2, PC3) based on mean values of each variable from 13 wetlands on the Yukon Flats, Alaska in summer 2002–2003

	PC1	PC2	PC3
Variance explained (%)	48	27	16
TN	0.612	0.277	0.245
TP	**0.926**	0.046	0.299
Na	**0.866**	−0.333	−0.349
Mg	**0.969**	−0.212	−0.068
Ca	0.087	0.039	**0.959**
K	**0.840**	−0.376	0.252
Alkalinity	**0.913**	−0.337	−0.201
Chl *a*	0.538	**0.806**	−0.138
TVS	0.634	**0.739**	−0.151

Loadings ≥0.7 are in bold type

TN total nitrogen, *TP* total phosphorus, *Chl* a chlorophyll *a*, *TVS* total volatile solids

Table 5 Results from multiple regressions of invertebrate biomass ($\log_{10}$(AFDM + 1)) on factor scores from principal component analysis of limnological measures from 13 wetlands on the Yukon Flats, Alaska, in June and August 2002–2003

Response variable			PC1		PC2		PC3	
	R^2	P	r^2	P	r^2	P	r^2	P
Chironomid larvae	0.75	<0.01	+0.38	<0.01	−0.06	0.19	+0.32	<0.01
Amphipods	0.57	0.05	+0.07	0.25	+0.22	0.06	−0.28	0.04

Coefficients of multiple determination (R^2) and P-values for regressions including all principal components, and partial regression coefficients (r^2) and P-values for individual principal components (with direction of correlation shown), are presented. PC1 represents increasing TP, Na, Mg, K, and alkalinity; PC2 represents increasing Chl *a* and TVS; and PC3 represents increasing Ca. Only invertebrate taxa showing some significant relationships are shown. Invertebrate data are from vertical sweep-net samples (protocol of Murkin and Kadlec, 1986); there were no significant relationships for core samples

chemistry and was positively correlated with TP, all cations except Ca, and alkalinity. Axis 2 (PC2) explained 27% of total variance, and was positively correlated with Chl *a* and TVS. Axis 3 (PC3) explained another 16% of total variation, and was positively correlated with Ca concentrations. Axis 1 separated wetlands with high TP and cations, particularly those wetlands where high Na and alkalinity limited productivity. Axis 2 separated more productive from less productive wetlands in terms of Chl *a* and TVS. Axis 3 separated wetlands based on study plot, reflecting spatial variation in Ca levels of alluvial deposits along the floodplain of the Yukon River (Heglund & Jones, 2003).

The PCA factor scores (Table 4) were used as dependent variables in multiple regressions to relate invertebrate biomass to water chemistry (Table 5). In vertical sweep-net samples (protocol of Murkin & Kadlec, 1986), chironomid larvae increased with increasing TP, cations, and alkalinity (PC1 and PC3). Amphipods in sweep-net samples were positively related to Chl *a* and TVS (PC2), and negatively related to Ca concentration. There were no significant relationships between water chemistry and invertebrates in core samples.

Discussion

Variation in wetland loss

Our results for wetland area loss are consistent with recent studies at northern latitudes indicating variability in wetland drying (Yoshikawa & Hinzman, 2003; Smith et al., 2005; Riordan et al., 2006). Water levels are highly influenced by the thickness of the active layer and the total thickness of the underlying permafrost. Recent studies indicate that wetland drying in regions of discontinuous permafrost is often driven by permafrost degradation and growth of taliks, defined as layers of unfrozen soil above permafrost and below ponds (Yoshikawa & Hinzman, 2003; Smith et al., 2005; Riordan et al., 2006). As taliks grow, they can merge and create pathways for horizontal water movement, which facilitates drainage to the subsurface. In regions of discontinuous permafrost in Siberia, wetland drying is a spatially patchy process with permanently drained lakes commonly found alongside undisturbed neighbors (Smith et al., 2005). A geologic reconnaissance of the Yukon Flats in the 1960s (Williams, 1962) indicated that soils on Plot C, where wetland loss was not documented in this study, were generally perennially frozen with many of the lakes formed by local thawing. Conversely, both Plot H and Plot M were located on stratified alluvial deposits and had many unfrozen zones, and on these plots we saw variable changes in wetland area, from gains of 5% to losses of 58% in surface water area. In our closed-basin wetlands, concentrations of most solutes increased more in wetlands that lost more surface area (Table 3); this pattern suggests that increased evaporation relative to precipitation was important, in addition to possible drainage through expanding taliks.

Long-term trends in nutrients and Chl *a*

Between 1952 and 2000, 1370 wetlands on the Yukon Flats lost an average 18% of the surface water area (Riordan et al., 2006). Our study shows that wetlands remaining in the early 2000s had experienced

important changes in chemistry and food web structure. From the 1980s to 2000s, TN, Na, Mg, and Ca increased, whereas Chl *a* declined, and these changes were greater in wetlands that lost >20% of open-water surface area. Increased nutrients are consistent with predictions of climate warming effects on closed-basin lakes, which are especially vulnerable in semiarid regions where groundwater inputs and outputs are small, and water levels and chemical concentrations respond quickly once evaporation exceeds water inputs. These patterns are also consistent with those over 20 years in the Experimental Lakes region of northern Ontario, where N and cations increased and Chl *a* declined relative to P levels, as expected in a P-limited system with heavy grazing of phytoplankton by invertebrates (Schindler et al., 1996; Schindler, 1998). In ponds that changed from having both surface inflows and outflows to being closed basins due to drying, Schindler (1997) attributed declines in P to longer water residence durations which increased the duration of biological removal processes. In wetlands we studied on the Yukon Flats which were closed basins during both periods, declines in P from the 1980s to 2000s are probably not explained by longer water residence durations.

Although P limitation is considered prevalent in Alaska and elsewhere at high latitudes (Pienitz et al., 1997; Gregory-Eaves et al., 2000), data from 129 wetlands on the Yukon Flats during the 1980s were equivocal (Heglund & Jones, 2003). Nutrient addition assays indicated that N limitation was more prevalent. Heglund & Jones (2003) concluded that top-down control by large-bodied zooplankton grazers, which dominated these wetlands in the absence of fish predation, was an important factor in the low yields of Chl *a* relative to nutrient levels in the 1980s. In our study, cladoceran biomass was dominated by large-bodied *Daphnia* spp. (90% of total cladoceran dry mass in 2001–2003), followed by *Ceriodaphnia* spp. (9%) and *Chydoridae* (1%).

Given the negative response of Chl *a* to nutrients, a possible explanation for the long-term decline in TP and Chl *a* in wetlands of the Yukon Flats is increased grazing by zooplankton. TP includes P in phytoplankton, and the increased zooplankton populations in June during the early 2000s (Fig. 3) probably removed much of both TP and Chl *a* from the water column (Strauss et al., 1994; Hann & Goldsborough, 1997). In shallow lakes, zooplankton recycling and release may be the major source of dissolved nutrients for phytoplankton production (Lehman, 1980, Den Oude and Gulati, 1988). Zooplankton grazers skew the ratios of nutrients they excrete from the ratios they ingest, with cladocerans (notably daphniids) retaining more and releasing less of P relative to N (Sterner, 1990; Hessen & Anderson, 1992). Thus, increases in zooplankton biomass between the decades might have been a factor in the divergent trajectories of TP and TN, with slight declines in TP corresponding to a four-fold increase in TN.

Differing trends of TP and TN in ponds might also be influenced by differing release of these nutrients from thawing permafrost soils in surrounding uplands. Thawing of permafrost in boreal forest uplands has been shown to increase substantially the mineralization and leaching of N to adjacent water bodies (van Breemen et al., 1998; Jones et al., 2005); however, we are aware of no similar studies of P mobilization in this environment. In soils of coastal tundra, enhanced mineralization is expected to be followed by greater immobilization into microbial biomass of inorganic P than of inorganic N (Gersper et al., 1980). Resulting greater retention of P in surrounding soils would be consistent with divergent trends in P and N in our study ponds, but definitive studies are needed in areas of melting permafrost around northwest boreal wetlands. Alternatively, suspended chlorophyll and TP can also be reduced if the increased density of submersed macrophytes suppresses the resuspension or growth of microalgae in the water column. Although we have no data on changes in macrophyte densities over this period, macrophytes were lacking in June after freezing of the water column during winter, so that effects of macrophytes on sediment resuspension or shading of the water column were minimal until later in the summer.

Change in trophic flows of microalgal production

Hypereutrophic conditions (generally >0.2 mg l^{-1} TP, as in our wetlands) can favor increased production of phytoplankton, with associated decrease in production of macrophytes and the substrate they provide for epiphytic algae (Scheffer et al., 1993; Bayley & Prather, 2003). In many macrophyte-dominated wetlands, most carbon available to macroinvertebrates comes from microalgae and not macrophyte tissue (Hart & Lovvorn, 2003, 2005),

so that decreases in epiphyton can reduce food for epiphytic scrapers and deposit-feeders such as snails, amphipods, and chironomids (Thomas & Daldorph, 1994). Lowered standing stock of phytoplankton as indexed by Chl *a*, which was observed in our study during the 2000s, does not preclude higher phytoplankton production. In shallow lakes, high zooplankton populations can filter the entire water column 1–2 times per day (Hanson & Butler, 1994), so that high algal production rates are not apparent based on standing stocks. This explanation is consistent with that of Heglund & Jones (2003), who concluded that chlorophyll levels in our area were much lower than expected given the high nutrient levels because of heavy grazing by large zooplankton. In fact, given that Chaoborid predators on zooplankton were also more abundant in the 2000s, we suggest that increased zooplankton populations could not have occurred without greater production of their phytoplankton foods, which were subsequently grazed to a low standing stock. High grazing rates in the water column can greatly reduce the amount of suspended algae that settle for use by surface feeders.

If phytoplankton production on the Yukon Flats was formerly limited by N (see preceding section), then the 141% increase in TN between decades may have increased the relative production of phytoplankton, thereby favoring zooplankton grazers over scrapers and deposit-feeders in June. Because the water column had frozen to the sediments during winter, submersed macrophytes were generally absent in June and developed only later in the summer. As the early-summer peak of phytoplankton production declined seasonally and was removed by zooplankton grazing, increased light availability for epiphytic algal production, and seasonal increase of submersed macrophytes as substrate for epiphyton and habitat for surface-feeders, might have promoted the late-summer increase in amphipods, gastropods, and chironomids in the 2000s (Fig. 3). Nevertheless, we suggest that increased N availability, and resulting increase in water-column production of microalgae and their grazers in early summer, caused much of the high early-season production to be consumed in the water column, with overall negative impacts on secondary production of scrapers and deposit-feeders. Although settling fecal pellets from zooplankton might fuel microbial food webs that support deposit-feeders, a very large fraction of the energy in fresh phytoplankton is lost in such conversions (Pomeroy & Wiebe, 1988).

Invertebrates and limnological variables

Relations between water chemistry and macroinvertebrates have been shown previously in boreal wetlands. In 17 boreal lakes in Alberta, Canada, amphipod, chironomid, and total benthic biomass were related to soluble reactive P, but not to dissolved inorganic N or color (Scrimgeour et al., 2001). In our study in 2002–2003, chironomid larvae increased with increasing TP, cations, and alkalinity, whereas amphipods were negatively related to Ca concentrations and positively related to Chl *a* and TVS (Table 5). This relationship for amphipods might help explain their decline between decades, as Chl *a* decreased over this period.

As noted in the preceding section, apparently negative effects of declining Chl *a* on amphipods might reflect re-routing of algal production through increased zooplankton grazers. However, zooplankton grazer biomass was not significantly related to any of our measures of water chemistry. We suspect that any relations between cladocerans and Chl *a* may have been masked by the timing of samples, particularly in June. Cladoceran biomass normally rises in spring in response to algal blooms, peaks during the clear water phase associated with high grazing pressure, and then declines in summer (e.g. Sommer et al., 1986). In some wetlands, sampling may have occurred early when cladoceran biomass was rising in response to algal peaks, indicating a positive relationship between cladoceran biomass and Chl *a*. In other wetlands we may have sampled during the clear water phase, after Chl *a* levels had declined due to grazing pressure, but cladoceran biomass was still high, resulting in a negative relationship. Although sampling in all wetlands was between 10 and 23 June in both years, we cannot eliminate differences between wetlands and years in the timing of algal blooms as a source of variation in cladoceran-Chl *a* relations.

Suggested changes in food web function

Our data show that in addition to major loss of surface area, wetlands in the Yukon Flats have experienced long-term changes in water chemistry

and food web structure associated with climate warming. On the basis of trends in water surface area over a much larger region (Riordan et al., 2006), these changes may be widespread throughout the western boreal forest. Increased levels of cations, and especially the 141% increase in TN, may be shifting primary production toward phytoplankton. Such an increase in phytoplankton production seems necessary to explain the large increase in zooplankton biomass during the spring bloom in June. These zooplankton appear to graze down the early-season bloom of phytoplankton, possibly decreasing energy flow to scrapers and deposit-feeders with negative impacts on their abundance. Scrapers and deposit-feeders tend to be much larger than zooplankton, and are often important prey for migrating and breeding waterbirds. Thus, increased zooplankton and reduced biomass of larger invertebrates may be impacting higher trophic levels, and altering productivity for a suite of boreal wetland species.

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