

LESSER SCAUP NESTING ECOLOGY IN RELATION TO WATER CHEMISTRY AND
MACROINVERTEBRATES ON THE YUKON FLATS, ALASKA

by

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Lesser scaup (*Aythya affinis*) populations have declined since the late 1970s, and proposed reasons for these declines include changes in food resources or breeding ground habitats. Most Lesser Scaup breed in the boreal forest zone of Alaska and Canada, but despite inordinate impacts to this vast and important region, little research has focused on effects of changing climate on aquatic ecosystems. Global warming is most pronounced at high latitudes, and the boreal forests of Alaska have experienced an average rise in temperature of 3°C since the 1960s. Climate change models for this region predict a reduction in the number of wetlands, increased eutrophication of remaining wetlands, and changes in aquatic food webs. On the Yukon Flats National Wildlife Refuge in northeast Alaska, we investigated the effects of changes in breeding habitat in the boreal forest on scaup nesting ecology.

Scaup nest success over three breeding seasons (2001–2003) was 12.3%. Nest survival rates varied based on habitat type in which the birds nested. Nest success was lowest on wetlands >10ha (7.6%), intermediate on wetlands <10ha (11.1%), and highest on wooded creeks (26.2%). Average duckling survival from 1-30 days was 0.201 (95% CI: 0.041 to 0.912), and most duckling mortality (94%) occurred in the first 10 days after hatch. Three of 10 marked hens moved all or part of their broods overland between nesting and brood-rearing wetlands for distances of 0.3–1.6 km.

We re-sampled water chemistry and macroinvertebrates in summer 2001–2003 from 9 wetlands where similar data were collected during 1985–1989. Total nitrogen and most metal cations (Na, Mg, and Ca, but not K) increased between these periods, while total phosphorus (TP) and chlorophyll *a* (Chl *a*) declined. These changes were greater in wetlands that had experienced more drying (decreased surface area). Compared to 1985–1989, biomasses of cladocerans, copepods, and ostracods were higher in both June and August 2002–2003, while biomasses of amphipods, gastropods, and chironomid larvae were generally lower. The latter taxa (especially amphipods) are thought to be critical prey for lesser scaup.

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Chapter I: NEST SUCCESS AND DUCKLING SURVIVAL OF LESSER SCAUP ON THE YUKON FLATS, ALASKA

Abstract: Over the last 20 years scaup numbers have declined, and these declines have been greatest in the northern boreal forests of Canada and Alaska where most lesser scaup (*Aythya affinis*) nest. We studied nest success and duckling survival of lesser scaup over three field seasons, 2001-2003, on the Yukon Flats National Wildlife Refuge (NWR) in northeastern Alaska. Daily survival rate (DSR) of nests on our study area across all 3 years was 0.943 (n = 177 nests, 95% CI: 0.930 to 0.954), corresponding to a nest success of only 12.3%, considerably lower than published estimates of an average nest success of 57% for lesser scaup in the northern boreal forest. With Mayfield logistic regression, we investigated effects on nest survival of year, clutch initiation date, and nesting habitat type (large wetlands >10 ha, small wetlands <10 ha, and wooded creeks). Neither year nor clutch initiation date influenced nest survival; however, the odds of nest success on large wetlands was 49% lower than on wooded creeks (odds ratio = 0.512, 95% CI = 0.286,0.918). Based on the model that used only habitat type for estimation, DSR on large wetlands was 0.931 (corresponding nest success = 7.6%), DSR on small wetlands was 0.941 (nest success = 11.1%), and DSR on wooded creeks was 0.963 (nest success = 26.2%). To estimate duckling survival, we monitored 10 broods (n = 75 ducklings) over 3 field seasons by radio-tagging hens at nest hatch. Most duckling mortality (94%) occurred in the first 10 days after hatch. Average duckling survival from 1-30 days was 0.201 (95% CI: 0.041 to 0.912). Three of 10 hens moved all or part of their broods overland between nesting and brood-rearing wetlands for distances of 0.3 km to 1.6 km. Our estimates of lesser scaup nest success and duckling survival on the Yukon Flats were among the lowest ever reported for ducks nesting at northern latitudes, even though the study site was in pristine boreal forest. This finding indicates that long-term trends in environmental conditions in the boreal forest ecosystem may be resulting in reduced reproductive success of scaup, thereby contributing to local population declines observed on the Yukon Flats.

INTRODUCTION

Continental populations of lesser and greater scaup combined (*Aythya affinis* and *A. marila*) have been declining for over 20 years, and the percentages of both females and juveniles in the population have decreased (Allen et al. 1999, Afton and Anderson 2001). The decline in total scaup numbers probably has resulted from declines of lesser scaup rather than greater scaup, because the latter represent only 10-15% of the continental scaup population and have more stable numbers (Afton and Anderson 2001). Lower female survival may result from higher hen mortality during the nesting season, when demands of nesting put females at greater risk of starvation or predation. The fewer juveniles currently observed in the population suggest that reproductive success is declining. Among various possible explanations, productivity and survivorship may have declined due to changes in boreal forest wetlands, poor nutritional condition upon arrival on the breeding grounds, or both (Rouse et al. 1997, Austin et al. 2000, Anteau and Afton 2004).

Most lesser scaup nest in the northern boreal forest of Alaska and Canada. Populations of scaup in the western Canadian boreal forest (Northwest Territories, northern Alberta, and northwestern British Columbia) have experienced the greatest declines. Trajectories of populations in boreal forest west of the Continental Divide (interior Alaska, Yukon Territory, and all but the northeastern corner of British Columbia) are mixed or stable (Austin et al. 2000). Aerial surveys of breeding scaup in interior Alaska from 1957-1994 showed highly variable population levels but no significant overall declines (Hodges et al. 1996). However, data from individual survey strata indicate that scaup breeding populations on Stratum 4 (Yukon Flats NWR) have experienced significant declines during the last 20 years ($r = -0.47$, $p = 0.037$) (Afton and Anderson 2001).

Most of what we know about lesser scaup nesting ecology comes from studies in the southern portion of their breeding range, either in the prairie parklands near the town of Erikson in southeastern Manitoba (Rogers and Korschgen 1966, Hammell 1973, Afton 1983, 1984, Afton and Ankney 1991, Afton and Hier 1991, Koons 2001) or on the St Denis National Wildlife Area in central Saskatchewan

(Dawson and Clark 1996). Few studies have been conducted in the boreal forest where most scaup nest (Trauger 1971, Grand 1995, Fournier and Hines 2001, Brook 2002) because of logistical difficulties of working in this remote region.

From the few studies conducted on boreal wetlands, reported nest success of lesser scaup has been as high as 57% for northern boreal forests (Austin et al. 1998), but data from this region show significant annual variations in local numbers and reproductive success (Trauger 1971). Mayfield-Green estimates of lesser and greater scaup nest success averaged 61% in recent studies near Yellowknife, NWT between 1990-1998, but nest success was estimated to be 18% on the study site most typical of lesser scaup habitat in that region (Fournier and Hines 2001). Additional research near Yellowknife, NWT in 1999 and 2000 yielded estimates of lesser scaup nest success of 14% (Brook 2002). During the 1989-1991 breeding seasons, overall nest success of a number of duck species on the Yukon Flats NWR ranged from near zero to 12% (Grand 1995). However, nest success increased to 100% for nests initiated after 30 June, indicating that later-nesting species like lesser scaup experienced high success. In contrast to the high lesser scaup nest success seen on Yukon Flats by Grand (1995), the Mayfield estimate of scaup nest success for the same time period on Minto Flats, AK, located about 100km south of the Yukon Flats, was 4.4% (Petrula 1994). Given the high degree of variability in nest survival, assessing productivity in various areas and habitats throughout the breeding range is critical to understanding scaup declines.

Even less is known about lesser scaup duckling survival on boreal forest wetlands than is known about nest survival. Three studies conducted in the prairie parklands, and only 1 study in the boreal forest have estimated survival of lesser scaup ducklings. In the prairie parklands, based on multiple counts of broods attended by marked hens, average duckling survival near Erickson, Manitoba during the first 28 days post-hatch was 0.617 from 1977 to 1980 (Afton 1984), but declined to 0.193 during the 1999 and 2000 breeding seasons (Koons 2001). At St Denis National Wildlife Area, Saskatchewan, average survival of ducklings was 0.38 during the first 48 days post-hatch (Dawson and Clark 1996). In

the one study of lesser scaup duckling survival conducted in the boreal forest, at sites near Yellowknife, NWT, the duckling survival probability for the first 47 days was 0.61, and daily survival rates (DSR) were significantly different between the first 17 days (DSR = 0.983) and the last 30 days (DSR = 0.993) of the pre-fledging period (Brook 2002). Although they did not measure duckling survival directly, Nudds and Cole (1991) suggested that, based on rate of within-year decline in brood sizes, survival of lesser scaup ducklings did not change between the 1960s and 1980s at the Yellowknife Study Area, NWT.

In this paper, we present information on lesser scaup nesting in the boreal forest of eastern interior Alaska on a pristine study site free of direct human disturbance outside of our research activities. Estimating and comparing scaup demographic rates from different geographic areas can contribute to improved conservation. Given the scarcity of information on scaup nesting in the boreal forest, basic nesting parameters are important to those trying to model scaup population dynamics. This information is also critical to managers making decisions concerning land exchanges and acquisitions as oil and gas corporations seek property for exploration in and around Yukon Flats NWR.

STUDY AREA

The Yukon Flats comprise a vast wetland basin bisected by the Yukon River in interior Alaska. The area encompasses over 20,000 wetlands scattered throughout 35,000 km² of mostly undeveloped wilderness. Elevation averages 180 m above sea level, with local relief of <45 m (King 1962). The basin is underlain by discontinuous permafrost and is heavily influenced by flooding and fire. The vegetation is largely open boreal forest with alkaline wet meadows that support some of the highest duck nesting densities in Alaska (Conant and Dau 1991).

The Yukon Flats have a continental subarctic climate characterized by great seasonal extremes in temperature and daylight. Summer temperatures can exceed 38°C and are warmer than at any other comparable latitude in North America; winter temperatures may reach extremes of -59°C or lower (U.S. Fish and Wildlife Service 1987). Annual precipitation ranges from 18 to 28 cm, and snow accumulation

rarely exceeds 76 cm (Bertram and Vivion 2002). Although the area has a short growing season of about 81 days, the long hours of sunlight during spring and summer produce lush vegetation.

Our study site (Plot M) was located on the eastern portion of Yukon Flats NWR between the Yukon and Porcupine Rivers (Fig. 1). This site was randomly selected along with 10 other plots for waterfowl brood surveys in the 1980s, and was used during a study of waterbird habitat selection conducted from 1984-1989 (Heglund 1988, 1992, Heglund et al. 1994). We expanded the original study site from that research (11.2 km²) to include all wetlands within a 54-km² area. The uplands of Plot M were dominated by dense stands of white spruce (*Picea glauca*), white birch (*Betula papyrifera*), and quaking aspen (*Populus tremuloides*). Shrub communities of alder (*Alnus* spp.) and willow (*Salix* spp.) dominated riparian sites and the edges of creeks and lakes. Wetland margins were dominated by sedges (*Carex* spp., *Eleocharis* spp.), grasses (*Calamagrostis* spp., *Glyceria* spp., and *Hordeum jubatum*), and cattail (*Typha latifolia*) (U.S. Fish and Wildlife Service 1987). Most wetlands on Plot M were <2 m deep and were nutrient-rich. In a study of 129 shallow wetlands on the Yukon Flats conducted from 1984-1990, over 70% were classified as eutrophic or hypereutrophic based on their nutrient content (Heglund and Jones 2003). Wetlands had extensive, dense beds of submersed plants dominated by *Potamogeton pectinatus*, *P. perfoliatus*, *P. filiformis*, and *Myriophyllum* spp. Creeks flowed between some wetlands on Plot M, and the Sucker River was located along the northern edge of the study site. These creeks and the river were extensively impounded by beavers (*Castor canadensis*), and had very low flow rates.

METHODS

Nest Survival

We imported the panchromatic band of a Landsat Enhanced Thematic Mapper+ (ETM+) satellite image (spatial resolution 15 m) taken on 24 June 2000 into a GIS software package (ArcView 3.4; ESRI, Inc., Redlands, CA) to digitize all wetlands within our 54-km² study plot. We estimated that Plot M encompassed 34 wetlands; applying an area-perimeter script, we determined that 15 of these wetlands exceeded 1 ha in area. Of these 15 wetlands, we selected 10 for scaup nest searches; 5 were classified as

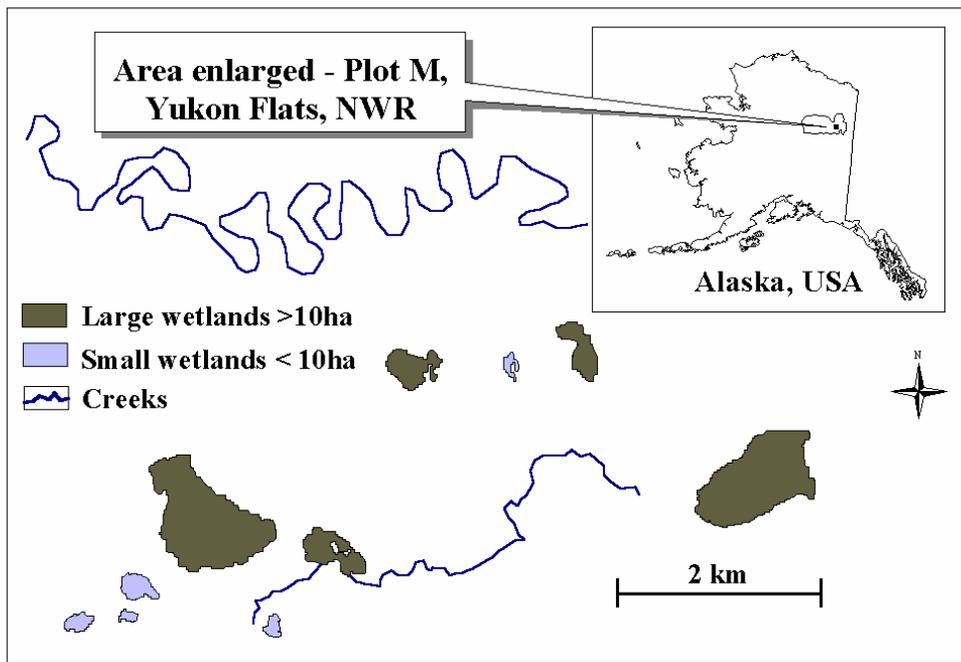


Fig. 1 . Yukon Flats National Wildlife Refuge (NWR), Alaska (inset) with Plot M enlarged to show the locations of study wetlands (n = 10) and creeks (n = 3).

large wetlands (area >10 ha; range = 10.8 – 69.7 ha), and 5 were classified as small wetlands (area <10 ha; range = 1.4 – 5.4 ha) (Fig. 1). In addition to the wetlands, we searched 3 wooded creeks: one creek that stretched 6.97 km between 2 of our largest wetlands, one smaller creek (0.78 km), and a portion of the Sucker River (19.27 km) that ran along the northern edge of the study area (Fig. 1).

Nest searches were conducted between 1 June and 25 July 2001, and between 10 June and 25 July 2002-2003. Nine of the 13 wetlands were searched in all 3 field seasons (2001-2003), whereas 4 of the wetlands were searched only in 2002-2003. Wetlands were searched 3 times during each nesting season at weekly intervals. Nests were located by crews of 2-5 people systematically searching wetland margins on foot and in kayaks in an effort to flush nesting hens. When a nest was located it was marked with a wooden stake about 20 m away, and a GPS reading was recorded to facilitate re-location. Dates of clutch initiation, initiation of incubation, and hatching were estimated by candling eggs (Weller 1956). The percent concealment of the eggs was estimated from eye level while standing directly above the nest, and was updated during subsequent visits; these values were averaged to obtain a single percent concealment value for each nest. The main cover type was recorded, and within 10 days after the nest either hatched or failed we measured average cover height, and distance from the nest to open water (area with no emergent vegetation), with a meter tape. Nests were monitored every 7-10 days. After a nest was located or checked, eggs were covered with nesting material to simulate natural incubation recesses by females (Gotmark 1992). The fate of clutches was determined by examining the nest contents for hatched egg membranes or evidence of predation (e.g. crushed egg shells). Nests which appeared to have been destroyed by predators were examined in an attempt to determine the predator species involved: we recorded the amount of disturbance around the nest as an indication of the size of the predator, and any trails to the nest which indicated mammalian predators.

Nest Survival Data Analysis.--We used Mayfield logistic regression (Hazler 2004) to estimate daily nest survival and to examine relationships between survival and explanatory variables. Mayfield logistic regression extends the traditional Mayfield estimator in a logistic regression framework. It accounts for

the number of exposure days for each nest, allows for censoring of nests with uncertain fates, and can incorporate explanatory variables at the group and nest level. To calculate the number of exposure days for each nest, we used hatch date as the last active day for successful nests, and assumed that failure occurred at 40% of the interval between observations for failed nests. We used this slight modification of the midpoint assumption (40% of exposure time rather than 50%) as recommended since the Mayfield estimator performs well unless the intervals between nest checks are long (7-10 days in our case) (Miller and Johnson 1978, Johnson 1979).

We developed 5 *a priori* candidate models to determine if the covariates year, clutch initiation date, or nesting habitat type influenced scaup nest survival. For the model that included all covariates, goodness-of-fit was assessed with the Hosmer and Lemeshow (2000) goodness-of-fit test. Models were evaluated with Akaike's Information Criteria after adjusting for small sample size and overdispersion (QAIC_c; Akaike 1973, Burnham and Anderson 2002). Under this framework, the model with the smallest QAIC_c value was interpreted as having the best fit to the data. We estimated overdispersion (\hat{c} = variance inflation factor) by dividing deviance by the degrees of freedom from our most highly parameterized model (year, initiation date, and habitat type). All models in our candidate set were scaled by this factor to adjust standard errors and AIC_c rankings.

We expected nest survival to differ among years due to annual variation in weather, predator numbers, and food availability. We included initiation date because early nesters tend to be older females and generally have higher nest success (Trauger 1971, Krapu and Doty 1979, Afton 1984, Lokemoen et al. 1990). We wondered if this pattern would hold for a species that is one of the latest-nesting ducks in the boreal forest, and for which there is evidence that ducklings that hatch later in the breeding season have higher probability of survival (Dawson and Clark 1996). We modeled scaup nest survival as a function of habitat type, because hens nested in three distinct habitats on our study site: (1) large wetlands (>10 ha, n = 5), (2) small wetlands (<10 ha, n = 5), and (3) wooded creeks (n = 3). Based on our experience searching for nests around different wetland types, we theorized that predator access

and movements might differ among these habitats. Large wetlands had larger open margins to search, and did not require extensive travel through dense forest to access them. In contrast, small wetlands offered less area to search, and were generally separated by large expanses of dense forest. Wooded creeks often had stretches without any open unforested margin, and we found that searching them was most efficient from kayaks; such conditions might discourage searching by some predators.

We implemented Mayfield logistic regression using PROC LOGISTIC in SAS software (SAS Institute, Cary, North Carolina). We used the events-trials syntax to model nest failure, where events were success (0) or failure (1), and trials were the number of exposure days for each nest. Signs on all coefficients and the intercept were reversed to interpret their effects on nest survival. We present the odds ratios and their 95% confidence intervals as a summary measure of the effect size of variables in our models. Odds ratios = 1.0 imply no survival differences, and therefore odds-ratio confidence intervals that include 1.0 indicate that the covariate does not significantly affect survival. As an example of interpretation, an odds ratio of 0.75 for the comparison of nest survival on large wetlands vs. wooded creeks would mean that the odds of nest survival on large wetlands was 25% lower than nest survival on wooded creeks.

After a model's intercept and coefficients had been estimated, we predicted survival based on the explanatory variables as:

$$\hat{S} = [1 + \exp(-(\hat{\beta}_0 + \hat{\beta}_1 X_1 + \hat{\beta}_2 X_2 + \dots + \hat{\beta}_n X_n))]^{-1}$$

where \hat{S} = daily survival rate (DSR), $\hat{\beta}_0$ is the model intercept, $\hat{\beta}_i$ are coefficients, and X_i are measured covariates (Hosmer and Lemeshow 1989, Allison 1999). Nest success was then estimated by raising the daily survival rate to an exponent equal to the average number of days it takes a scaup to lay and incubate a clutch (36 days).

Duckling Survival

Female lesser scaup were nest-trapped after 10 days into incubation in 2001, and when the eggs were fully pipped in 2002 and 2003, using a Weller trap placed over the nest (Weller 1957). Captured

adult females were weighed, aged by eye color (Trauger 1974), measured (width of bill nail, and length of bill, culmen, tarsus, and wing chord), and banded with a standard U.S. Fish and Wildlife Service aluminum leg band. They were fitted with an individually-numbered nasal disc, and a 5.5-g radio transmitter was mounted subcutaneously on the upper back. A local anesthetic (Lidocaine) was used at the site of attachment of the radio package. We implanted transmitters aseptically into a subcutaneous pocket formed by blunt dissection through a 20-mm incision between the scapulas. The antenna exited through a small hole created with an 18-gauge catheter about 20 mm distal to the incision site. We closed the incision with synthetic, absorbable 4-0 Vicryl sutures, and used surgical glue to close the hole through which the antenna exited the skin. Females nest-trapped were anesthetized with Propofol at the end of the banding and radio-tagging procedure to reduce nest abandonment (Rotella and Ratti 1990, Machin and Caulkett 2000).

Marked hens that hatched clutches were located every 2 days to attempt brood counts for the first week after hatch, and then weekly until total brood mortality occurred or up to 30 days after hatching. Previous studies indicated that almost no mortality of lesser scaup ducklings occurs after 4 weeks of age (Afton 1984, Dawson and Clark 1996). After hatch, females were carefully approached by 1 to 2 observers in kayaks at a distance that did not flush them from their ducklings, and were observed with binoculars until a complete brood count was obtained. Although brood amalgamation is not uncommon in this species (Hines 1977, Afton 1993), we did not observe any permanent brood mixing or brood abandonment by our marked hens.

Duckling Survival Data Analysis.--We used Mayfield's procedure modified by Flint et al. (1995a) to investigate the effects of duckling age on survival. To account for lack of independence between brood-mates, this method considers broods as clusters and bases the standard error estimator on cluster sampling. We calculated daily survival rate (DSR) from 1-30 days after hatch, assuming that daily survival was constant and mortality occurred halfway between observations from 1-10 days, and at 40% of the time period between observations from 11-30 days after hatch (Miller and Johnson 1978, Johnson

1979). Previous studies indicated that most mortality of scaup ducklings occurs within the first 2 weeks of hatch (Dawson and Clark 1996, Koons 2001, Brook 2002); consequently, we also calculated DSR separately for 3 periods: 0-10 days, 11-20 days, and 21-30 days after hatch. Survival estimates were calculated by raising DSR to the power of the period length in days, and confidence intervals were calculated by determining the 95% CI for DSR of each period and raising the upper and lower bounds to the power of the period length (Johnson 1979, Flint et al. 1995a).

Nest and Brood Density

To assess the frequency of scaup brood occurrence on different wetland types (large wetlands, small wetlands, wooded creeks) we conducted brood surveys on all wetlands that were searched for nests from 2001-2003. Brood surveys were conducted each season during the first week of August, when previous waterfowl production surveys on Plot M indicated high brood densities of scaup. The number of adults, number of ducklings, and duckling age were recorded during surveys from shorelines and from kayaks.

We used wetland and creek perimeters as determined by GIS from the 24 June 2000 ETM+ satellite image to calculate densities of both nests and broods on the 13 wetlands searched and surveyed. Wetland perimeters reflected the area searched for nests because only narrow (5-30 m) transition zones of cattail, sedge, and grass between open water and dense boreal forest were searched for nests. Forested habitats were not searched because a study conducted on Minto Flats, AK, where areas of both open meadows and forested sites were searched, indicated that scaup do not use woody vegetation for nesting; only open habitats were used in both high and low water years from 1989-91 (Petrula 1994). Although wooded habitats were not systematically searched for scaup nests on our study site, we did travel through this habitat type extensively when moving between wetlands and scaup nests were never encountered.

We used nest and duckling densities as response variables to explore differences between habitat types (large wetlands, small wetlands, wooded creeks) and years (2001-2003) using a split-plot analysis of variance (ANOVA) to account for repeated measurements in different habitat types over years. We

tested for habitat and year main effects and habitat \times year interactions with PROC GLM (SAS Institute 2001). We used least significant difference tests for post-hoc analyses to identify specific differences when ANOVA revealed significant factor effects. Before analysis, duckling densities were log-transformed to normalize residuals and increase homogeneity of variance.

RESULTS

We monitored a total of 177 scaup nests on Yukon Flats NWR during three breeding seasons, 2001-2003. The nesting season, from first clutch initiated until last clutch hatched, ranged from 27 May to 6 August (72 days) across all years. The mean clutch initiation date of scaup for all years combined was 15 June ($n = 177$, 95% CI: 14 June to 16 June). There was no significant difference in clutch initiation date between 2002 and 2003 (14 June: $n = 135$ nests, 95% CI: 12 June to 15 June), but clutch initiation date was significantly later in 2001 (19 June: $n = 42$, 95% CI: 17 June to 21 June). Clutch initiation, from first to last clutch initiated, lasted 41 days (27 May to 5 July). Mean clutch size was 8.3 eggs ($n = 141$, 95% CI: 8.0 to 8.6), with no significant difference between years. Intra- and interspecific parasitism were rare on our study site; only 1 nest contained redhead (*Aythya americana*) eggs (3 redhead eggs, 5 scaup eggs), and 5 clutches exceeded 12 eggs, indicating that the latter clutches probably resulted from more than one scaup hen laying in the nest (Weller et al. 1969). Most nests (71.4%) were located within 0.5 m of open water (mean distance to open water for all nests = 3.67 m, SE = 0.65 m), and only 7 of 177 nests were over 25 m from the edge of open water. Most nests were well concealed (mean percent concealment = 71.2%, SE = 2.3%) in either *Carex* spp. (70%) or *Calamagrostis canadensis* (26%). Cover height at nests averaged 1.02 m (SE = 0.07).

Predation was the major factor in nest failure, causing 68% of nest loss across all years. Avian predators most frequently seen in the area were mew gulls (*Larus canus*), great horned (*Bubo virginianus*) and great gray owls (*Strix occidentalis*), northern harriers (*Circus cyaneus*), and common ravens (*Corvus corax*). Potential mammalian predators included red squirrels (*Tamiasciurus hudsonicus*), wolves (*Canis lupus*), red foxes (*Vulpes vulpes*), grizzly and black bears (*Ursus horribilis*

and *U. americanus*), martens (*Martes americana*), short-tailed and least weasels (*Mustela erminea* and *M. rixosa*), minks (*Mustela vison*), and lynxes (*Lynx canadensis*). Mammalian predators seen in the area during this study were red squirrels, grizzly and black bears, wolves, lynxes, and short-tailed weasels. Identifying predators of nests is difficult; however, due to extensive disturbance at and around depredated nests, large mammals were suspected in at least 21 of the 84 nest losses due to predation. The only predator observed depredating a nest was a wolf. In 2003, 4 scaup hens were killed on the nest, probably by bears.

Nest Survival

Of the 177 scaup nests monitored, 12 were right censored due to abandonment in response to nest trapping of hens before hatch. The Hosmer and Lemeshow (2000) goodness-of-fit test indicated that the global model fit the observed values ($\chi^2 = 8.87$, $df = 8$, $p = 0.353$). The estimated \hat{c} (variance inflation factor) based on the global model was 1.36, and we used the $\sqrt{\hat{c}}$ to adjust all models in our candidate set because the SAS software squares the SCALE factor when calculating the covariance matrix. Based on the constant survival model for estimation, daily survival rate (DSR) of scaup nests was 0.943 (95% CI: 0.930 to 0.954), corresponding to a nest success of 12.3%. The best model included habitat as a predictor of nest survival (Table 1) and indicated that nest survival was highest on creeks ($n = 42$ nests), intermediate on small wetlands (<10 ha) ($n = 42$ nests), and lowest on large wetlands (>10 ha) ($n = 93$ nests). The odds of nest survival were 49% lower on large wetlands than on creeks (Table 2). The odds of nest survival were 40% lower on small wetlands than on creeks, but the 95% CI for the odds ratio overlapped 1.0 in this case (Table 2). Using coefficients from the model that used only habitat type for estimation, DSR on wooded creeks was 0.963 (corresponding nest success = 26.2%), DSR on small wetlands was 0.941 (corresponding nest success = 11.1%), and DSR on large wetlands was 0.931 (corresponding nest success = 7.6%). There was no difference in nest survival between years (Akaike $w_i = 0.12$, $\chi^2 = 2.51$, $p = 0.29$), and initiation date did not affect chances of survival (Akaike $w_i = 0.09$, $\chi^2 = 0.14$, $p = 0.71$) (Table 1).

Table 1. Model selection results for survival of lesser scaup nests (n = 177) on the Yukon Flats, Alaska, 2001-2003. Models are ranked by ascending ΔQAIC_c , with the best-fitting model listed first.

Nest survival model	K^a	ΔQAIC_c^b	w_i^c
Habitat	3	0.00	0.51
Constant	1	1.91	0.20
Year	3	2.92	0.12
Initiation date	2	3.41	0.09
Global	6	3.81	0.08

^a The number of estimated parameters.

^b Quasi-likelihood Akaike's Information Criterion corrected for small sample sizes and overdispersion ($\hat{c} = 1.36$). ΔQAIC_c is the difference between QAIC_c of the current model and the minimum observed QAIC_c value.

^c Akaike weights are the relative likelihood of the model given the data.

Table 2. Odds ratios and 95% confidence intervals (CI) for explanatory variables from the Mayfield logistic regression analysis predicting nest survival of lesser scaup (n = 177 nests) on the Yukon Flats, Alaska, 2001-2003. As an example, the odds ratio of 0.512 for large wetlands vs. creeks indicates that the odds of nest survival on large wetlands was 48.8% lower than on wooded creeks.

Variable	Odds ratio	CI
Large wetlands vs. creeks	0.512	0.286, 0.918
Small wetlands vs. creeks	0.603	0.306, 1.189
Large wetlands vs. small wetlands	0.850	0.489, 1.479
Year (2001 vs. 2003)	0.826	0.459, 1.485
Year (2002 vs. 2003)	1.329	0.793, 2.229
Year (2001 vs. 2002)	0.621	0.337, 1.145
Initiation date	0.995	0.970, 1.021

Duckling Survival

Ten lesser scaup hens that were radio-tagged in 2001-2003 hatched broods, and we monitored the fate of the 75 ducklings in these broods. Most duckling mortality (94%) occurred in the first 10 days after hatch. Five of the 10 radio-marked hens lost their entire broods, 3 within 2 days of hatching. Daily survival of ducklings from 1-30 days was 0.948 (SE = 0.025), corresponding to survival probability over this period of 0.201 (95% CI = 0.041 to 0.912). Mortality was greatest during the first 1-10 days after hatch; however, confidence intervals for the 1-10 day and 21-30 day intervals barely overlapped (Table 3).

Although only 10 marked hens were monitored, 3 made substantial overland movements when the ducklings were less than 10 days old, indicating that such movements are not rare. Two hens moved at least 0.3 km overland, and 1 hen moved at least 1.6 km overland. One hen moved immediately following hatch with the possible loss of 1 duckling, and the other 2 hens moved their broods when the ducklings were between 7 and 10 days old without losing any ducklings.

Nest and Brood Density

The interaction between wetland type and year was not significant for either nest density or duckling density in the split-plot ANOVA, and no difference was seen between years in either of the density estimates (Table 4). There were no significant differences between wetland types in nest density (Fig. 2); however, there was a significant main effect for wetland type in duckling density ($F_{2,6} = 54.62$, $p < 0.001$). A post-hoc least significant difference test indicated that duckling densities were higher on large wetlands than on small wetlands or creeks (Table 5), with no difference in density between the latter habitat types (Fig. 2).

Table 3. Daily survival rates (DSR) and associated standard errors (SE), and interval survival probabilities (S) and associated 95% confidence intervals (CI), for lesser scaup ducklings based on data collected from radio-marked females (n = 10 broods, 75 ducklings) on the Yukon Flats, Alaska, 2001-2003.

Interval	DSR	SE	S	CI
1-10 days	0.892	0.042	0.321	0.122, 0.772
11-20 days	0.996	0.004	0.964	0.891, 1.040
21-30days	0.992	0.009	0.923	0.769, 1.041

Table 4. Results of split-plot analysis of variance testing the effects of habitat type (large wetlands >10 ha, small wetlands <10 ha, wooded creeks) and year (2001-2003) on the density of lesser scaup nests and ducklings (no./km of shoreline) on the Yukon Flats, Alaska. F-values were calculated with Type III sums of squares.

Predictors	<i>F</i>	df	<i>P</i>
Nest density			
Habitat	0.35	2, 6	0.719
Year	1.68	2, 8	0.247
Habitat × year	2.56	4, 8	0.120
Duckling density			
Habitat	54.62	2, 6	< 0.001
Year	2.01	2, 8	0.196
Habitat × year	1.43	4, 12	0.283

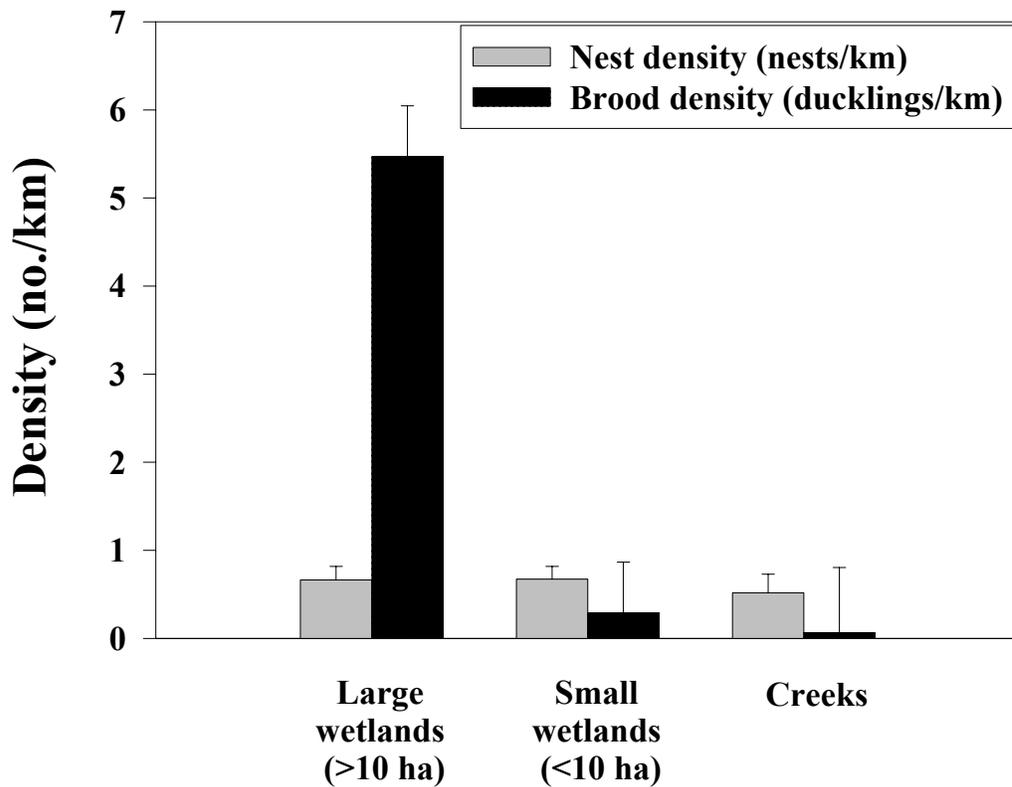


Fig. 2. Mean densities (no./km of shoreline) of lesser scaup nests and ducklings by habitat type on the Yukon Flats NWR, Alaska, 2001-2003. Error bars = 1 SE. No significant differences were seen between habitat types in nest density; however, brood density was significantly higher on large wetlands than on small wetlands or creeks ($F_{2,6} = 54.62$, $p < 0.001$).

Table 5: Results of the post-hoc least significant difference test ($\alpha = 0.05$) of the effect of habitat type (large wetlands >10 ha, small wetlands <10 ha, wooded creeks) on lesser scaup duckling density (no./km of shoreline) on the Yukon Flats, Alaska, 2001-2003.

Duckling density habitat comparisons	Difference between means	95% Confidence Interval
Large wetland – Creek	5.30	(3.66 to 6.93) ***
Large wetland – Small wetland	5.34	(3.92 to 6.75) ***
Creek – Small wetland	0.04	(-1.60 to 1.68)

*** Comparisons significant at $\alpha = 0.05$.

DISCUSSION

Clutch Initiation Date and Clutch Size

Mean clutch initiation date of lesser scaup on the Yukon Flats was within the range of estimates reported for the boreal forest. The mean clutch initiation date across all years was 15 June, very close to estimates on the Yellowknife Study Area (hereafter Yellowknife), NWT, where peak clutch initiation dates ranged from 7-13 June in 1967-1970 (Bellrose 1980), and from 19-21 June in 1999-2000 (Brook 2002).

However, on Minto Flats, AK, about 100 km south of Yukon Flats, mean clutch initiation date was 7 June from 1989-1991 (Petrula 1994), about a week earlier than our estimate.

Mean clutch size of lesser scaup on the Yukon Flats of 8.3 eggs was on the low end of estimates for the boreal region. Previous studies of lesser scaup nesting in Alaska estimated clutch size at 9.5 eggs (Nelson 1953) on the Yukon Flats in 1953, and 9.6 eggs on Minto Flats in 1989-1991 (Petrula 1994).

Estimates of lesser scaup clutch size from the Canadian boreal forest were 9.0 eggs on the Saskatchewan River Delta and 8.7 eggs at Yellowknife in 1990-1995 (Fournier and Hines 2001), and 7.8 to 8.6 eggs on the same Yellowknife study site in 1999-2000 (Brook 2002). Declines in clutch size over time would support the spring-condition hypothesis (Anteau and Afton 2004). If hens are arriving on the breeding grounds in poor condition, nesting may be delayed and clutch sizes reduced. However, inferring declines from Nelson's (1953) estimate for clutch size on the Yukon Flats (9.5 eggs) is problematic since it was based on only 16 nests. Average clutch size in the same study for scaup nesting on Minto Flats was 8.5 (4 nests), and on the Yukon Delta was 8.4 (59 nests), values quite similar to ours.

Distance of Nests to Open Water

Most scaup nests located on the Yukon Flats NWR were within 0.5 m of open water (mean distance to open water = 3.7 m, SE = 0.7). This value is quite different from nests found on Minto Flats, AK, where mean distance to water was 60.3, 58.8, and 17.3 m for 1989, 1990, and 1991 respectively (Petrula 1994). This large disparity reflects differences in nesting habitat in the 2 locations: on Minto Flats frequent flooding helps maintain large meadows, whereas on our study site, nesting habitat was

largely restricted to small strips bordering wetlands. Flooding also affected nest survival on Minto Flats, where 14-18% of all nest losses in high-water years resulted from flooding. During three years on our study site, water levels remained relatively stable within and between seasons, and only 1 nest was lost to flooding across all field seasons. On Minto Flats, channel habitats were infrequently used by scaup for nesting: only 11 of 244 nests (4.5%) were located near a channel. On our study site, 42 of 177 nests (23.7%) were found on creeks, but these results may reflect differences in habitat availability and search effort on the 2 study areas.

Nest Survival

Our overall estimate of nest success for lesser scaup breeding on the Yukon Flats was 12.3%, considerably lower than the average of 57% for lesser scaup in the northern boreal forest from the summary by Austin et al. (1998). However, recent scaup nesting studies in the boreal forest have documented low nest success. From 1990-1998, estimated scaup nest success was 18% at Yellowknife, NWT, on a site considered typical habitat of lesser scaup in that region (Fournier and Hines 2001). Additional research on this site in 1999 and 2000 yielded a nest success estimate of 14% (Brook 2002). Also, the Mayfield estimate of lesser scaup nest success on Minto Flats, AK from 1989-1991 was 4.4% (Petrula 1994), indicating that even in remote, undisturbed habitats in the boreal forest, scaup nest success may be very low.

In our study, the odds of nest survival on large and small wetlands were lower than on wooded creeks. The sedge/grass margin used by nesting scaup was in general narrower on wooded creeks, perhaps being less attractive to predators because of the smaller area available to search and the difficulty of moving through dense cover between open areas. Mammalian predators may find searching the margins of large and small wetlands more efficient than traveling through dense spruce forest between and bordering creeks.

There is evidence that body condition of lesser scaup upon arrival at nesting areas has been declining in recent years, perhaps due to reduced availability or quality of food on northern spring

stopover sites (Anteau and Afton 2004). If all birds are arriving lean, then late nesters might have had longer to build up reserves before nesting and therefore be more successful than earlier nesters. We did not see a relationship between clutch initiation date and nest survival, but this result is not completely unexpected since scaup are one of the latest-nesting species on boreal wetlands and have a contracted nesting period. All clutches on our study site were initiated over a 41-day period from 27 May to 5 July, and this range may not be large enough to detect differences in survival given our sample size. There is also evidence that scaup ducklings from nests that hatch later in the season have higher probability of survival (Dawson and Clark 1996); thus, for a late-nesting species like scaup, it may be beneficial to nest as late as possible, while still avoiding stranding of flightless young and molting adults due to ice-up of wetlands in early fall. Food resources for duckling growth and survival are thought to be the main factor favoring late nest initiation (Austin 1983, Dawson and Clark 2000), and this factor may mask any effects of clutch initiation date on nest survival.

Duckling Survival

Our estimate of duckling survival to 30 days of 0.201 (95% CI: 0.041 to 0.912) was considerably lower than the value of 0.61 (95% CI: 0.51 to 0.70) reported by Brook (2002) for lesser scaup in the boreal forest at Yellowknife. However, our value was similar to the low estimate from a recent study in the prairie parklands of Manitoba (0.193, 95% CI: 0.108 to 0.323) (Koons 2001). The pattern of high mortality early in brood-rearing also agrees with other studies of lesser scaup ducklings (Dawson and Clark 1996, Koons 2001, Brook 2002), and of juvenile waterfowl in general (Savard et al. 1991, Flint et al. 1995*b*, Grand and Flint 1996, Korschgen et al. 1996, Flint and Grand 1997). Of duckling mortalities in our study, 94% occurred within 10 days of hatch, and 3 of 10 broods suffered total brood loss within 2 days of hatching.

It was not possible to determine the causes of duckling mortality, but we suspect both predation and weather had a role. Weather when most scaup nests were hatching was relatively benign during this study; however, cool temperatures and rain may have contributed to duckling mortality. Potential

predators of ducklings included all nest predators noted earlier, as well as herring gulls (*Larus argentatus*) which were uncommon and seen only during the brood-rearing period, but were observed depredating scaup broods.

Three of 10 hens successfully moved their ducklings overland, 2 from smaller to larger wetlands, and 1 from a creek nest to a large wetland, indicating that overland movements are not rare. All brood movements occurred before the ducklings were 10 days old. Movement of broods via creeks connecting wetlands is not unexpected, but the 3 brood movements during this study were through boreal forest since no creeks connected the wetlands involved. Total brood loss occurred in 5 instances, and the possibility that ducklings died while traveling between wetlands cannot be ruled out. However, after losing their ducklings, radio-marked hens were always re-located on the wetlands where they were last observed with broods or nests, suggesting that the duckling deaths occurred on that wetland. We believe it is not uncommon for scaup to nest away from brood-rearing wetlands and move broods shortly after hatch. Scaup nesting on the Sucker River, for instance, would need to move ducklings a minimum overland distance of 1.2 km to the nearest wetland where broods were encountered during surveys.

We assumed that nasal markers and radio transmitters did not affect the females' behavior or ability to raise their broods; however, changes in waterfowl body mass and behavior have been associated with carrying radio transmitters (Greenwood and Sargeant 1973, Pietz et al. 1993). In a study of breeding scaup, nasal markers and subcutaneously implanted radio transmitters did not affect behavior except for head shaking, which was more likely related to nasal markers than to transmitters (Brook and Clark 2002). Although we observed radio-tagged females for 5-30 min during duckling counts, and there was no obvious behavioral response, we cannot be certain that there were no effects of nasal markers or transmitters on the behavior or brood-rearing ability of females.

Nest and Brood Density

Little is known about scaup nesting habitat in the northern boreal forest. Studies suggest that scaup prefer larger wetlands for breeding and particularly brood-rearing (Toft et al. 1982, van Horn 1991,

Heglund 1992, Decarie et al. 1995, Fast et al. 2004). On our study site, nest densities did not differ significantly between wetland types (large wetlands, small wetlands, wooded creeks), indicating that scaup were willing to nest in the wetland types we searched. However, duckling densities did differ significantly between wetland types. Previous studies in the boreal forest have concluded that lesser scaup prefer wetlands >1 ha in area for brood rearing (vanHorn 1991, Heglund 1992, Fast et al. 2004), but results from our brood surveys on the Yukon Flats indicate that wetlands over 10 ha in area were used much more frequently than smaller wetlands, even though smaller wetlands were >1 ha (range = 1.4 - 5.4 ha). We observed high nest densities on creeks compared to the few studies conducted in the boreal forest, but this pattern may be because creeks were not searched in previous studies. There are no published accounts of scaup in the boreal forest using creeks for brood-rearing, and on our study site scaup broods were rarely encountered on creeks. Although scaup might attempt to raise ducklings on small wetlands and creeks but suffer high mortality, our telemetry data on brood movements indicate that hens were willing to move their broods, sometimes long distances, from smaller wetlands and creeks to larger wetlands where brood densities were high. Since scaup that nest on large brood-rearing wetlands suffer higher nest losses, a better strategy may be to nest on creeks not used for brood-rearing where nest survival is higher, and then move ducklings shortly after hatch.

Females should select habitat where their chances of success are high, and they may move their ducklings to large wetlands due to better food resources or protection from predators. We did not consider differences in invertebrate communities between wetland types in this analysis; however, creeks had distinctly less emergent vegetation and fewer invertebrates than small or large wetlands. Amphipods are an important food of scaup, especially for older ducklings (Bartoneck and Hickey 1969, Bartoneck and Murdy 1970, Sugden 1973), and habitat selection by scaup has been linked to the density of amphipod prey (Afton and Hier 1991, Lindeman and Clark 1999). Larger wetlands had high amphipod densities, perhaps because they tended to be deeper and the chance of over-winter survival of amphipods was greater (Fast et al. 2004). Also, on larger wetlands the risk of predation may be lower. Female

scaup did not use concealing vegetation to hide ducklings; rather, they moved ducklings to open water when disturbed, and larger wetlands offered more open water for this function.

MANAGEMENT IMPLICATIONS

Information about vital rates for declining species may provide valuable insights into causes of declines. Research on lesser scaup, however, has been limited by the remoteness and logistical difficulties of working in the boreal forest. Nest success and duckling survival of lesser scaup on the Yukon Flats were among the lowest reported for ducks nesting at northern latitudes, even though the study site was in pristine boreal forest. This finding indicates that long-term trends in environmental conditions in the boreal forest ecosystem may be resulting in reduced reproductive success of scaup, thereby contributing to local population declines observed on the Yukon Flats.

Loss of habitat may be playing a role in lesser scaup declines on the Yukon Flats, especially for scaup nesting on small wetlands and creeks that are more rapidly affected by drying due to warming temperatures. The boreal forest region has experienced an average rise in temperature of 3°C since the 1960s (Hansen and Lebedeff 1987, Lashof and Ahuja 1990, Chapin et al. 1995, Weller et al. 1999). Climate change models project a decline in small wetlands and shallow creeks with increasing evapotranspiration rates, and increased infiltration and water-holding capacity in boreal forest soils due to melting of permafrost (Woo et al. 1992, Rouse et al. 1997). Between 1952 and 2000, the Yukon Flats lost 18% of its wetland area (Riordan 2005). Although large brood-rearing wetlands experience less impact, the loss of small wetlands and particularly creeks (where scaup nest success appears to be higher) could result in local declines in productivity. Efforts to project habitat trends and resulting population trajectories of scaup should perhaps consider such differences among habitat types.

Development within the Yukon Flats is limited to native in-holdings, and subsistence use by local residents and recreational hunters and trappers represents the only current consumptive use of natural resources. However, oil and gas corporations have expressed interest in land exchanges for exploration

in and around the Yukon Flats. The value of large wetlands used by breeding and molting waterfowl on the refuge has long been recognized. However, our study demonstrates that lesser scaup use small wetlands and creeks for nesting activity and that these habitats near large wetlands are of high value.

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Chapter II: Long-term change in limnology, invertebrates, and avian predators in Alaskan boreal wetlands.

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 pristine boreal forest of northeast Alaska, we re-sampled water chemistry and macroinvertebrates in summer 2001–2003 from 9 wetlands where similar data were collected during 1985–1989. These wetlands lost an average 18% of surface water area between decades, results very similar to other studies over much larger areas. Total nitrogen and most metal cations (Na, Mg, and Ca, but not K) increased between these periods, while total phosphorus (TP) and chlorophyll *a* (Chl *a*) declined. These changes were greater in wetlands that had experienced more drying (decreased surface area). Compared to 1985–1989, densities of cladocerans, copepods, and ostracods in both June and August were higher in 2002–2003, while densities of amphipods, gastropods, and chironomid larvae were generally lower. The latter taxa (especially amphipods) are thought to be critical prey for lesser scaup (*Aythya affinis*), a diving duck that nests mainly in the boreal forest and whose numbers have been declining for over 20 years. 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 long-term decline in Chl *a* corresponded to greatly increased zooplankton density in June, suggesting a shift in carbon flow from scrapers/deposit-feeders that are eaten by scaup to water-column grazers that are not. In 2003, the density of lesser scaup ducklings among wetlands was not related to any of our measures of macroinvertebrate biomass. However, declines in benthic and epibenthic deposit-feeders that are key prey for lesser scaup suggest important foodweb effects of climate change in otherwise pristine wetlands of the boreal forest.

Introduction

Winter temperatures in the boreal forest of Alaska have increased by as much as 3 to 4 °C over the past 60 years, compared with a mean increase of 0.6 °C over the past 100 years for the rest of the world (Hansen and Lebedeff 1987, Lashof and Ahuja 1990, Chapin et al. 1995, Environment Canada 1995, Weller et al. 1999). By the end of the 21st century, the Arctic is expected to warm by more than twice the global average (Arctic Climate Impact Assessment 2004). The boreal forest is the largest terrestrial ecosystem on earth, covering about 17% of the earth's land surface. Numerous lakes cover about 10% of the boreal area (Molot and Dillon 1996, Schindler 1998). With close coupling between air and water temperatures in shallow lakes, 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 in this region (Carvalho and Kirika 2003). In this paper, we examine trends in limnology and macroinvertebrate communities over 19 years, and associated effects on an avian predator of invertebrates, in boreal wetlands of northwest North America.

Long-term monitoring data in the boreal region are rare, but the few available studies suggest that increased warming is already causing major changes in the physical, chemical, and biological characteristics of boreal lakes (review in Schindler 1997). The northwest boreal zone of North America receives relatively little precipitation (often <30 cm/y), and the abundant wetlands result largely from two factors: (1) cool, short summers with low evapotranspiration, and (2) an impermeable permafrost layer which prevents infiltration and impedes drainage of the upper unfrozen layer (Livingstone 1963, Ford and Bedford 1987). Widespread melting of permafrost which has already been documented (Hinzman and Kane 1992, Osterkamp and Romanovsky 1999, Jorgenson et al. 2001), and increased evapotranspiration, will result in fewer, more nutrient-rich wetlands (Rouse et al. 1997, Kankaala et al. 2000, Moser et al. 2002, Riordan 2004). Nutrients will be concentrated as wetlands dry (lose water volume); and as permafrost underlying wetlands and adjacent uplands melts, rates of nutrient

mineralization and leaching into surface waters will increase. Resulting changes in trophic structure may cause major shifts in community structure (Bayley and Prather 2003).

Climate also influences the timing of important life-history events. In a review of phenological shifts, 62% of 677 species showed trends toward spring advancement (Parmesan and Yohe 2003). If different species exhibit unique responses to changes in temperature, their interactions with other species in the food web may be altered. An example is the temporal mismatch that has developed between peak food demands of nestling songbirds and peak insect availability, due to advanced leaf flush resulting from warmer springs in Europe (Visser et al. 1998, Thomas et al. 2001).

Such changes have already been documented in aquatic food webs. A longer ice-free season in boreal lakes of Ontario has resulted in higher total nitrogen and phosphorus concentrations, and increased populations and diversity of phytoplankton despite overall declines in chlorophyll concentrations (Schindler et al. 1990, Schindler et al. 1996a). At Toolik Lake in Alaskan arctic tundra, 16 years of physical, chemical, and biological data showed potential negative impacts of global warming on lake trout (*Salvelinus namaycush*), the keystone predator in many arctic and boreal lakes (McDonald et al. 1996, Gunn et al. 2003). In polar semi-desert and tundra heath in Spitsbergen, the phenology of chironomid abundance changed with differences in temperature between years (Hodkinson et al. 1996, 1998). Under normal conditions, chironomid emergence was spread evenly across the summer; however, higher temperatures resulted in a large early emergence. 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).

Studies in north-temperate lakes have revealed divergent responses of zooplankton to earlier spring algal blooms resulting from warmer temperatures. In Lake Washington (Seattle, USA), temperatures in the upper 10 m of the water column in spring have increased by an average 1.39°C since 1969, onset of stratification now occurs 21 days earlier than it did 4 decades ago, and timing of the spring phytoplankton bloom advanced accordingly by 27 days between 1962 and 2002. Timing of peak

densities of the herbivorous rotifer *Keratella* advanced 21 days in response to the earlier peak of spring algal blooms; however, *Daphnia* failed to respond, resulting in long-term declines in spring and summer densities (Winder and Schindler 2004). Lack of a response by *Daphnia* to match peak food availability might be explained by use of hatching cues disconnected from the increase in water temperature (Winder and Schindler 2004). In contrast to patterns in Lake Washington, *Daphnia* populations in Loch Leven, a large shallow lake in lowland Scotland, did shift their seasonality to match the earlier and smaller spring peaks in phytoplankton that resulted from warming temperatures over 34 years (Carvalho and Kirika 2003).

A common predator of macroinvertebrates in boreal wetlands is the lesser scaup duck (*Aythya affinis*), whose populations have declined substantially over the last 20 years (Afton and Anderson 2001). A proposed reason for this decline is decreased breeding productivity due to changes in boreal forest habitats where most lesser scaup nest (Austin et al. 2000). Breeding parameters such as nest success and rate of renesting depend on females acquiring adequate mineral, protein, and lipid reserves for producing and incubating eggs. Use of stored reserves by incubating scaup is lower than by other waterfowl of similar size (Afton and Ankney 1991, Esler et al. 2001), and greater reliance on exogenous resources may make scaup more susceptible to changes in amounts or timing of invertebrate prey. Body reserves of female lesser scaup at northern stopover sites during spring migration in 2000 and 2001 were lower than in the 1980s (Anteau and Afton 2004), and females arriving at breeding grounds in poorer condition are expected to be more sensitive to changes in local food availability.

Lesser scaup are also one of the latest-nesting duck species in North America, with nest initiation in northern boreal forests not occurring until early to mid June. Lesser scaup ducklings from nests hatched later in the season appear to have higher probability of survival (Dawson and Clark 1996), and better food resources for duckling growth and survival are thought to be a factor favoring late nest initiation (Austin 1983). Amphipods are an important food of scaup, especially for older ducklings (Bartonek and Hickey 1969, Bartonek and Murdy 1970, Sugden 1973), and habitat selection for brood-rearing has been

linked to the density of amphipod prey (Afton and Hier 1991, Lindeman and Clark 1999, Fast et al. 2004). Given the unprecedented warming in the boreal forest biome, it is reasonable to expect changes in abundance and timing of availability of aquatic invertebrates, with consequent effects on nesting scaup (Rouse et al. 1997, Sorenson et al. 1999, Roy and Sparks 2000, Walther et al. 2002).

To evaluate possible impacts of climate warming, we studied trends in drying, water chemistry, and macroinvertebrates in boreal wetlands of the Yukon Flats in eastern interior Alaska. Assessment of long-term changes on the Yukon Flats was possible because of existing data on limnology and invertebrates in these wetlands from the 1980s (Heglund 1988, 1992, Heglund and Jones 2003). From 1985 through 1989, data were collected on macrophytes and limnology of 129 wetlands on the Yukon Flats National Wildlife Refuge (NWR) for use in developing a regional wetland classification (Heglund 1992), and for modeling use of wetland types by aquatic birds (Heglund et al. 1994). Scaup used nearly all wetland types on the refuge, but were found most often on large, highly productive, slightly brackish wetlands. Wetlands of different nutrient status and salinity are expected to differ in the abundance and community structure of invertebrates (Voights 1976, Lancaster and Scudder 1987, Murkin et al. 1991, Jorgenson et al. 1992, Lovvorn et al. 1999, Verschuren et al. 2000, Hart and Lovvorn 2005). Recent and expected climate change may decrease the number of less eutrophic vs. highly eutrophic wetlands, while reducing the sum of both combined. The Yukon Flats lost 18% of surface water area between 1952 and 2000 (Riordan 2004). Given this high rate of wetland area loss, it becomes important to know what effects, if any, climate warming may be having on relations between water chemistry, macroinvertebrates, and their predators such as lesser scaup.

In this study, we determined whether changes in water chemistry and macroinvertebrate communities occurred between 1985–1989 vs. 2001–2003 in wetlands of the Yukon Flats. As there were few published studies on invertebrate taxa 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. Finally, we compared densities of lesser scaup

ducklings with macroinvertebrate biomass in 2003 to explore how changes in boreal wetlands may be contributing to scaup declines.

Study area

The Yukon Flats comprise a vast wetland basin bisected by the Yukon River in interior Alaska (65.7–67.5°N, 142.5–150.0°W). The area encompasses over 20,000 wetlands scattered throughout 35,000 km² of mostly undeveloped wilderness. Elevation averages 180 m above sea level, with local relief of <45 m (King 1962). The basin is underlain by discontinuous permafrost and is heavily influenced by flooding and fire. Vegetation is largely open boreal forest with alkaline wet meadows that support some of the highest duck nesting densities in Alaska (Conant and Dau 1991).

The Yukon Flats have a continental subarctic climate characterized by great seasonal extremes in temperature and daylight. Summer temperatures can exceed 38 °C and are warmer than at any other area with similar latitude in North America (U.S. Fish and Wildlife Service 1987). Winter temperatures may reach extremes of –59 °C or lower, annual precipitation ranges from 18 to 28 cm, and snow accumulation rarely exceeds 76 cm (Bertram and Vivion 2002). Although the area has a short growing season of about 81 days, the long hours of sunlight during spring and summer yield lush vegetation.

A study in the 1980s found that wetlands on the Yukon Flats were among the most nutrient-rich in Alaska, with over 70% of 129 representative water bodies classified as eutrophic or hypereutrophic (Heglund and Jones 2003). Reasons for these high nutrient levels include the geologic setting in carbonate alluvium, shallow water depths, and resulting high mixing rates of the water column. Ratios of total nitrogen (TN) to total phosphorus (TP) (mean 12.3) suggested that N was limiting in about half the wetlands sampled. Ratios of chlorophyll *a* (Chl *a*) to N (mean 12.1) and Chl *a* to P (mean 0.11) were low relative to other regions, probably because of grazing of microalgae by invertebrates. Most lakes in the area have maximum depth <2 m and freeze to the sediments each winter; resulting lack of permanent fish communities allows abundant invertebrates.

Methods

In our study, water chemistry, macroinvertebrates, and densities of lesser scaup ducklings were measured in wetlands on three study plots on the Yukon Flats NWR (Fig. 1). In the 1980s, these sites were randomly selected along with 8 other plots for waterfowl production surveys, and were used in a study of waterbird habitat selection from 1985–1989 (Heglund 1988, 1992, Heglund et al. 1994, Heglund and Jones 2003). To assess water chemistry changes since the 1980s, we re-sampled 9 wetlands: 2 wetlands on Plot C, 2 wetlands on Plot H, and 5 wetlands on Plot M (Fig. 1). These 3 plots were chosen for re-sampling because waterfowl production surveys indicated high numbers of lesser scaup. To examine relations between water chemistry, macroinvertebrate biomass, and density of scaup ducklings during our study, we included 4 additional wetlands adjacent to Plot M, increasing our sample size for comparisons to 13 wetlands.

Changes in Wetland Area

Aerial photographs taken in June 1952 were compared to (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 3 images were imported into a GIS software package (ArcView 3.4; ESRI, Inc., Redlands, CA) after georectification with ERDAS IMAGINE 8.6 (Leica Geosystems, Heerbrugg, Switzerland). 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) sampling periods, limnological sampling was repeated according to the protocols of Heglund (1992). Monthly (June, July, August) water samples were collected from 9 wetlands, and analyzed for total nitrogen (TN), total phosphorus (TP), sodium (Na), magnesium (Mg), calcium (Ca), potassium (K), pH,

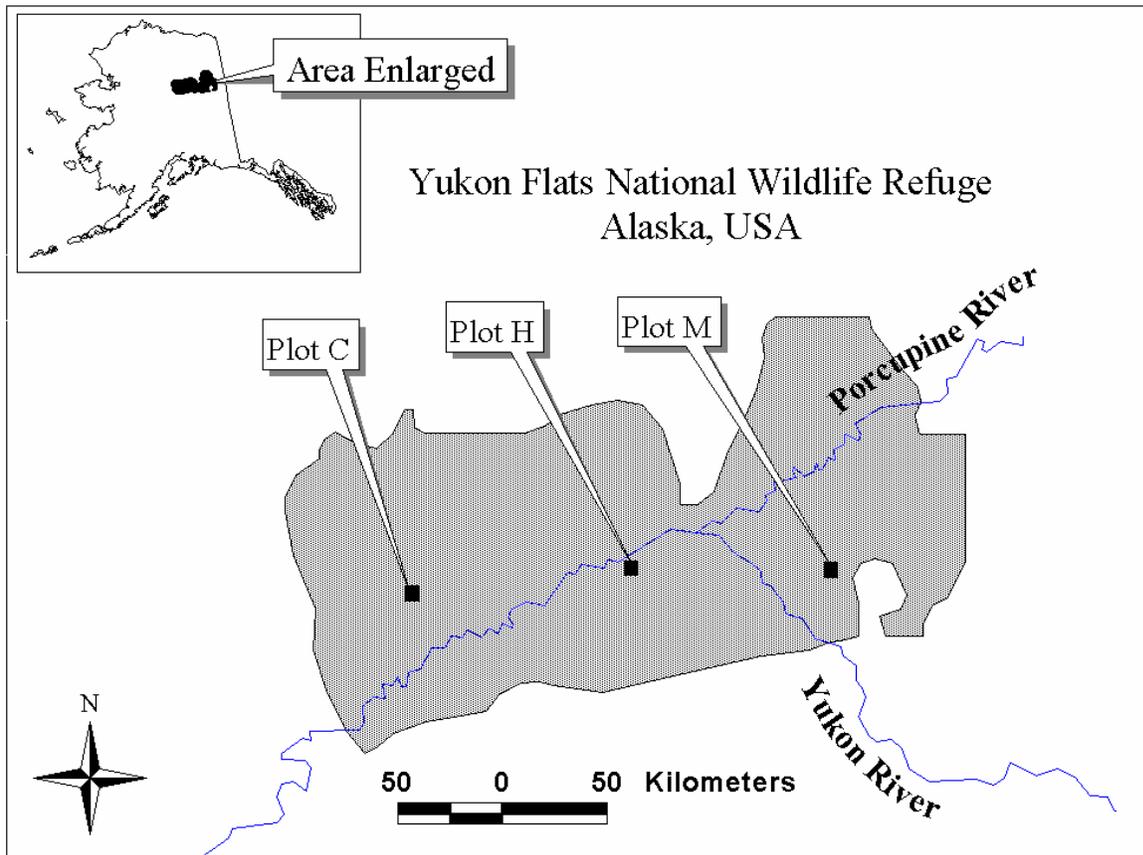


Fig. 1: Location of study plots C, H, and M on the Yukon Flats National Wildlife Refuge (NWR), Alaska, USA.

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. The pH was measured on site using a Hach wide-range Color Comparator (Hach Company, Loveland, CO). 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 H₂SO₄ 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- μ m glass-fiber filters, and concentrations were determined fluorometrically after extraction in buffered ethanol. TSS and TVS were sampled by pre-filtering water through a 500- μ m filter (in 2001–2003 but not 1985–1989), and then collecting the remaining suspended solids on 1.5- μ m Whatman filters that had been pre-ashed and pre-weighed. To estimate TSS (mg/L), 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 determine TVS (Hoyer and Jones 1983).

To test for differences between the two decades (1980s vs. 2000s), we used repeated-measures analysis which accounts for the correlation among dates, and multivariate analysis of variance (MANOVA) which analyzes the response of several correlated dependent variables. Data were first paired by year, with data from the earliest year that a wetland was sampled in the 1980s (1985 or 1986) paired with data from 2001. Although data from the 1980s were collected over 5 years, all wetlands in this analysis were sampled in only 2 or 3 of those years; for all 9 wetlands, 1989 data were paired with data from 2003. After matching years between decades, data were then paired by month (June, July, August). With 9 wetlands sampled once each month for 3 months over 3 field seasons, our total possible sample size was 81. Considering missing data, we were able to make 43 comparisons. We did not test

for differences over time in pH, total suspended solids (TSS), or total volatile solids (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. Because we were interested in 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. Wetland area loss was used as the between-subjects factor in the MANOVA. To compensate for low power inherent in MANOVA, and given the exploratory nature of our study, we set $\alpha = 0.10$ for all analyses (Scheiner and Gurevitch 2001).

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 were re-sampled twice each year: in early June to correspond to scaup nest initiation, and in early August to correspond to peak densities of scaup ducklings. 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. From a randomly selected starting point, sampling was conducted at 20-m intervals beginning 10 m toward open water from the edge between emergent vegetation and open water. In August, the dominant submersed macrophytes were identified to genus at each sampling point along each transect (macrophytes were absent or poorly developed in June). 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 2 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 per liter) 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.

For each wetland in 2002–2003 during June and August separately, the dry mass (DM) of a subsample of each taxon was determined by drying at 105°C. These samples were then ashed in a muffle furnace at 500 °C for 8 h to determine ash-free dry mass (AFDM). Biomass was calculated for each taxon as $\text{AFDM} \times \text{numerical density}$ for sweep-net samples (yielding mg per liter). We did not have AFDM information for samples collected in the 1980s, so we used the wetland- and season-specific AFDM estimates from 2002–2003 to convert these data from density (number/L) to biomass (mg/L). The mean AFDM/individual (± 1 SE) for each taxon averaged over all 9 wetlands was 0.08 ± 0.03 mg for cladocerans, 0.06 ± 0.01 mg for copepods, 0.94 ± 0.22 mg for ostracods, 2.49 ± 0.23 mg for *Gammarus* spp., 0.84 ± 0.06 mg for *Hyaella azteca*, 1.39 ± 0.13 mg for physid snails, 3.21 ± 1.62 mg for lymnaeid snails, 0.94 ± 0.29 mg for planorbid snails, 1.71 ± 0.22 mg for coenagrionid (damselfly) larvae, 0.52 ± 0.05 mg for chaoborid (phantom midge) larvae, and 0.28 ± 0.11 mg for chironomid larvae. Note that we used values determined for each wetland and sampling period (June and August) separately when calculating AFDM for analyses.

Changes in macroinvertebrate biomass between decades were evaluated with paired t-tests on log-transformed means for each wetland. Although 9 wetlands were sampled, 1 wetland was sampled only in June, and a second only in August, yielding 8 wetland comparisons between the 1980s and 2000s. Biomasses of the following invertebrate taxa were compared by wetland: Cladocera, Copepoda, Ostracoda, Amphipoda, Gastropoda, larval Coenagrionidae, larval Chaoboridae, and larval Chironomidae. These taxa were chosen because (1) they accounted for an average 92% of total biomass

in all wetlands sampled in 2002–2003, and (2) several of these taxa (amphipods, gastropods, and chironomid larvae) are considered the most important foods for both breeding adult scaup and their ducklings (Austin et al. 1998). Given high variability and the exploratory nature of our study, we set $\alpha = 0.10$ for all analyses, and a Dunn-Sidak correction (Sokal and Rohlf 1995) was used to adjust the α level to correct for multiple comparisons.

Macroinvertebrate biomass vs. water chemistry

To examine relations between macroinvertebrate biomass and water chemistry during the 2000s, we used invertebrate sampling protocols developed by Murkin and Kadlec (1986). The 9 wetlands used for long-term studies, and 4 additional wetlands adjacent to Plot M, were sampled. Eight of the wetlands were sampled in June of both 2002 and 2003, 6 were sampled in August of both years, and 5 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 the protocols of Murkin and Kadlec (1986). A net (0.5-mm mesh, rectangular frame 20 × 45 cm) was modified by bending the handle 45° upwards from the horizontal. With the mesh bag folded closed to prevent catching invertebrates, the net was lowered until the net frame lay flat on the bottom. With the bag still closed the net was moved along the bottom 0.75 to 1.0 m from the area disturbed, and then quickly raised through the water column to the surface with the net's mouth open upward. During June sampling there were no submersed macrophytes, and during August the occurrence of macrophytes varied among samples. Sweep-net data were converted to volumetric densities (number per liter) based on the net frame dimensions and water depth at the sampling site. For benthic invertebrates (collected only in 2003), a core sample (5 cm wide, 5 cm long) was taken at each of the 10 sites during each of the two sampling periods (June and August), and washed through a 0.5-mm sieve. Invertebrates were preserved in formalin for later analysis. In about 40% of sweep-net samples, cladoceran and copepod numbers were >500, so we subsampled these groups by quartering the sample after other taxa had been removed and counted.

For each wetland during June and August separately, the dry mass (DM) of a subsample of each taxon was determined by drying at 105°C. These samples were then ashed in a muffle furnace at 500 °C for 8 h to determine ash-free dry mass (AFDM). For analyzing relations between invertebrate biomass and water chemistry, biomass was calculated for each taxon as AFDM × numerical density for both sweep-net samples (yielding grams per liter) and core samples (yielding grams per cm³). Because adult scaup can forage in both the water column and sediments, we compared biomass between sweep-net and core samples by converting data from both sample types to g AFDM/m². 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 9 wetlands used for long-term comparisons, monthly samples of water chemistry were also collected from four wetlands off 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 were highly autocorrelated, 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 comprising 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.

Scaup duckling density vs. macroinvertebrate biomass

To assess scaup duckling density, we conducted brood surveys on all wetlands that were sampled for invertebrates in 2003. Twelve wetlands were included: the 8 wetlands used for long-term studies plus the 4 additional wetlands off Plot M. Brood surveys were conducted during the first week of August, when previous studies indicated high densities of scaup broods. Number of adults, number of ducklings, and duckling age (7 age classes: Ia–III, Gollop and Marshall 1954) were recorded during surveys with spotting scopes and binoculars from shorelines and from kayaks. Relations between scaup duckling density and the biomasses of different invertebrate taxa were examined with linear regression. We ran 5 linear regressions with duckling density (ducklings/ha) as the response variable. Predictor variables were: wetland area, amphipod biomass, gastropod biomass, chironomid biomass, and total wetland macroinvertebrate biomass. Biomasses of amphipods, gastropods, and chironomid larvae were included in analyses because previous studies identified these taxa as important prey for both adult scaup and their ducklings (review in Austin et al. 1998). The June and August biomasses from both sweep-net and core samples for each invertebrate taxa were combined for analysis. Because there were no existing data on the particular invertebrate taxa eaten by scaup on the Yukon Flats, we also included total wetland invertebrate biomass in the regressions. Duckling densities and all invertebrate biomass data were $\log_{10}(x + 1)$ transformed before analysis.

Results

Changes in wetland area: 1950s to 2000s

The two wetlands studied on Plot C (Fig. 1) did not lose surface water area between any of the time periods; in fact, wetland C722 had a net gain in area of about 33% between 1952 and 1978 (Table 1). Wetland area loss was high for the two wetlands on Plot H, and was consistent over time with losses of 20 to 27% between both time periods for cumulative losses 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. Most (91%) wetland loss on Plot M, and 93% of loss for all wetlands combined, occurred between 1978 and

Table 1: Area (ha) of 9 wetlands located on 3 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 (open surface water excluding emergent vegetation) was calculated with a GIS from aerial photographs taken in June 1952, high-resolution color-infrared photographs taken in June 1978, and the panchromatic band of a Landsat Enhanced Thematic Mapper+ satellite image taken on 24 June 2000. Percent change = $[(\text{final} - \text{initial})/\text{initial}] \times 100$.

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

2000. Mean area loss for all 9 wetlands between 1952 and 2000 was 19%, very close to the 18% area loss estimated by Riordan (2004) based on 1370 wetlands on the Yukon Flats over the same period.

Changes in water chemistry: 1980s to 2000s

Over the 9 wetlands studied, TN increased by 141% between the 1980s and 2000s, while TP declined by 17% and Chl *a* declined by 52% (percent change = $[(\text{final} - \text{initial})/\text{initial}] \times 100$). All metal cations studied except K increased by 33 to 34%, while 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, while 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, decreasing in wetlands with low area loss while increasing 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. By this experiment-wise α level, the interaction was significant for both Mg (Wilks' Lambda, $F_{(1,41)} = 8.97$, $p < 0.01$) and alkalinity (Wilks' Lambda, $F_{(1,41)} = 11.03$, $p < 0.01$).

Changes in macroinvertebrate biomass: 1980s to 2000s

In horizontal sweep-net samples collected near the water surface (protocol of Heglund 1992), only copepod biomass in June (mg/L) changed significantly between decades, increasing 31-fold (from 0.014 to 0.427 mg/L) between the 1980s and 2000s (paired *t*-test, $p < 0.02$, Fig. 2). Small sample size (9 wetlands) and the typically high variability in aquatic invertebrate populations contributed to lack of statistical significance between decades. For example, there were 5700 to over 7200-fold differences in cladoceran biomass between wetlands (from 0.0003 to 2.1807 mg/L in the 1980s, and from 0.0005 to 2.8696 mg/L in 2002–2003). Consequently, we inspected the data for trends in invertebrate taxa that 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 important as

Table 2: Means (± 1 SE) of water chemistry variables in 1985–1989 vs. 2001–2003 for 9 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). TN = total nitrogen, TP = total phosphorus, and Chl *a* = chlorophyll *a*. Percent difference = $[(\text{final} - \text{initial})/\text{initial}] \times 100$.

Measure	1980s	2000s	% difference	p
TN (mg/L)	1.93 \pm 0.17	4.65 \pm 0.32	+141	<0.01
TP (mg/L)	0.45 \pm 0.08	0.37 \pm 0.07	-17	0.04
Na (mg/L)	63.71 \pm 9.58	85.54 \pm 9.95	+34	<0.01
Mg (mg/L)	48.28 \pm 6.25	64.59 \pm 6.44	+34	<0.01
Ca (mg/L)	27.80 \pm 1.89	36.93 \pm 2.86	+33	<0.01
K (mg/L)	14.91 \pm 1.76	15.68 \pm 1.88	+5	0.56
Alkalinity (meq/L)	8.92 \pm 1.02	8.63 \pm 0.84	-3	0.33
Chl <i>a</i> (μ g/L)	23.22 \pm 3.63	11.13 \pm 2.62	-52	<0.01

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. 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, and Chl *a* = chlorophyll *a*. Percent difference = [(final – initial)/initial] × 100.

Measure	% difference		p
	<20% area loss	>20% area loss	
TN (mg/L)	+118	+163	0.38
TP (mg/L)	-28	+5	0.02
Na (mg/L)	+39	+32	0.53
Mg (mg/L)	+11	+56	<0.01
Ca (mg/L)	+14	+53	0.09
K (mg/L)	-8	+19	0.05
Alkalinity (meq/L)	-23	+14	<0.01
Chl <i>a</i> (µg/L)	-44	-62	0.84

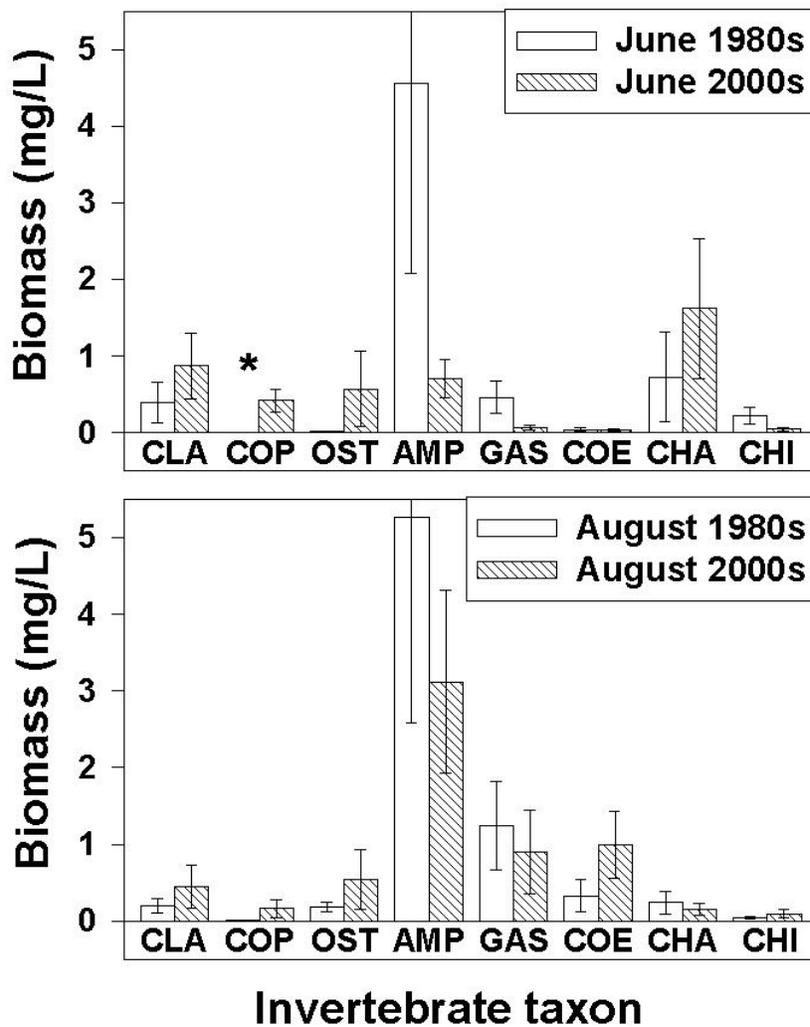


Fig. 2: Mean biomass (AFDM, mg/L) of different invertebrate taxa in horizontal sweep-net samples (protocol of Heglund 1992) in 1985–1989 vs. 2002–2003 for 9 wetlands on the Yukon Flats, Alaska. Error bars = ± 1 SE. CLA = cladoceran, COP = copepod, OST = ostracod, AMP = amphipod, GAS = gastropod, COE = 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, $n = 8$, $p = 0.016$).

prey for scaup: amphipods, gastropods, and chironomid larvae (Fig. 2). Because of several thousand-fold changes in the biomass of some invertebrates, we used relative percent difference ($RPD = [(final - initial)/0.5(final + initial)] \times 100$) rather than percent difference to express changes between decades. RPD standardizes values between 0 and 200%, using the mean of the two values being compared as the denominator and thereby avoiding the problem of zero values for initial biomasses. In June and August, respectively, mean biomass of amphipods declined by 146% and 51% (RPD) between decades, and the biomass of gastropods by 150% and 32%; chironomid biomass declined by 129% in June but increased by 77% in August. In contrast, June and August biomasses of the 2 major zooplankton taxa increased (RPD) by 75% and 79% (cladocerans) and 193% and 192% (copepods), while the biomass of chaoborid larvae that prey on zooplankton increased by 76% in June. These values indicate an important decadal shift in relative biomass from scrapers/deposit-feeders toward zooplankton and their predators.

To examine relations between June zooplankton biomass, Chl *a*, and wetland area loss, we graphed the RPD for these measures between decades (Fig. 3). Chl *a* increased in the only wetland where zooplankton biomass declined (C722), which was also the only wetland that gained surface water area between 1952 and 2000. Chl *a* was unchanged in M620, which had higher nutrient levels and far higher cladoceran levels than the other wetlands in both decades. In general, increases in biomass of zooplankton grazers were greater (mean RPD = 163%) in wetlands that had lost >20% surface water area between 1978 and 2000 than in wetlands that did not dry (mean RPD = 76%). The relative percent decline in June Chl *a* concentrations was also greater (mean RPD = 103%) in wetlands with >20% area loss than in wetlands with <20% area loss (mean RPD = 33%). Thus, greater increases in zooplankton were associated with greater decreases in phytoplankton.

Macroinvertebrate biomass: 2002–2003

During 2002–2003, we collected 377 sweep-net samples (vertical sweep from the sediments to the water surface, protocol of Murkin and Kadlec 1986) and 248 benthic cores from 13 wetlands. Considering only sweep-net samples for both years combined, the largest percent biomass (AFDM) in

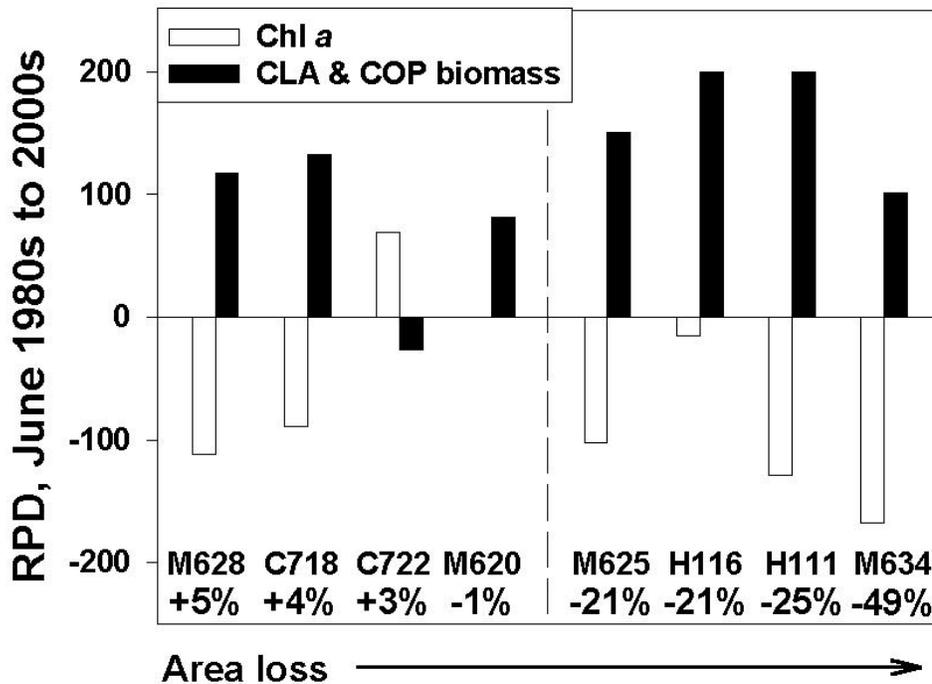


Fig. 3: Relative percent difference, $RPD = [(final - initial)/0.5(final + initial)] \times 100$, in June Chlorophyll *a* (Chl *a*) concentrations and the biomass (AFDM) of cladocerans (CLA) and copepods (COP) combined in 1985–1989 vs. 2002–2003 in 8 wetlands on the Yukon Flats, Alaska (data from horizontal sweep-net samples, protocol of Heglund 1992). Wetlands are presented in order of increasing area loss from left to right, and wetland designations along the x-axis are annotated by % loss of surface water area from 1978 to 2000 (Table 1). Wetlands to the right of the vertical dashed line lost >20% of surface area.

June was made up of cladocerans (43%) and amphipods (20%) (Fig. 4). In August, biomass was dominated by amphipods (24%), gastropods (20%), coenagrionid larvae (14%), cladocerans (13%), and chironomid larvae (12%). Cladocerans were mostly large-bodied *Daphnia* spp. (90% of total cladoceran biomass in 2002–2003), followed by *Ceriodaphnia* spp. (9%), and Chydoridae (1%). *Hyalella azteca* made up 63%, and *Gammarus* spp. 37%, of amphipod biomass. Although individual *Gammarus* spp. were generally larger than *H. azteca* (3 to 4 times higher AFDM), *H. azteca* outnumbered *Gammarus* spp. almost 3 to 1. In vertical sweep-net samples, there was a trend for the biomass of all taxa to increase from June to August, except for cladocerans and copepods which decreased (Fig. 5).

In core samples, chironomid larvae, amphipods, gastropods, Hirudinidae (leeches), and coenagrionid larvae accounted for about 90% of total biomass (Fig. 6). In June and August combined, chironomid larvae averaged 38% of benthic biomass (AFDM, range 7 to 89% among wetlands), amphipods 26% (range 0 to 65%), and gastropods 15% (range 0 to 54%). Because adult sculpin can forage in both the water column and sediments, we compared the biomass between sweep-net and core samples (5 cm deep) by converting data from both sample types to grams per m² of wetland (Fig. 7). Biomasses of cladocerans, copepods, ostracods, and chaoborid larvae were greater in sweep-net samples than in cores, while the biomasses of amphipods, gastropods, coenagrionid larvae, and chironomid larvae were greater in cores than in sweep-net samples (Fig. 7). Chironomid biomass was on average 10 times greater, gastropod biomass 6 times greater, and amphipod biomass 2 times greater in cores than in the water column above the same area of bottom.

Macroinvertebrate biomass vs. water chemistry: 2002–2003

Nutrient concentrations in the 13 wetlands sampled during 2001–2003 on the Yukon Flats were highly variable, but indicated that most wetlands were eutrophic to hypereutrophic. Based on the criteria of Nürnberg (1996), all wetlands were classified as hypereutrophic in terms of TN (Table 4). In terms of TP, 11 wetlands (85%) were eutrophic or hypereutrophic. 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

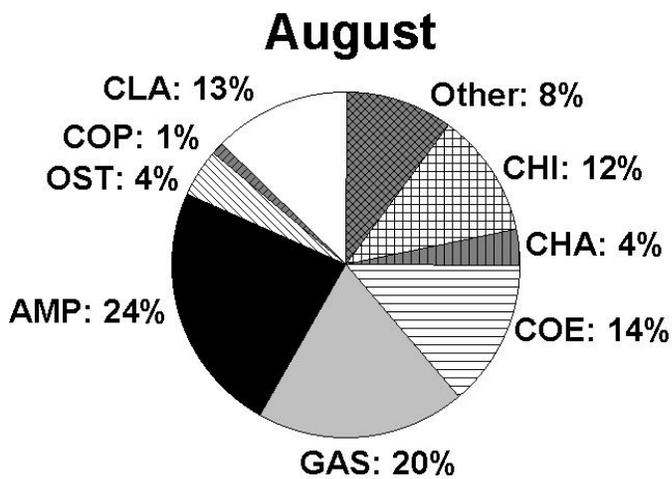
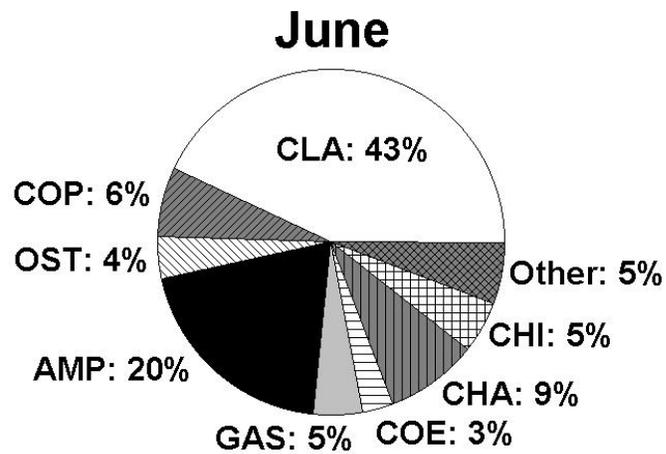


Fig. 4: Percent total biomass (AFDM) of major invertebrate taxa in vertical sweep-net samples (protocol of Murkin and Kadlec 1986) during June and August 2002–2003 in 13 wetlands on the Yukon Flats, Alaska. CLA = cladoceran, COP = copepod, OST = ostracod, AMP = amphipod, GAS = gastropod, COE = coenagrionid (damselfly) larvae, CHA = chaoborid (phantom midge) larvae, CHI = chironomid larvae.

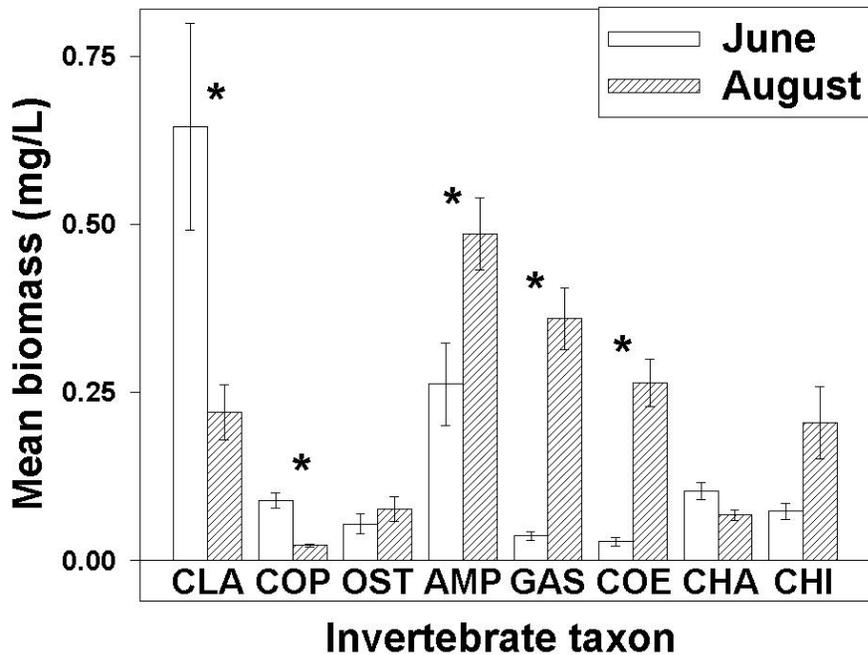


Fig. 5: Mean biomass (AFDM) of major invertebrate taxa in vertical sweep-net samples (protocol of Murkin and Kadlec 1986) in June and August 2002–2003 in 13 wetlands on the Yukon Flats, Alaska. CLA = cladoceran, COP = copepod, AMP = amphipod, GAS = gastropod, COE = coenagrionid (damselfly) larvae, CHA = chaoborid (phantom midge) larvae, CHI = chironomid larvae. Error bars = ± 1 SE. Asterisks indicate significant differences between months (paired t-tests on samples at the same stations, $n = 170$, all $p < 0.013$).

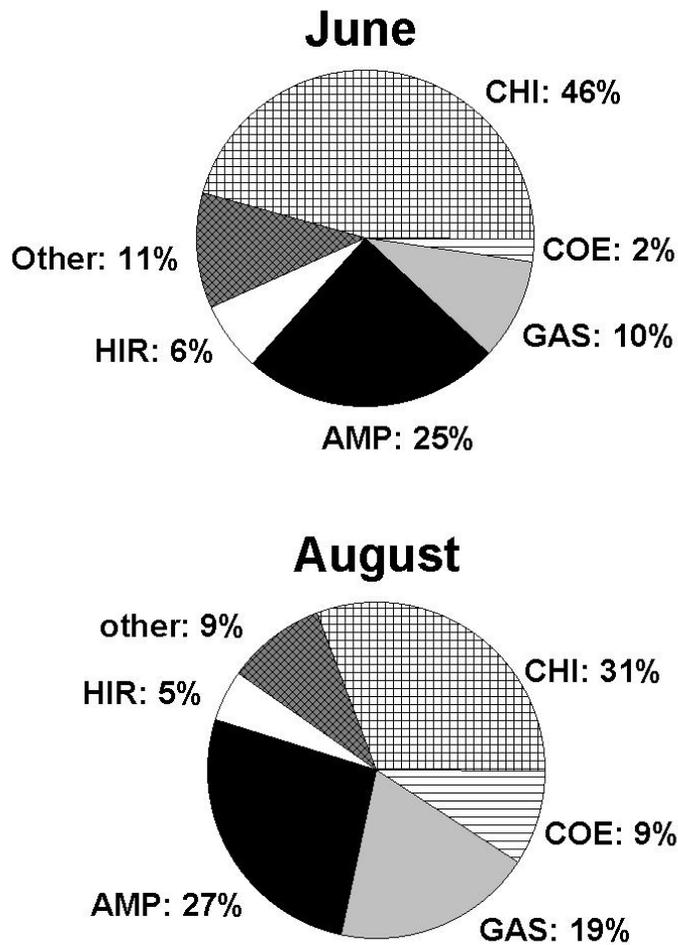


Fig. 6: Percent total biomass (AFDM) of major invertebrate taxa in core samples (5 cm deep) during June and August 2003 in 13 wetlands on the Yukon Flats, Alaska. HIR = hirudinidae (leeches), AMP = amphipod, GAS = gastropod, COE = coenagrionid (damselfly) larvae, CHI = chironomid larvae.

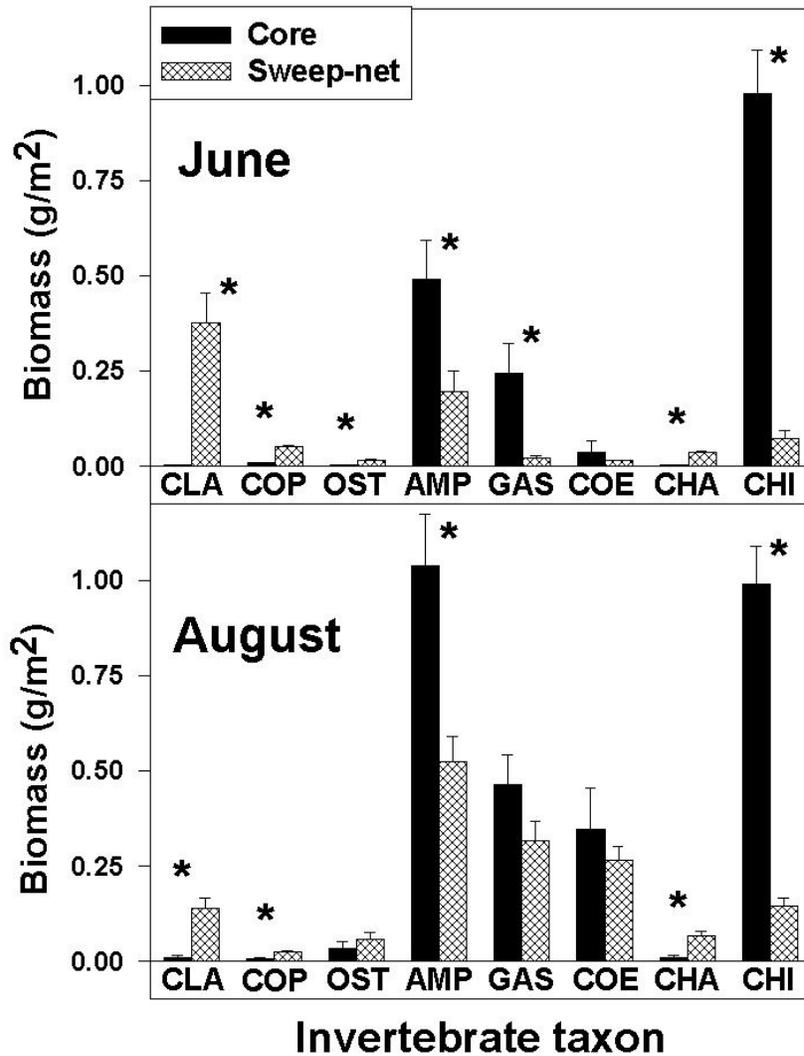


Fig. 7: Invertebrate biomass (g AFDM/m²) in cores (5 cm deep) vs. vertical sweep-net samples (protocol of Murkin and Kadlec 1986) during June and August 2003 in 13 wetlands on the Yukon Flats, Alaska. CLA = cladoceran, COP = copepod, AMP = amphipod, GAS = gastropod, COE = coenagrionid (damselfly) larvae, CHA = chaoborid (phantom midge) larvae, CHI = chironomid larvae. Error bars = 1 SE. Asterisks indicate significant differences between cores and sweep-net samples (paired t-tests on samples at the same stations, n = 129 in June, n = 107 in August, all p < 0.007).

(Prairie et al. 1989); consequently, only 5 wetlands (39%) were classified as eutrophic to hypereutrophic based on Chl *a* (Table 4). The only significant seasonal trend was in TP, which increased between June (mean \pm 1 SE = 0.399 ± 0.127 mg/L) and August (0.550 ± 0.165 mg/L) (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 (cf., Fig. 3).

To examine relations between invertebrate biomass and water chemistry, we used principal component analysis (PCA) on 9 limnological variables (Table 5). The first axis (PC1) explained 48% of the total variation in water 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 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 and Jones 2003). The PCA factor scores (Table 5) were used as dependent variables in multiple regressions to relate invertebrate biomass to water chemistry (Table 6). In vertical sweep-net samples (protocol of Murkin and 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 (Table 6). There were no significant relationships between water chemistry and invertebrates in core samples.

Scaup duckling density vs. macroinvertebrate biomass: 2003

Lesser scaup broods were surveyed on 13 wetlands sampled for invertebrates in 2003. One wetland sampled for invertebrates in June could not be re-sampled in August due to low water levels, and data from this wetland were excluded because June and August biomasses were combined for regressions. Lesser scaup broods were recorded on all but 4 of the wetlands; 3 of the 4 wetlands with no ducklings

Table 4: Percentages of 13 wetlands in different trophic states based on criteria of total nitrogen (TN), total phosphorus (TP), and chlorophyll *a* (Chl *a*) of Nürnberg (1996). Values are means for June, July, and August 2002 and 2003 on the Yukon Flats National Wildlife Refuge, Alaska.

Trophic state	Total nitrogen		Total phosphorus		Chlorophyll <i>a</i>	
	Criterion (mg/L)	%	Criterion (mg/L)	%	Criterion (µg/L)	%
Oligotrophic	<350	0	<10	0	<3.5	15
Mesotrophic	350-650	0	10–30	15	3.5–9	46
Eutrophic	651–1200	0	31–100	31	9.1–25	24
Hypereutrophic	>1200	100	>100	54	>25	15

Table 5: Loadings of water chemistry variables on the first 3 principal components (PC1, PC2, PC3) based on mean values from 13 wetlands on the Yukon Flats, Alaska in summer 2002–2003. Loadings ≥ 0.7 are in bold type. TN = total nitrogen, TP = total phosphorus, Chl *a* = chlorophyll *a*, and TVS = total volatile solids.

	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 <i>a</i>	0.538	0.806	-0.138
TVS	0.634	0.739	-0.151

Table 6: Results from multiple regressions of invertebrate biomass ($\log_{10}(\text{AFDM} + 1)$) on factor scores from principle component analysis (Table 5) of limnological measures from 13 wetlands on the Yukon Flats, Alaska, in June and August 2002–2003. Coefficients of multiple determination (R^2) and p-values for regressions including all principle components, and partial regression coefficients (r^2) and p-values for individual principle 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.

Response variable	R^2		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

were the smallest wetlands included in the study and were under 3.1 ha in area (range 1.7 to 3.1 ha). Mean density (± 1 SE) of lesser scaup broods (including wetlands with no ducklings) was 1.1 ± 0.4 ducklings/ha. We ran 5 simple linear regressions with duckling density on each wetland as the response variable and wetland area, total amphipod biomass, total gastropod biomass, total chironomid larvae biomass, and total wetland macroinvertebrate biomass as the response variables. Duckling density was not significantly related to wetland area or the biomass of particular macroinvertebrate taxa (wetland area: $r^2 < 0.01$, $p = 0.92$; amphipod biomass: $r^2 = 0.19$, $p = 0.15$; gastropod biomass: $r^2 = 0.02$, $p = 0.687$; and chironomid biomass $r^2 < 0.01$, $p = 0.80$). However, duckling density increased with increasing biomass of all macroinvertebrates combined ($r^2 = 0.26$, $p = 0.09$).

Discussion

Between 1950 and 2002, wetlands in the Yukon Flats lost about 18% of surface water area (Riordan 2004). Our study shows that wetlands remaining in the early 2000s had dried appreciably since the 1980s, and had experienced important changes in chemistry and foodweb structure. In wetlands that were often N-limited (see next section), increased levels of cations and TN should have favored increased algal production, and the large increase in zooplankton grazers in June may reflect such a change. In such cases, increased production of phytoplankton could be obscured by increased grazing pressure, which would lower standing stocks of phytoplankton and of TP which includes P in phytoplankton. Concurrent long-term declines in deposit-feeders such as amphipods, snails, and chironomid larvae suggest redirection of carbon flow from benthic and epiphytic deposit-feeders to zooplankton grazers. Dispersion of lesser scaup ducklings among wetlands was not clearly related to the abundance of deposit-feeding invertebrates they depend on for food. However, trends in their invertebrate prey might still have had a role in long-term declines of scaup.

Changes in water chemistry: 1980s to 2000s

From the 1980s to 2000s, TN, Na, Mg, and Ca increased, while TP declined and Chl *a* declined more than did P. These changes were greater in wetlands that lost >20% of surface area. Increased nutrients

are consistent with predictions of climate warming effects on closed-basin lakes, which are especially vulnerable in arid 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). Schindler (1997) attributed declines in P to longer water residence times, which increased the duration of biological removal processes. In the closed-basin wetlands of the Yukon Flats, declines in P are probably not explained by longer water residence times.

Although P limitation is considered prevalent in Alaska and elsewhere at high latitudes (Pienitz et al. 1997a, 1997b, Gregory-Eaves et al. 2000), data from 129 wetlands on the Yukon Flats during the 1980s were equivocal (Heglund and Jones 2003). Ratios of Chl *a* to TP were low relative to other regions, with Chl *a* yields per unit of TP being a third to half the levels commonly found in lakes (Prairie et al. 1989). The response of Chl *a* to nutrient-addition assays was also generally weak (Heglund and Jones 2003). In 74 nutrient stimulation bioassays where initial TP:TN averaged 36, Chl *a* increased in 11% of assays with P addition, and in 38% of assays with N addition, indicating that N limitation was more prevalent. Heglund and Jones (2003) concluded that top-down control by large-bodied zooplankton grazers, which dominated these wetlands in the absence of fish predation, were an important factor in the low yields of Chl *a* to nutrients in the 1980s.

Given the inconsistent response of Chl *a* to nutrients, the most likely 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 much increased zooplankton populations in June during the early 2000s (Fig. 2) probably removed much of both TP and Chl *a* from the water column (Sterner 1990, Sarnelle 1992, Strauss et al. 1994, Hann and Goldsborough 1997). The relative percent difference (RPD) in Chl *a* concentrations between decades was more negative in wetlands where cladoceran biomass increased

between the 1980s and 2000s (Fig. 3). We suspect that in the 2000s, although zooplankton probably increased more in the spring in response to greater primary production, they subsequently grazed down the standing stock (Strauss et al. 1004, Hann and Goldborough 1997).

Changes in macroinvertebrate biomass: 1980s to 2000s

At intermediate levels of nutrient availability in shallow lakes, increased nutrients can result in divergent states of primary production and foodweb structure (Scheffer et al. 1993). Increased nutrient levels can lead to (1) persistence of submersed macrophytes, but with increased periphyton for epiphytic and benthic scrapers and deposit-feeders, or (2) decline of submersed macrophytes, with increased phytoplankton or metaphyton and an increase in water-column grazers (Daldorph and Thomas 1991, Thomas and Daldorph 1991, 1994). Similar alternative states can result from drying of wetlands and associated changes in permanence and water chemistry (Lovvorn et al. 1999, Hart and Lovvorn 2000, 2005).

In shallow, nutrient-rich wetlands of the northwest boreal forest, there is evidence for alternative stable states (Bayley and Prather 2003). Submersed aquatic vegetation (SAV) is abundant at intermediate to high nutrient levels. However, under hypereutrophic conditions (generally >0.2 mg/L TP), dense phytoplankton reduces penetration of light to submersed macrophytes. Loss of SAV can reduce epiphytic scrapers and deposit-feeders (snails, amphipods, and some chironomids), which typically achieve far higher biomass than either benthos or zooplankton when macrophytes are present (Wollheim and Lovvorn 1995, and references therein).

In the western boreal forest of Canada, Bayley and Prather (2003) classified wetlands very similar to those in our study based on levels of Chl *a* and P. By their scheme, 5 of 6 of our wetlands classified as having intermediate to high phytoplankton levels in the 1980s shifted to lower phytoplankton status in 2001–2003. TP declined in 7 of 9 of our wetlands between decades; however, in the 2000s, TP in all these wetlands (range 0.022 to 1.193 mg/L) was still above the suggested cutoff of 0.020 mg/L for transition from SAV to phytoplankton dominance. Although Chl *a* levels suggest that these wetlands

were starting to shift toward SAV dominance, they continued to be very nutrient-rich, with high but declining TP and increasing TN. Lowered standing stock of phytoplankton as indexed by Chl *a* does not preclude high or even increased cell-specific rates of phytoplankton production. In fact, the increased zooplankton populations might have resulted largely from increased phytoplankton production, which was subsequently grazed to a lower standing stock.

In the 1980s, ratios of Chl *a* to N and P on the Yukon Flats were a third to half those expected based on typical Chl *a*:nutrient ratios in lakes (Prairie et al. 1989), possibly because of zooplankton grazing (Heglund and Jones 1993). If N limits wetland productivity on the Yukon Flats (see preceding section), then the 141% increase in TN between decades may be shifting primary production toward phytoplankton. This change would favor zooplankton grazers over epiphytic scrapers and deposit-feeders. Even in shallow waters where phytoplankton is a small component of the ecosystem's organic mass balance, organic matter derived mainly from phytoplankton production can be the dominant food source for zooplankton (Sobczak et al. 2002). In macrophyte-dominated wetlands, most carbon available to macroinvertebrates comes from algae and not macrophyte tissue, and the diets of both amphipods and chironomids are often dominated by algal-derived material (Hart and Lovvorn 2000, 2005). In Lake Michigan, 61% of all carbon deposited during spring diatom blooms was assimilated by abundant benthic amphipods (*Diporeia* sp.) (Fitzgerald and Gardner 1993). However, the impact of increased grazing by zooplankton on the carbon supply to benthic invertebrates, an effect well recognized in marine systems (review in Lovvorn et al. 2005), has received little study in wetlands. In lakes and estuaries, removal of phytoplankton from the water column by abundant filter-feeding bivalves appears to have caused declines in zooplankton as well as some benthic invertebrates (Ludyanskiy et al. 1993, Kimmerer and Orsi 1996), suggesting that changes in flows of algal production can greatly affect foodweb structure in shallow waters.

Beyond foodweb effects, declines in amphipods may be directly related to higher water temperatures resulting from both higher air temperatures and shallower water depths. In *Hyaella azteca*,

reproduction begins when water temperature reaches 20°C (de March 1977, Panov and McQueen 1998). However, net growth efficiency for larger individuals is maximal at lower temperatures (Panov and McQueen 1998). At water temperatures >20°C, metabolic rates of the largest individuals exceed energy intake, causing loss of larger individuals (Lozano and Kitchell 1978, Hogg and Williams 1996, Panov and McQueen 1998). Because fecundity increases with increasing body size in amphipods, the presence of large females may be important to producing a strong first generation in early summer, or a strong cohort of young in late summer that grow through winter to breed the following season. Numbers of larger individuals with higher fecundity may be reduced by slower growth rates at higher temperatures, especially during the summer.

Macroinvertebrate biomass vs. water chemistry

Water chemistry affects the abundance and diversity of macrophytes and algae, thus controlling the physical structure and food resources available to invertebrates (Friday 1987, Rasmussen and Kalff 1987, Rasmussen 1988, Jeffries 1991, Brodersen et al 1998, Hart and Lovvorn 2003, 2005). Species richness often decreases at extreme levels of nutrients and other solutes (Hammer et al. 1990, Williams et al. 1990). However, at intermediate solute concentrations, habitat structure and variability may have greater effects than water chemistry on the structure of littoral macroinvertebrate assemblages (Lovvorn et al. 1999, Heino 2000). In a study of 45 lakes in arctic Alaskan tundra, variations in zooplankton species composition were related more to latitude, lake morphometry, and biotic interactions than to water chemistry (Kling et al. 1992).

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, while amphipods were negatively related to Ca concentrations and positively related to Chl *a* and TVS (Table

6). This relation for amphipods might help explain their decline between decades, as Chl *a* decreased over this period.

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, we may have sampled early when cladoceran biomass was rising in response to algal peaks, indicating a positive relationship. 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 was done in all wetlands 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.

Scaup duckling density vs. macroinvertebrate biomass

Diets of nesting scaup are variable, but are usually dominated by gastropods, chironomid larvae, and especially amphipods (review in Austin et al. 1998). Habitat selection by adult scaup depends on the density of amphipod prey (Afton and Hier 1991), and wetland use by scaup broods may also be linked to amphipod availability (Lindeman and Clark 1999, Fast et al. 2004). Nevertheless, we found no relation between scaup duckling density and amphipods, or the biomass of any other macroinvertebrate taxon, in sweep-net and core samples from the Yukon Flats. Our inability to detect such relations may be related to our small sample size of 12 wetlands. Previous studies linking scaup brood use to amphipod availability involved over 100 wetlands each (Lindeman and Clark 1999, Fast et al. 2004). In our study, more of the variation in duckling density was explained by total amphipod biomass ($r^2 = 0.19$, $p = 0.15$) than by the biomass of gastropods ($r^2 = 0.02$, $p = 0.68$) or chironomid larvae ($r^2 < 0.01$, $p = 0.80$). Duckling density increased with increasing biomass of all macroinvertebrates combined ($r^2 = 0.26$, $p =$

0.09), suggesting that scaup ducklings may have consumed a wider range of taxa (see Bartonek and Murdy 1970, Sugden 1973, Afton and Hier 1991).

It is also possible that food is not the major factor affecting wetland selection by scaup broods. In Alberta prairies, lesser scaup ducklings shifted over time from smaller ponds (<0.8 ha) to larger and deeper ponds (>2 ha) (Sugden 1973). However, this shift appeared to result not from food availability, but rather the need for security from predators. Food in small ponds appeared adequate, and older scaup regularly used larger ponds (2 to 6 ha) where amphipods were lacking and the birds ate mainly benthic insect larvae (Sugden 1973). On the Yukon Flats, avoiding predation may also be a dominant force in wetland selection by scaup broods. Low scaup nest success due to predation on hens, and low duckling survival due to predation on entire broods after hatch, suggest that predators are quite important in this area (Chapter 1). Another factor that might confound effects of invertebrate abundance on wetland use by scaup broods is preference for large wetlands that will freeze later in the fall. Lesser scaup nest late in the season, increasing the risk that flightless young and molting adults will become stranded by early freeze-up.

Although some scaup nested on small wetlands where nest success was higher than on large wetlands, all scaup moved to large wetlands for brood-rearing (Chapter 1). Whether movement from small to large wetlands resulted from food availability, vulnerability to predators, or avoidance of early freeze-up is unclear. However, small (<10 ha) and large (>10 ha) wetlands did not differ in the mean biomass of invertebrate taxa important to scaup (amphipods, gastropods, and chironomid larvae). Note that if avoidance of predators or early freeze-up overrides food availability in the selection of wetlands by broods, food availability might still affect brood production and survival.

For adult scaup and older ducklings which can feed in both the water column and sediments, availability of preferred foods may be greater in the sediments (Fig. 7); however, only sweep-net samples were available for comparisons between decades. Energy costs of diving by scaup increase with dive depth (Kaselloo and Lovvorn 2005), and intake rates of prey in the water column vs. sediments have not

been measured (cf., Giles 1990, Richman and Lovvorn 2004). For ducklings, these factors probably change over the period of growth, with very buoyant young ducklings restricted to feeding only in shallow water or in the upper water column (Bartonek and Murdy 1970). Studies of future long-term changes in invertebrate prey for scaup should consider benthic as well as water-column prey.

Conclusions

Our data show that in addition to major loss of surface area, wetlands in the Yukon Flats are experiencing long-term changes in water chemistry and foodweb structure. Based on trends in water surface area over a much larger region (Riordan 2004), 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 dominance by phytoplankton. This change may explain the greatly increased biomass of zooplankton during the spring bloom in June, which graze down standing stocks of phytoplankton and perhaps divert carbon flow away from scrapers and deposit-feeders which have concurrently declined. The latter taxa, especially amphipods, are thought to be the major foods of both adult and young lesser scaup. Given the confounding effects of predation on wetland selection by scaup broods, more study is needed to determine the role of climate-related changes in foodweb structure in the long-term decline of this aquatic predator.

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