Project Period	04/01/2009 - 12/31/2011
Award Amount	$108,952.91
Matching Contributions	$67,981.00
Project Location Description (from Proposal)	Assess climate-related changes in food resources for Steller's eider/shorebirds/passerines at Barrow 1970s to 2009-10; Compare abundance & seasonality of tundra insect prey near Kaktovik & Atqasuk, AK
Project Summary (from Proposal)	Compare current insect prey resources to existing data and engage citizens in monitoring ecological resources susceptible to climate change. Project will inform resource managers and avian researchers concerned with tundra-nesting birds in arctic Alaska.
Summary of Accomplishments	We've assessed potential impacts of climate change on the food base for avian consumers on Alaska's Arctic Coastal Plain, where abundant shallow ponds produce much of the prey needed by Arctic-breeding waterfowl including threatened Steller's and Spectacled Eiders, plus many other species of tundra-nesting shorebirds and passerines. We've collected 3yrs of new data on invertebrate communities in tundra ponds at Barrow, permitting comparison across four decades of both the availability of aquatic prey and the seasonal timing of insect emergence. By sampling at other sites besides Barrow, we've expanded baseline knowledge of this crucial avian food resource on the ACP. We've documented thermal characteristics of both coastal (Barrow) and inland (Atqasuk) tundra ponds, revealing warmer temperatures and a longer growing season in ponds at Barrow relative to four decades ago. The pond fauna at Barrow has changed little over this time, but some species appear to grow faster and the timing of insect emergence in Barrow ponds averages four days earlier than in the 1970s. Adult insects emerge in a short summer pulse that makes years of aquatic production available to a broad spectrum of avian consumers. We've learned much about how emergence timing responds to pond thermal characteristics, findings that will enable development of models to predict how future climatic conditions may be expected to alter the magnitude and timing of this ecologically significant event.
Lessons Learned	Demonstrating the value of understanding all parts of the tundra food web is both a challenge and an opportunity. We've worked hard to communicate, both to the public and to researchers in other disciplines, potential contributions our aquatic studies can make to more evident conservation issues. Cooperation with avian ecologists has helped to keep our research focused on questions of significant concern to broader constituencies. Our plans to engage local students in this study proved too optimistic, but we had success engaging older residents, with some participation in field work and strong attendance at our local outreach activities. While success of such program elements cannot be guaranteed, it is clearly important for researchers in remote communities to be receptive to potential community engagement. Facultative collaborations with other researchers have contributed substantially to project success. Several goals of this project were enhanced by volunteer efforts of students engaged in other research projects at Barrow and at Atqasuk. Although such assistance can't be presumed in a proposal, in this case such generous help has allowed us to collect much more complete data than our budget would otherwise have allowed.

We’re uncovering scientific results at an increasing rate as we continue to work with samples and data collected over the past 3 summers. Many of our ideas about how seasonality of tundra insects responds to climate are being validated by these findings.

Conservation Activities Progress Measures Value at Grant Completion	Engage graduate students in MS thesis reseach Number of students educated/involved 2
Conservation Activities Progress Measures Value at Grant Completion	Involve NDSU undergraduate students in arctic field work Number of students educated/involved 2
Conservation Activities Progress Measures Value at Grant Completion	Involve NDSU undergraduate students in sample analysis Number of students educated/involved 11
Conservation Activities Progress Measures Value at Grant Completion	Involve local residents in field research at Barrow, AK Number of volunteers contacted/involved 3
Conservation Activities Progress Measures Value at Grant Completion	Help with field sample collection by student researchers on related arctic projects Number of volunteers contacted/involved 7
Conservation Activities Progress Measures Value at Grant Completion	Present public outreach talks at Barrow, AK (# of events) Number of people engaged in public education, training, and outreach programs 3
Conservation Activities Progress Measures Value at Grant Completion	Audience at public outreach talks in Barrow, AK (estimated total attendance over 3 dates) Number of people engaged in public education, training, and outreach programs 65
Conservation Activities Progress Measures Value at Grant Completion	Scientific presentations on research project (# talks & posters presented) Number of people engaged in public education, training, and outreach programs 7
Conservation Activities Progress Measures Value at Grant Completion	Publish research findings in refereed scientific journals Other (Research publications) 2

Final Programmatic Report Narrative

Instructions: Save this document on your computer and complete the narrative in the format provided. The final narrative should not exceed ten (10) pages; do not delete the text provided below. Once complete, upload this document into the on-line final programmatic report task as instructed.

1. Summary of Accomplishments

In four to five sentences, provide a brief summary of the project's key accomplishments and outcomes that were observed or measured.

To assess how climate change may alter the availability of the food base for avian consumers, we've documented the current status of invertebrate communities in tundra ponds on Alaska's Arctic Coastal Plain. Both aquatic and terrestrial stages of this fauna are crucial prey resources for most tundra-nesting birds, including threatened species like Steller's and Spectacled Eiders, plus many shorebirds and passerines. Thermal characteristics of both coastal (Barrow) and inland (Atqasuk) tundra ponds were documented, revealing warmer temperatures and a longer growing season at Barrow relative to four decades ago. The pond fauna at Barrow has changed little, but some species appear to grow faster and the timing of insect emergence in Barrow ponds averages four days earlier than in the 1970s. We've learned a great deal about how insect emergence timing responds to pond temperature; these findings will support development of models predicting how the magnitude and timing of this ecologically important event may change under future climatic conditions.

2. Project Activities & Outcomes

Activities

- Describe and quantify (using the approved metrics referenced in your grant agreement) the primary activities conducted during this grant.

Because basic information on invertebrate prey resources for tundra-nesting birds was largely restricted to Barrow, AK and over 30yrs old, we proposed (A) to collect new data from Barrow tundra ponds on (1) seasonal water temperatures, (2) densities, composition, and biomass of insect larvae commonly consumed by shorebirds and waterfowl, and (3) emergence timing of aquatic insects. Each of these ecological variables could then be compared to historical data collected at Barrow in the 1970s. We proposed (B) to broaden the scope of such ecological knowledge by sampling both tundra pond thermal behavior (response 1) and invertebrates (responses 2 & 3) at other sites on the Arctic Coastal Plain, which might differ from the comparatively well-studied tundra ecosystem of the Barrow Peninsula. We also proposed (C) to collaborate with avian researchers studying breeding birds at Barrow and other sites on the Arctic Coastal Plain, whose work would benefit from this information. We planned to (D) engage local residents in this work as much as possible, via public outreach presentations and potential recruitment of student interns from North Slope villages. The initial two-year grant was extended through 2011 to permit a third field season, needed in part due to late funding of the initial award in 2009.

Successful activities completed over the 33mo duration of this project are detailed below:

(A-1, B-1) <u>Thermal data from tundra ponds on the Arctic Coastal Plain</u>: We monitored hourly water temperatures in ten ponds near Barrow and ten ponds near the inland village of Atqasuk during 2009, 2010, and 2011, with Hobo Pro® loggers. Additional temperature data are also available for some ponds from loggers placed during preliminary work in 2007&2008, before NFWF #1549.

(A-2, B-2) <u>Sampling of tundra pond invertebrate communities</u>: In June 2010, we collected 30 core samples in each of five randomly- selected tundra ponds in the Barrow Environmental Observatory and five ponds near the Village of Atqasuk, 100km inland from Barrow. Sampling locations represented both vegetated and open-water strata in each

pond. All cores were preserved and processed to determine abundance, composition, biomass, and size-structure of the invertebrate community serving as a prey resource for benthic-feeding birds such as eiders and other waterfowl. These samples also provide quantification of the pond insect fauna whose emergence phenology we monitored at both locations (below). We also collected less quantitative samples of pond invertebrates at Barrow (2009-11), and in 2009 at another coastal location (Peard Bay – 100km west of Barrow) plus a second inland site on the Arctic Coastal Plain (Olak – 160km SE of Barrow;160km E of Atqasuk). These opportunistic samples help to assess the generality of the coastal vs. inland contrasts revealed by the quantitative sampling of tundra ponds at Barrow & Atqasuk.

(A-3, B-3) Insect emergence phenologies: We monitored seasonal patterns of insect emergence at both Barrow and Atqasuk during 2009, 2010, and 2011. Dip-net samples of leeward flotsam contain larvae, pupae, and adults of pond insects, but also the floating pupal exuviae (shed pupal skins) that indicate recent (past 2-3 days) emergence of individual species. Standardized samples collected every 2-3 days reveal the seasonal progression of insect emergence at the species level. Our samples extended to at least mid-late July each year, and at Barrow we detected the last insect species anticipated to emerge (based on sampling in the 1970s). Some later sampling (mid-late July and August) was possible thanks to the efforts of volunteers working on other projects at Barrow, and especially at Atqasuk.

(C) Collaboration with arctic bird reseachers: The 2009 opportunity to sample pond invertebrates at the Olak site arose when a team from the University of Alaska –Fairbanks asked for help with a study of King Eiders breeding on the Arctic Coastal Plain near Teshekpuk Lake. Butler was able to join the team for two days at the beginning of their final field season, to assess the composition and abundance of invertebrates in ponds where feeding activity by this species had been studied intensively in prior years. Field work was cut short by grizzly bear activity at the site, and plans to monitor insect emergence that season had to be dropped. Butler did collect useful quantitative data at Olak that appeared in a paper published in *The Condor* on King Eider foraging during the breeding period (Oppel et al. 2011). Butler also developed pond-invertebrate sampling protocols used in 2010 & 2011 by field crews with the Arctic Shorebird Demographic Network, to monitor the availability of aquatic prey for breeding shorebirds at multiple arctic sites across Alaska and Canada. We also collaborated with a group of aquatic ecologists repeating limnological measurements in Barrow ponds that were studied intensively in the early 1970s during the International Biological Program. Butler & McEwen contributed to a paper recently published in *Ambio* on changes to these ponds over a 40yr span (Lougheed et al. 2011).

(D) Community outreach and engagement: The Barrow Arctic Science Consortium (BASC) provided most logistic support for this work, and helped with permitting required by the Ukpeagvik Inupiat Corporation and the North Slope Borough. Project members made a total of four public presentations on this research to the Barrow community, through the BASC-sponsored Saturday Schoolyard Seminar Program (Butler in 2010 & 2011; McEwen in 2011). Butler visited Mrs. E.B. Roseberry's biology class at Barrow High School in September 2010. Although efforts to recruit local student interns were unsuccessful, several adult Barrow residents showed interest in the study and participated in some field work. We attended local activities at Barrow and Atqasuk each year, and enjoyed cordial relations with the residents of both villages. The North Slope Borough's Department of Wildlife Management showed strong support for the project, helping with Butler's transport to the Olak study site and providing short-term housing for a student's extended stay at Barrow in 2009.

- Briefly explain discrepancies between the activities conducted during the grant and the activities agreed upon in your grant agreement.

Several anticipated elements of this study did not come to pass, primarily due to unforeseen logistical constraints and funding limitations. Estimated costs for the work turned out to be considerably higher than anticipated when the proposal was prepared. Personnel and operating procedures at BASC changed markedly in 2009, and some (very legitimate) costs had not been quoted to Butler in late 2008. Other costs of field work increased during the study, including airfares, housing costs, and BASC overhead.

We were able to economize in multiple ways. The PI drew none of his budgeted summer salary funds, committing the entire salary budget to student support. NFWF also provided a $10,000 supplement to Project #1549 that permitted planning for a third field season. Synergism with a one-year grant from the Arctic Landscape Conservation Cooperative for related work at Barrow permitted us to successfully complete a third field season in 2011.

We did not conduct any sampling of terrestrial soil invertebrates, due in part to loss of essential equipment sent to BASC in June of 2009. The missing shipment turned up in 2011, having been received on time in 2009, but delivered to other researchers who stored the carton in an obscure location and did not report its presence. It is now clear that the aquatic portion of the study required all available time and manpower, and including terrestrial sampling would not have been feasible. Nor did we sample at Barter Island as initially proposed, given time and funding constraints. In compensation, samples collected by Butler at Olak, and at Peard Bay by a University of Alaska student working on the King Eider study, provided relevant information about pond invertebrate communities from locations away from the well-studied ponds at Barrow.

Outcomes

- Describe and quantify progress towards achieving the project outcomes described in your grant agreement. (Quantify using the approved metrics referenced in your grant agreement or by using more relevant metrics not included in the application.)

The scientific questions driving this project fall under four topics, which together address the overarching question of **how climate change may alter the availability of invertebrate prey for tundra-breeding birds**. These four topics are outlined below, followed by an overview of key findings from this study to date. Some results have been published already, and work will continue on these samples and data through the completion of two MS theses and ultimate publication in refereed journals. **Figures referred to in this narrative can be found in *Project Documents*.**

1) **Is there evidence that the thermal environment in tundra ponds at Barrow has been altered in response to climate change?** Despite an abundance of data on climate change throughout the Arctic, including at Barrow, no prior studies have addressed this question by comparing historic and recent temperatures in the shallow tundra pond habitats that produce aquatic invertebrate prey so essential for many arctic-nesting birds. These ponds are thermally dynamic, and do not accumulate heat through the summer as do deeper lakes. Pond temperatures show pronounced daily oscillations, and most heat gained during any one day is typically lost overnight, even during 24hr daylight (Hobbie 1980). This variability limited the collection of useful thermal data until the recent advent of inexpensive, reliable temperature loggers. For example, while monitoring insect emergence at Barrow during 1975-77, Butler (1980a) used max-min thermometers to monitor the daily amplitude of pond temperatures for 41 days during 1977, with one reading per day producing two data points. Collecting season-long, hourly data temperature would have required an expensive recording thermistor. Fortunately, such a recorder was in place during the IBP Tundra Biome project, and hourly temperature data were collected from one Barrow pond for much of the summer during 1971-73. Those data are a baseline record against which we can now assess our new temperature data, to look for changes in the thermal behavior of the same ponds studied four decades ago.

2) **Has the aquatic invertebrate community of tundra ponds at Barrow changed since it was studied 35-40 years ago?** Studies in the 1970s (Butler et al. 1980) showed that tundra ponds at Barrow supported a relatively high abundance of large insect larvae and other invertebrates likely consumed by a range of pond-feeding birds including ducks, eiders, and phalaropes. Both adults and juveniles of other tundra-nesting bird species have access to this aquatic food resource during emergence of adult insects. Loss or gain of dominant prey species, or significant change in available prey biomass, might alter the value of coastal tundra ponds as producers of avian food. Potential changes in life histories of important (high biomass) prey species could alter spatial and temporal patterns of pond invertebrate biomass (Butler 1982a,b) , with consequences for birds seeking high concentrations of large prey items for efficient foraging. One goal of this study was to update the status of the pond fauna at Barrow, both in terms of taxonomic composition and the overall biomass available to foraging birds.

3) **Is the aquatic invertebrate fauna at Barrow representative of tundra ponds at other locations across the Arctic Coastal Plain?** The composition, abundance, and biomass structure of prey organisms in Barrow ponds may be

unusual, due to unique characteristics of that northern, coastal locale. In this study, we set out to make comparisons between the pond fauna at Barrow, and any other sites on the ACP that we could efficiently access for pond sampling.

4) **Have there been changes in the seasonal phenology of insect emergence in ponds at Barrow?** Insect emergence timing is crucial to arctic-nesting birds, whose broods have historically hatched in synchrony with the period of greatest adult insect abundance. Successful reproduction by both birds and insects at Barrow is restricted to the early weeks of the short arctic summer, apparently due to low predictability of favorable weather conditions in the later weeks when warmest temperatures often occur (Myers & Pitelka 1979). If avian arrival on the tundra breeding grounds is regulated by day length but insect development is regulated by temperature, a warming climate may uncouple the historic seasonal synchronicity of predator and prey (Visser & Both 2005). Emergence timing of tundra pond insects at Barrow was documented during 1975-1977 (Butler 1980a,b), with some data available from 1972 (unpublished IBP records). During this study we've been able to monitor insect emergence in those same ponds, plus others, at Barrow. We've also collected three years of baseline data on seasonal emergence patterns in inland ponds near the village of Atqasuk, 100km south of Barrow.

Discussion of this topic requires an overview of our working hypothesis regarding regulation of emergence timing for tundra insects, as well as the implications of changes in this phenomenon for avian consumption of adult insect biomass. Resource availability for an avian consumer foraging at a pond surface or margin, such as an eider duckling or a juvenile shorebird, will depend on the temporal pattern of adult biomass produced by all species in the aquatic insect community. That seasonal pulse of prey biomass may vary in both its magnitude and its distribution over time. Simply quantifying such patterns in multiple years, or at different sites, may reveal little about what regulates the observed patterns, or how climate change might be expected to alter the timing or magnitude of the food pulse. Our approach has not been to merely measure insect emergence, but to learn enough to support making reasonable predictions about how the timing and magnitude of emerging insect biomass may be expected to change under altered climatic conditions.

Benthic invertebrates in Barrow ponds are mostly insects, primarily chironomid midges. About 15 species are common at Barrow (Butler et al. 1980, Lougheed et al. 2011), with fewer than a dozen taxa comprising most of the total biomass - due to either their large size or high abundance. Insect species at Barrow emerge in a fairly consistent sequence each year, with each population appearing for only a few days. Not all species emerge from every pond, so the duration of total emergence in any pond will depend partly on which species are present. Emerging insect biomass available to foraging birds is a regional resource, integrated across many ponds that may vary in thaw date, temperature pattern, and species composition. By analyzing emergence of important insect species at the population level, in ponds with known thermal characteristics, we are learning how insect emergence responds to tundra pond thermal variation.

Individual midge species spend 1-6 or more years as larvae in pond sediments, before reaching a stage when they can emerge during their final summer. Following pond thaw that last year, larvae in the maturing cohort of each species complete remaining growth (if any) and development, undergo pupation, and then emerge as short-lived adults. Temperature appears to be the primary environmental factor regulating these events that lead up to adult emergence. **Our working hypothesis has been that cumulative temperature exposure following pond thaw in the final year determines the timing of emergence for each population, and thus collectively for the entire insect community.** Species-specific differences in emergence dates that produce the observed seasonal sequence may result from (a) different threshold temperatures for larval or pupal development, (b) different temperature-dependent rates of growth or development, (c) different amounts of growth or development remaining following overwintering, (d) some combination of these factors, or (e) some other mechanism(s). **We've conducted some simple field and lab experiments to test some of these assumptions. We are analyzing our field data to evaluate support for this hypothesis about regulation of pond insect emergence.**

- Briefly explain discrepancies between what actually happened compared to what was anticipated to happen.

Samples and data collected during this project, plus during preliminary work at Barrow in 2007-08, provide a wealth of new information about changes in tundra pond limnology and invertebrate ecology at Barrow. We have also been able to sample extensively at the inland site of Atqasuk, with additional data from Olak and Peard Bay, to make comparisons to Barrow at present. In our work with this extensive material, we've focused primarily on the topics outlined below. Here we give a brief account of major findings under each of the four topics described above. Many of the analyses are underway, so final results may differ from what we report here. Two graduate students have worked on the project since 2010, and their MS theses should be finished during 2012. We anticipate publishing several papers in refereed journals during the next two years, in addition to our two publications to date (Oppel et al. 2011; Lougheed et al. 2011) and a third manuscript (McEwen & Butler, in prep) nearly ready for submission.

1) **Comparison of tundra pond thermal environment at Barrow over four decades.**
We've analyzed temperature data collected during our recent studies, relative to similar thermal data collected during 1971-73. These findings are reported in our contribution to Lougheed et al. (2011), and in more detail in a manuscript soon to be submitted to *Limnology & Oceanography* (McEwen & Butler, in prep). Major findings include the observation of warmer mean and maximum pond temperatures in recent years, most notably early and late in the summer, plus a longer growing season. Average daily pond temperature during the open-water season has increased by 2°C over the four decades, and the season is now about two weeks longer, with a 30% increase in growing degree days. Limitations of the available pond temperature data (the 1970s data begin after pond thaw) prevented detection of any long-term change in timing of pond thaw. However, Stone et al. (2002, 2011) present data showing a very strong pattern of earlier snow melt at Barrow since the mid-1970s. Our pond melt dates at Barrow, based on loggers in place since 2008, show a high correlation (r=0.99) between pond thaw and Barrow snow melt as determined by Stone et al. Thus invertebrates in tundra ponds at Barrow may now grow and develop faster than in the past, potentially completing life cycles in fewer years, and/or emerging with different seasonal timing.

2) **Changes in the aquatic invertebrate community of Barrow tundra ponds.**
We reported on the composition of the aquatic invertebrate community at Barrow ponds in our contribution to Lougheed et al. (2011), based on sampling of benthic organisms and insect emergence during 2009-10. We found essentially the same community of insects and other invertebrates in the Barrow ponds as was documented during the International Biological Program and subsequent work in the 1970s (Butler et al. 1980). None of the invertebrate taxa known from that earlier era has yet been lost, and at least one new chironomid midge species has appeared in the Barrow ponds. Thus thermal changes seen to date are not of a magnitude to greatly alter community composition. We continue to analyze samples for possible life history changes in major taxa, which may alter the biomass structure of the community. Our quantitative sampling of aquatic invertebrate biomass at Barrow indicates similar quantities of available prey biomass to that seen during the IBP studies (1972: (3 ponds) mean B = **3.5**, range 1.5-5.4 g dry wt m^{-2}; 2010: (5 ponds) mean B = **2.7**, range 1.5-3.5 g dry wt m^{-2}).

3) **Comparison of tundra pond communities at Barrow and other Arctic Coastal Plain sites.**
Qualitative samples were collected by UAF student G.P. Sartz in mid-June of 2009 from several tundra ponds at Peard Bay, on the coast 100km west of Barrow. These exploratory samples produced the same fauna known from similar pond types at Barrow. In early June of 2009, Butler made qualitative and semi-quantitative collections from ponds at Olak in association with S. Oppel and A. Powell's King Eider study. Some of those data are published in Oppel et al. 2011. Figure 1 shows the size distribution of invertebrate biomass found in Pond Ω at Olak, on a $\log_2$ scale. This first size spectrum analysis produced a slightly bimodal distribution. About 88% of total benthic biomass fell in the larger mode, representing chironomid larvae >5mm in length, other large dipteran larvae, and oligochaete worms. Although we don't know the minimum prey size a King Eider (or any other waterfowl species) can detect while foraging, it seems likely that most of these larger invertebrates could be consumed. If an eider could not efficiently filter the smaller larvae from pond sediment, only about 10% of potential prey biomass might be missed. Total biomass in the Olak sample was low relative to our 2010 data from more intensive, quantitative sampling at Barrow and Atqasuk. We've produced similar plots showing the distribution of benthic invertebrate biomass at those two sites (Figures 2a&b). Total biomass of benthic invertebrates was considerably higher at both Barrow and Atqasuk than in the one minimally-sampled pond at Olak, although qualitative sampling in other sites at Olak did not

reveal habitats with notably higher abundance of potential avian prey. More samples from Atqasuk have yet to be fully processed for biomass estimation, but it seems clear that total benthic biomass will be approximately half that found in ponds at Barrow. The Barrow pond fauna also includes more of the larger prey sizes, especially large chironomid, plecopteran, and trichopteran larvae. Some large midge and caddisfly species do live in the Atqasuk ponds, but they are less abundant than at Barrow and stoneflies are rare. We continue to explore these contrasts between Barrow and Atqasuk, as they may reflect a general pattern of differing abundance of aquatic invertebrate prey to be found in coastal, versus inland, regions of the Arctic Coastal Plain.

4) Changes in seasonal phenology of insect emergence at Barrow.

We've made exciting progress in documenting and understanding variation in insect emergence timing. Chironomid emergence in tundra ponds at Barrow was monitored as early as 1972, and studied more intensively during 1975-77. We now have comparable data from the past three years, plus some observations from 2008 thanks to a series of qualitative samples collected by Barrow resident Ralph Davis. Emergence timing for a given species can vary from pond to pond and from year to year, but Barrow pond midges are quite predictable in having (a) high within-population synchrony, and (b) a consistent seasonal sequence of adult emergence. Figures 3&4 illustrate this seasonal phenology, by comparing the sequence of peak emergence dates for the dominant midge species in a single Barrow pond (Pond J) over all eight years for which we have records. In Figure 3 one can see the effect of annual variation in snow melt (and thus pond thaw) on the overall timing of midge emergence. Both early- and late-thawing years occur in both decades. In Figure 4, the time scale for each year is shifted to align pond thaw dates, based on the correlation (r=0.99) between observed thaw date in Pond J during 2008-2011 and annual snow melt date at Barrow reported by NOAA's Earth System Research Laboratory (Stone et al. 2002; Stone 2011). This graphical adjustment for year-to-year differences in pond thaw accounts for much of the observed annual variation in insect emergence timing. Additional variation in emergence of each species can be accounted for statistically, by considering differences in the seasonal pattern of degree-day accumulation, both between and among ponds. It's interesting that the simple adjustment for date of thaw better aligns emergence timing of early- and mid-season species, while late-emerging species are more variable from year to year. Regulation of overall life cycle phenology for these later-emerging chironomids may differ from mechanisms used by early-season species. The abundant midge *Tanytarsus nearcticus* is always the latest species to emerge, thus defining the end of the insect emergence period each year. Butler observed juvenile phalaropes feeding on these late-emerging midges every season in 1975-77, suggesting the potential importance of an abundant single species with a distinctive phenology. Although we report here primarily on the abundant chironomids, we have similar data on emergence of two caddis fly species and one stonefly, larger but less-abundant tundra pond insects that also serve as avian prey.

We're currently analyzing variation in emergence phenology in Barrow ponds statistically, using all data from every pond in every year. Treating emergence as a time-to-event phenomenon, we're using survival analysis techniques to test for differences in emergence timing among years, ponds, and decades. Pooling all emergence data from all available years, we find a significant shift between the decades in median emergence date, with the average chironomid emerging four days earlier in the recent (2009-11) summers relative to the mid-1970s (Figure 5). This figure also shows Kaplan-Meier curves illustrating cumulative emergence patterns by decade for five individual species. Four of these species showed significantly earlier median emergence dates in the recent years. We're using variance partitioning techniques to identify and rank factors most responsible for observed differences in phenology. To date we've found evidence for some regulation of emergence timing by most of the anticipated variables, in the following order of priority: species > pond > thaw date > degree days. Our experimental work appears to confirm many of the assumptions in our working hypotheses (see Outcomes: Point 4 above) about how emergence is regulated at the population level. For example, we've found that the abundant early-emerging midge *Trichotanypus alaskensis* requires about 1500 degree-hours for pupation, regardless of whether the rearing environment is cold or warmer, with daily temperatures constant or fluctuating. Such information is important to developing predictive models of how insect emergence may change in response to future climatic trends.

- Provide any further information (such as unexpected outcomes) important for understanding project activities and outcome results.

Some topics under study as part of this project are not detailed here. For example, we're still working with emergence samples from Atqasuk, becoming familiar with the fauna at that inland site. As at Barrow, the invertebrate community in Atqasuk ponds is dominated by midge larvae, along with a few other insects, oligochaete worms, a snail, and a water mite. Genera are similar between ponds at Atqasuk and Barrow with some species found at both sites, but Atqasuk has many new species. We're also seeing life cycle differences in some dominant species at Barrow (1970s data vs. recent), and between Barrow and Atqasuk. Even in the warmer inland ponds, many of the larger aquatic insects appear to have life cycles requiring several years of growth and development before emergence. Thermal data from Atqasuk show general concordance of temperatures in these inland ponds with seasonal patterns at Barrow, but mean and peak temperatures are higher. Some pond taxa common at Barrow are missing or rare at Atqasuk, such as the stonefly *Nemoura arctica* and the midge *Trichotanypus alaskensis* – likely due to insufficient dissolved oxygen during periods of high temperature. The pond fauna at Barrow may not be unique to the Barrow Peninsula, but is likely characteristic of cooler tundra ponds at coastal sites across much of the ACP. Such ponds appear to support higher abundance and biomass of potential prey for foraging birds, both as aquatic animals and during insect emergence.

Much of what we've learned about insect emergence at Barrow conforms to our expectations, but many of our ideas were largely speculation prior to the documentation and testing supported by this grant. Some outcomes were unanticipated, such as our need to modify the "absolute spring species" concept proposed by Danks & Oliver (1972) as a life history mechanism regulating emergence timing for arctic chironomids. Synchronous emergence by *T. alaskensis* is clearly *not* the result of the population overwintering as prepupal larva, needing only to pupate and emerge following spring thaw as pond temperatures dictate (the ASS hypothesis of Danks & Oliver). Instead, larvae of this important species overwinter in the early stages of the final instar (or even late in the penultimate instar). Following pond thaw, larvae of *T. alaskensis* feed actively at a time when mean daily pond temperatures rarely exceed 6°C. Within 10-14 days these larvae have doubled their body mass and become prepupae. Pupation then takes another 1500 degree-hours, or 7-14 days depending on mean temperature. Thus this chironomid completes much of its 1-year life cycle in the first weeks of its final year, achieving characteristic synchrony of emergence during the final stages of larval development. Butler (1980a, 2000) documented a similar developmental pattern for the late-emerging midge *Tanytarsus nearcticus* (as *Tanytarus inequalis*), where a similar fraction of larval growth and development occurred in the final year – but over a period of 4-6 weeks.

Understanding essential facts about the biology of these animals is essential to our ability to interpret, and to predict, their responses to environmental change. Certainly we can't expect to explain ecosystem or community patterns one species at a time! Yet study of a few select invertebrates may reveal general patterns of ecological control over this arctic fauna. Such knowledge provides a basis for understanding (and anticipating) potential community-level responses to environmental change – and ecosystem-wide consequences of such change.

3. Lessons Learned

Describe the key lessons learned from this project, such as the least and most effective conservation practices or notable aspects of the project's methods, monitoring, or results. How could other conservation organizations adapt their projects to build upon some of these key lessons about what worked best and what did not?

This has been a research project in support of conservation goals. As such, we have targeted scientific outcomes of relevance to important conservation objectives, and have worked to communicate the relationships between science and conservation to all concerned parties. Findings that could seem inconsequential to some observers may be very important to explaining ecological outcomes of great consequence. Public outreach activities have helped us maintain a two-way flow of information and perspective, not only with the non-science public, but also across science disciplines. Working with avian ecologists helps us to keep our research focused on questions of significant concern to broader constituencies in environmental research and management. It also provides both the challenge and the opportunity to demonstrate the importance of learning more about animals that some may initially view as "just bugs that the birds eat".

Plans to engage local students in this project proved to be too optimistic, despite early encouragement from a successful pilot project in 2007 (Butler et al. 2008). We had better success engaging older residents, with two village elders participating in field work during the overall study. Attendance at our local outreach activities at Barrow and Atqasuk

has always been strong, with Butler's 2011 Saturday Schoolyard Seminar at Barrow drawing a record attendance, according to the BASC host. It is clearly important for researchers in remote communities to be receptive to potential community engagement, as fruitful outreach depends on the serendipity of connecting with the right individuals. Success of such program elements thus cannot be guaranteed, but under fortunate circumstances can be very beneficial for all parties.

Similarly, facultative collaborations with other researchers can be crucial to project success. Several goals of this project benefited greatly from volunteer efforts by seven students engaged in other research projects at Barrow and at Atqasuk. These individuals helped by downloading temperature data from loggers, or by collecting emerging insect samples at times when we could not be present. Although such assistance can't be presumed in a proposal, in this case such generous help has permitted us to collect much more complete data than our budget would otherwise have allowed. We owe a debt to our colleagues for whom these students worked, and have expressed our appreciation to both them and to the students directly.

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4. Dissemination

Briefly identify any dissemination of lessons learned or other project results to external audiences, such as the public or other conservation organizations.

Publications (cited above):

- Oppel et al. (2010) includes a contribution by Butler of 2009 data on invertebrate food availability for nesting King Eiders in tundra ponds on the Arctic Coastal Plain.
- Lougheed et al. (2011) includes contributions by Butler and McEwen on changes in both the thermal regime and the macroinvertebrate community of tundra ponds at Barrow, re-studied in 2009-10, four decades after the International Biological Program studies of 1970-73.

Public and scientific presentations about this project:

Sept 25, 2010 Tundra pond invertebrates in the Arctic Coastal Plain ecosystem. Schoolyard Saturday Outreach seminar by M.G. Butler, BASC, Barrow, AK.

Sept 29, 2010 Climate Effects on Food Resources for Tundra-Nesting Birds in Arctic Alaska. Poster by S.D. Braegelman, D.J. Peterson, & M.G. Butler, ND EPSCoR Conference, Grand Forks, ND.

Oct 1, 2010 Tundra pond invertebrates in the Arctic Coastal Plain ecosystem. Seminar by M.G. Butler to Institute of Arctic Biology, University of Alaska, Fairbanks, AK.

April 7, 2011 Emergence phenology of Chironomidae (Diptera) and prey availability for tundra breeding birds. Poster by S.D. Braegelman, M.G. Butler, & D.C. McEwen. 8th Northern Plains Biological Symposium, Grand Forks, ND.

May 24, 2011 Tundra pond chironomids reduce life cycle duration as arctic climate warms. Oral presentation by M.G. Butler at Annual Meeting of North American Benthological Society, Providence, RI.

June 25, 2011 What's for dinner? Tundra pond insects! Schoolyard Saturday Outreach seminar by M.G. Butler, BASC, Barrow, AK.

July 2, 2011 Climate Change Impacts on Tundra Ponds - A Historical Perspective. Schoolyard Saturday Outreach seminar by D.C. McEwen, BASC, Barrow, AK.

Mar 29, 2012 Emergence phenology and life history analysis of some high arctic insects. Oral presentation by S.D. Braegelman, Greenbag Lunch Seminar, Environmental & Conservation Sciences Program, Fargo, ND.

April 19, 2012 Understanding arctic insect emergence: A multivariate approach. Oral presentation by S.D. Braegelman, M.G. Butler, & D.C. McEwen, on program for 9th Northern Plains Biological Symposium, Fargo, ND.

May 24, 2012 Emergence phenologies of arctic chironomids: Comparison across three decades. Oral presentation by S.D. Braegelman and M.G. Butler, on program for Annual Meeting of North American Benthological Society, Louisville, KY.

5. Project Documents

Include in your final programmatic report, via the Uploads section of this task, the following:

- 2-10 representative photos from the project. Photos need to have a minimum resolution of 300 dpi;
- report publications, GIS data, brochures, videos, outreach tools, press releases, media coverage;
- any project deliverables per the terms of your grant agreement.

POSTING OF FINAL REPORT: *This report and attached project documents may be shared by the Foundation and any Funding Source for the Project via their respective websites. In the event that the Recipient intends to claim that its final report or project documents contains material that does not have to be posted on such websites because it is protected from disclosure by statutory or regulatory provisions, the Recipient shall clearly mark all such potentially protected materials as "PROTECTED" and provide an explanation and complete citation to the statutory or regulatory source for such protection.*

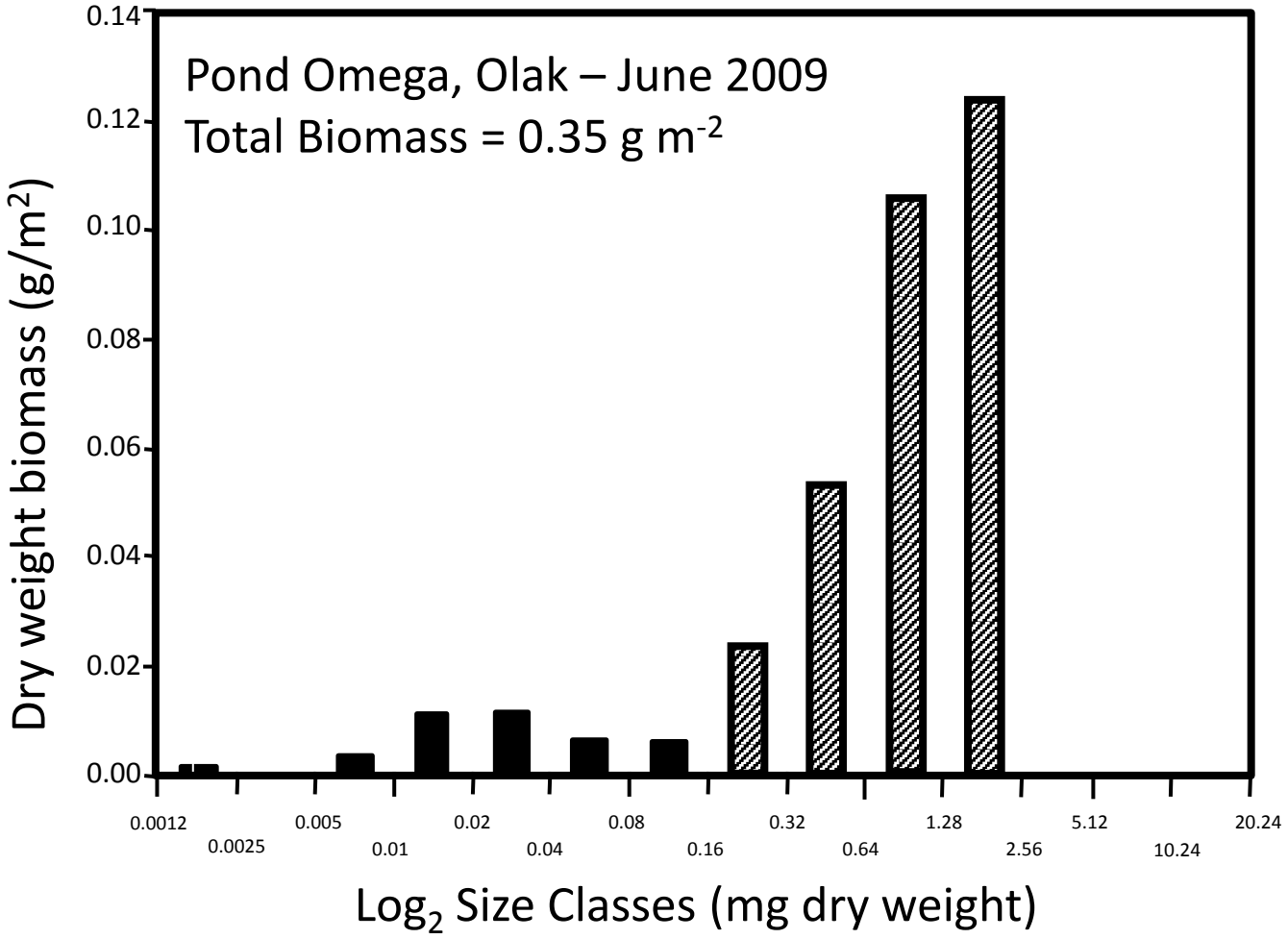


Figure 1. Size distribution of benthic invertebrate biomass at a King Eider feeding site in Pond Ω at Olak, near Teshekpuk Lake, on the Arctic Coastal Plain. See Oppel et al. (2011) for details of sampling. Hatched bars include animals >0.16mg dry weight, or ~ 5mm long.

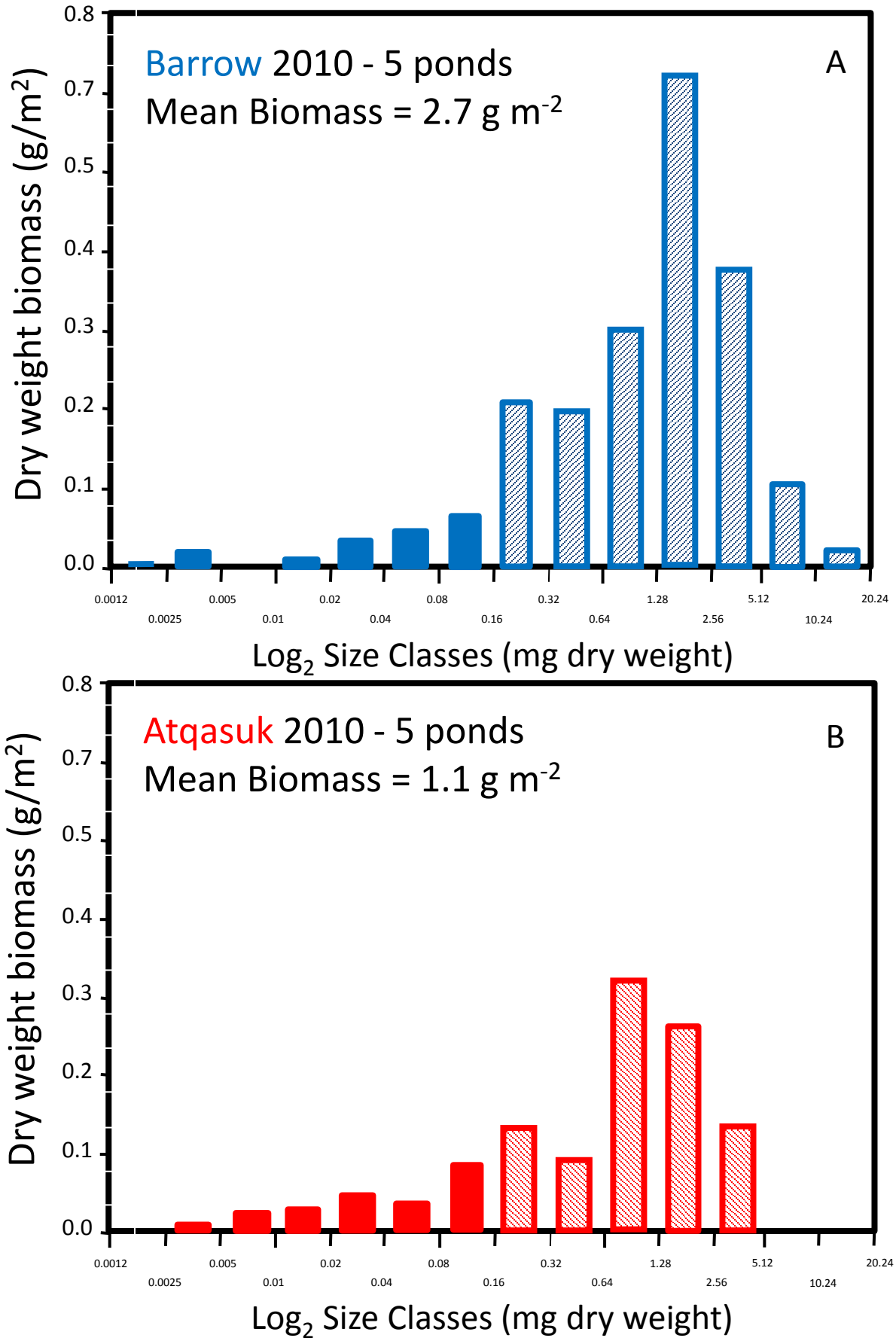


Figure 2. Size distribution of benthic invertebrate biomass in ponds at Barrow (A) and at Atqasuk (B) in June 2010. Note scale differs from Fig. 1. Hatched bars include animals >0.16mg dry weight, or ~ 5mm long.

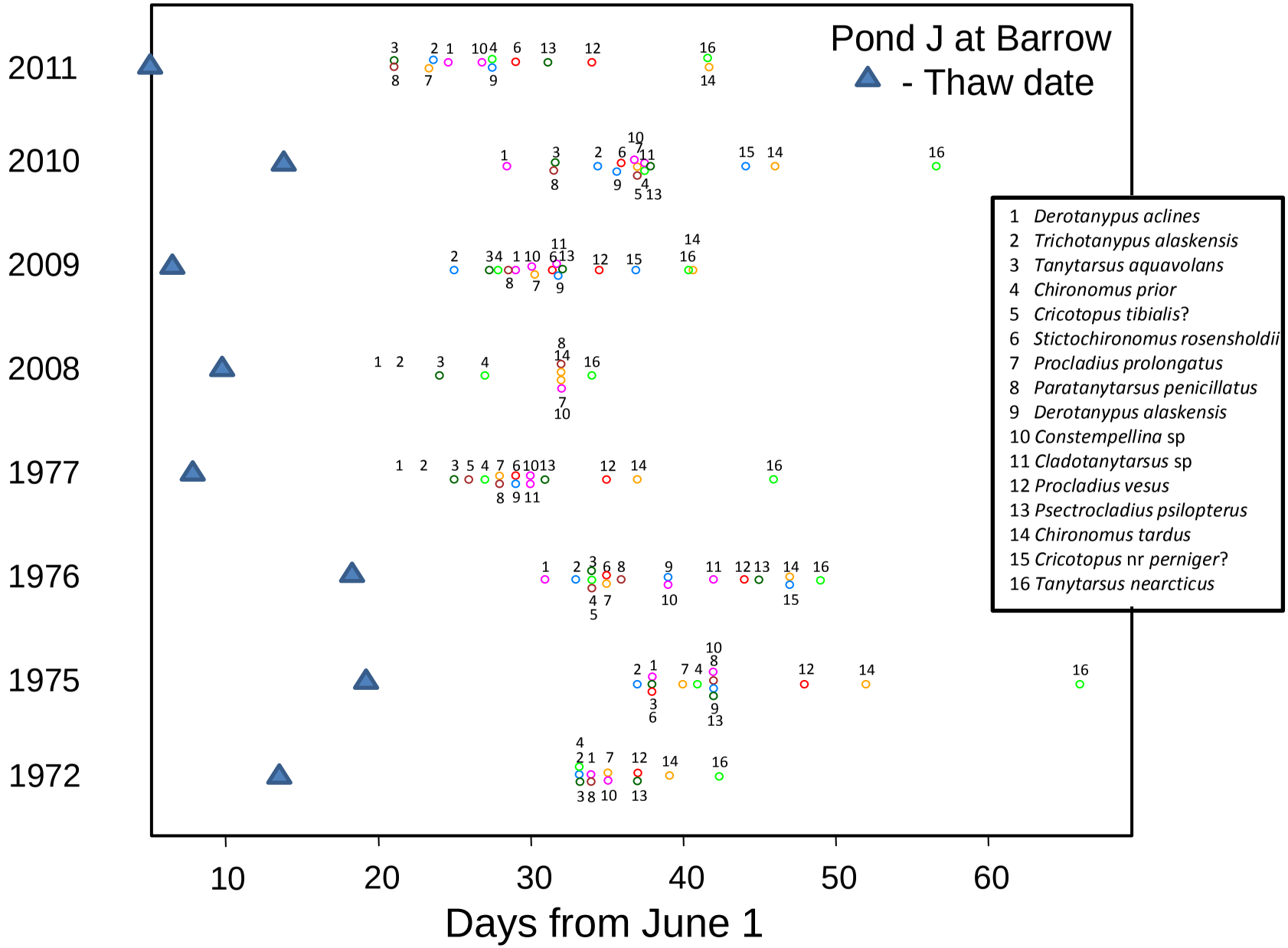


Figure 3. Dates of peak emergence for the 16 most-abundant chironomid taxa in Pond J at Barrow, AK during 1972 (unpublished IBP data), 1975, 1976, & 1977 (from Butler 1980a,b) and 2009, 2010, & 2011 (data collected in this study). Limited data from 2008 are from sporadic samples collected by a local volunteer.

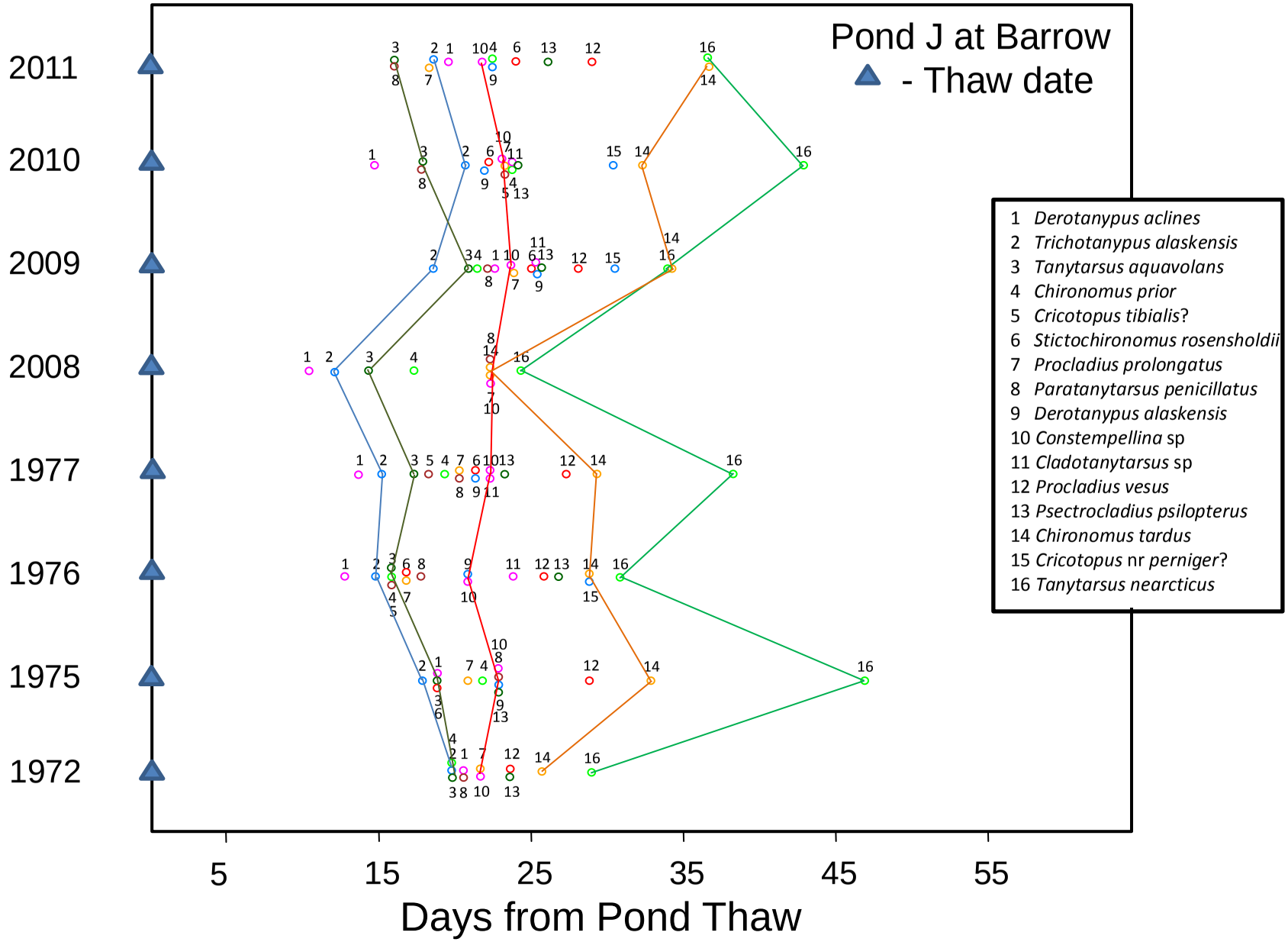


Figure 4. Peak chironomid emergence in Pond J at Barrow as in Fig. 3, but with time line for each year shifted to align estimated dates of pond thaw (see text for procedure). Lines connect five abundant taxa that were abundant in all years, representing early, mid-season, and late-emerging midge species.

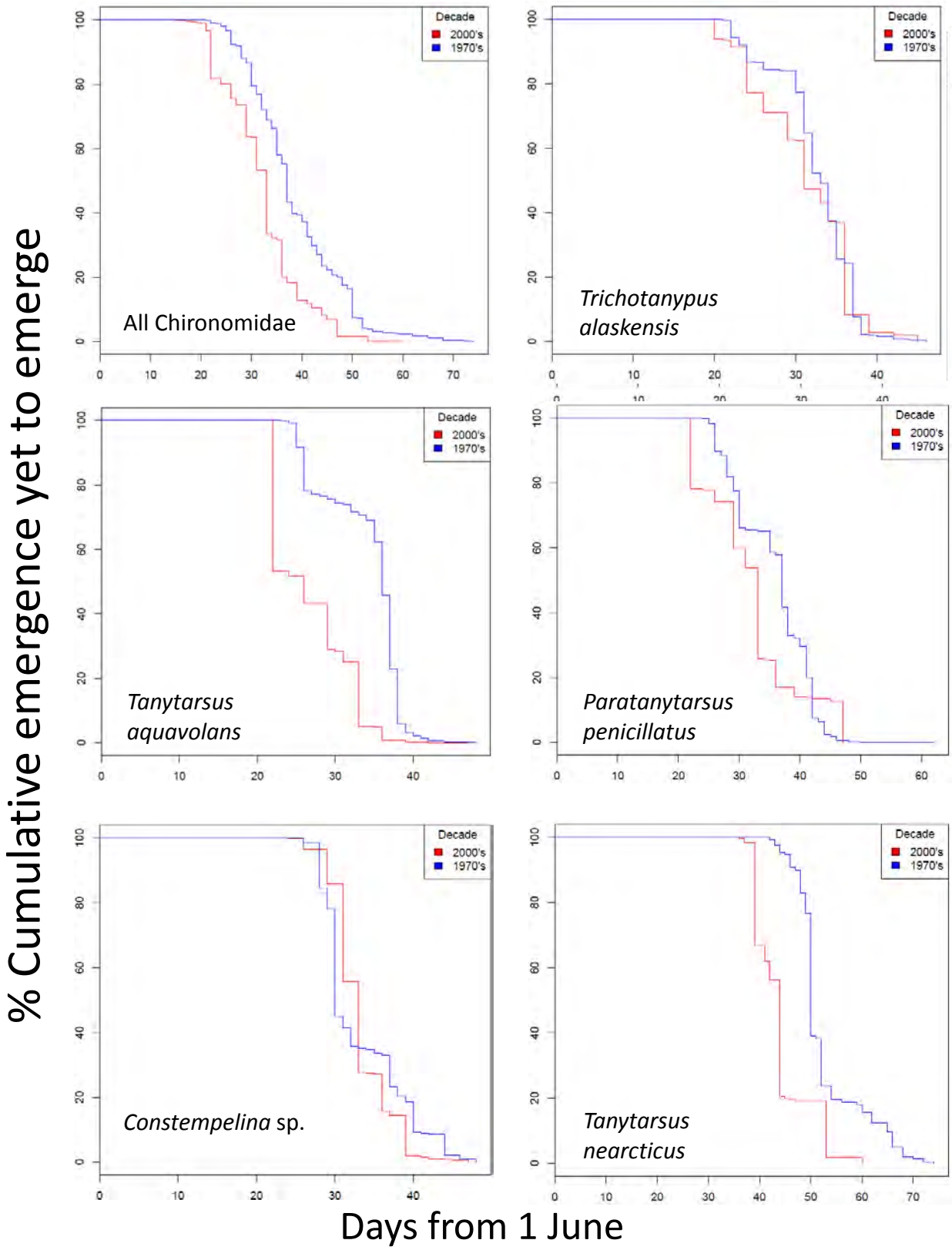
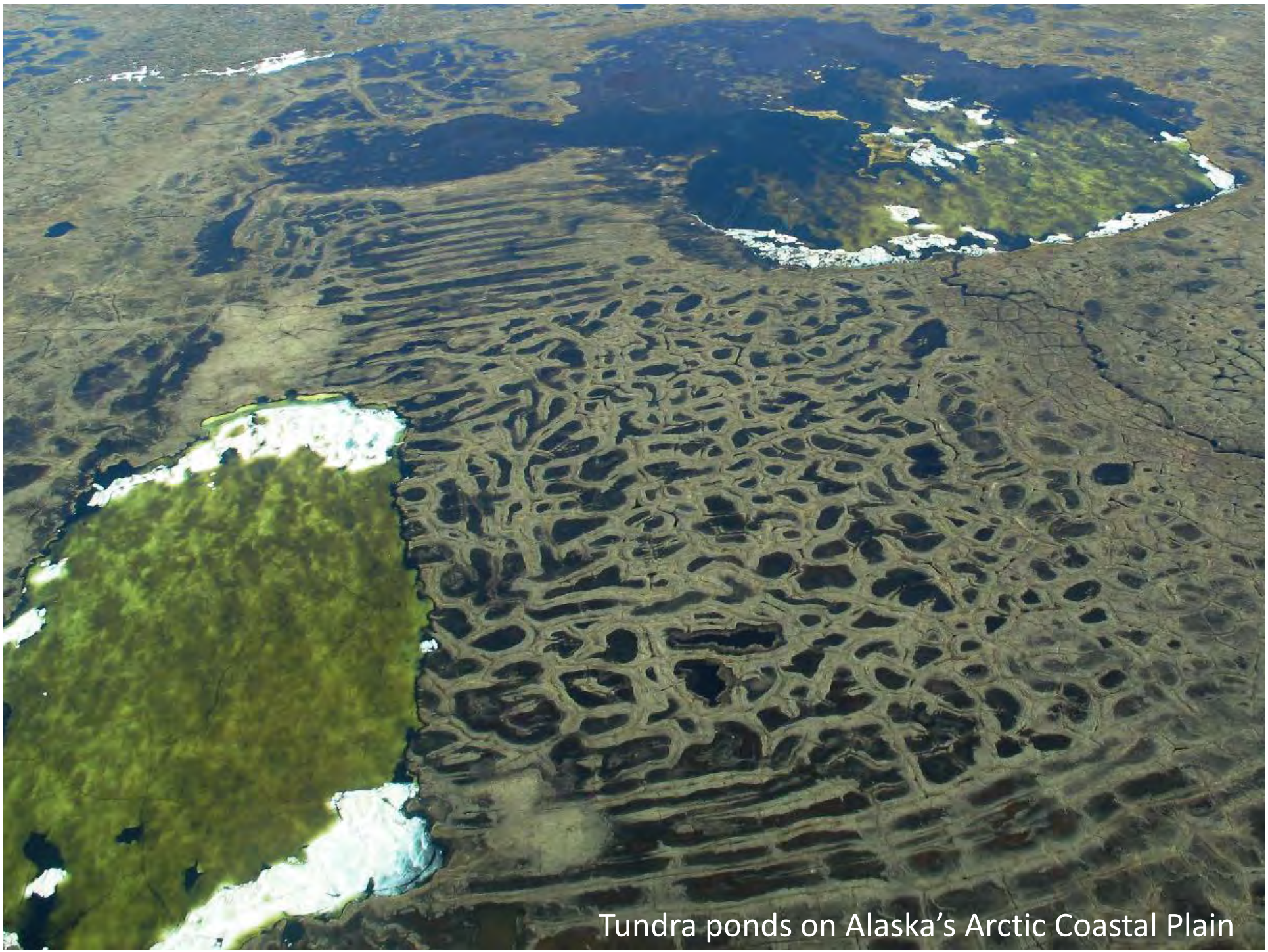


Figure 5. Chironomid emergence in IBP ponds at Barrow during 1970s and 2000s: Kaplan-Meier estimates of cumulative emergence in all ponds sampled during 1972, 1975, 1976, & 1977 (blue curves); and during 2009, 2010, & 2011 (red).



Tundra ponds on Alaska’s Arctic Coastal Plain

Top: Adult chironomid midges emerge from pupal stage.

Left: Mass chironomid emergence in a tundra pond at Barrow, Alaska in 1977.

Predators & prey: Steller's Eider hen forages on insect larvae in pond bottom; ducklings and phalaropes can access adults at surface.

Butler samples insect emergence in Pond J at Barrow, 1976 (left) and 35 years later in 2011.

Butler & Dan McEwen sample a pond at Barrow, June 2009

Butler samples prey base at Olak,
UAF King Eider study site, June 2009

Butler samples a Barrow pond at freeze-up, September 2010

NDSU student Eric Herman monitors insect emergence in a Barrow pond, June 2011

Butler gives Schoolyard Saturday talk to Barrow audience at BASC, June 2009

Barrow elders and Butler at Nalukataq, June 2009

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King Eider Foraging Effort During the Pre-Breeding Period in Alaska

Author(s): Steffen Oppel, Abby N. Powell and Malcolm G. Butler
Source: The Condor, 113(1):52-60. 2011.
Published By: Cooper Ornithological Society
URL: http://www.bioone.org/doi/full/10.1525/cond.2011.100077

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The Condor 113(1):52–60
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KING EIDER FORAGING EFFORT DURING THE PRE-BREEDING PERIOD IN ALASKA

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Abstract. For reproduction, many arctic-nesting migratory birds rely on nutrients obtained on the breeding grounds, so they devote sufficient time to foraging immediately prior to nesting. However, little is known about the increase in foraging effort necessary to meet the energetic requirements of reproduction. In early June 2006 and 2008, we quantified the proportion of time spent foraging before breeding by a large sea duck, the King Eider (*Somateria spectabilis*), on its breeding grounds in northern Alaska. During >235 hours of behavioral observations, both male and female King Eiders spent >50% of the day loafing (resting, sleeping, comfort behavior, or being alert). Females foraged on average 30% of the time (mean 7.2 hr day^{-1}, 95% CI 6.0–8.4 hr day^{-1}), three times as much as males (9%; 2.3 hr day^{-1}, 95% CI 1.5–2.8 hr day^{-1}). The most common prey in ponds where the eiders foraged were chironomid larvae and worms ranging in length from 1 to 30 mm. If the King Eider's daily energy expenditure on its breeding grounds is similar to values published for related species, it would need to ingest only 0.2–0.6 g dry mass of invertebrates per minute of foraging to meet its energetic requirements. Males did not lose body mass before breeding, and we assume that their foraging effort was sufficient for energy balance. Therefore, female King Eiders appear to triple their foraging effort over maintenance requirements to meet the energetic challenges of egg formation.

Key words: *behavior, chironomid, foraging, intake rate, King Eider, sea duck,* Somateria spectabilis.

Esfuerzo de Forrajeo de *Somateria spectabilis* Antes del Periodo Reproductivo en Alaska

Resumen. Muchas especies de aves migratorias que nidifican en el Ártico dependen de nutrientes presentes en las áreas de reproducción, por lo que dedican bastante tiempo al forrajeo justo antes de iniciar la anidación. Sin embargo, se sabe poco sobre el aumento del esfuerzo de forrajeo que sería necesario para alcanzar los requerimientos energéticos de la reproducción. A comienzos de junio de 2006 y 2008, cuantificamos la proporción de tiempo gastado en forrajeo por parte de un pato marino de gran tamaño, *Somateria spectabilis*, en su área reproductiva en el norte de Alaska. Durante >235 hr de observaciones de comportamiento, tanto las hembras como los machos gastaron >50% del día en comportamientos no activos (descansando, durmiendo, comportamiento de confort, o estando alerta). Las hembras forrajearon en promedio el 30% del tiempo (media 7.2 hr día^{-1}, IC de 95% 6.0–8.4 hr día^{-1}), tres veces más que los machos (9%; 2.3 hr día^{-1}, IC de 95% 1.5–2.8 hr día^{-1}). La presa más común en las lagunas en que estos patos forrajearon fueron larvas de chironomidos y gusanos que variaron en largo entre 1 y 30 mm. Si el gasto energético diario de *S. spectabilis* en sus áreas de reproducción es similar a la de los valores publicados para especies relacionadas, éstos necesitarían ingerir sólo 0.2–0.6 g de masa seca de invertebrados por minuto de forrajeo para alcanzar sus requerimientos energéticos. Los machos no perdieron masa corporal antes de la reproducción, y asumimos que su esfuerzo de forrajeo fue suficiente para lograr su balance energético. Por eso, las hembras de *S. spectabilis* parecen triplicar su esfuerzo energético por sobre sus requerimientos de mantenimiento para alcanzar las demandas energéticas de la formación de los huevos.

INTRODUCTION

Arctic-breeding birds face the challenge of a short summer for raising offspring, which requires nest initiation shortly after arrival on breeding grounds (Perrins 1996, Klaassen et al. 2006). As food resources may be limited during this time of the year, many migratory bird species breeding in the Arctic have long been assumed to rely for egg formation on stored body reserves (Ankney and MacInnes 1978, Meijer and Drent 1999). More recently, however, several arctic migrants have been found to use mostly nutrients obtained on the tundra for egg formation (Klaassen et al. 2001, Gauthier et al. 2003, Schmutz et al. 2006). This pattern implies that these birds forage extensively upon their arrival on arctic

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The Condor, Vol. 113, Number 1, pages 52–60. ISSN 0010-5422, electronic ISSN 1938-5422. © 2011 by The Cooper Ornithological Society. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, http://www.ucpressjournals.com/reprintInfo.asp. DOI: 10.1525/cond.2011.100077

nesting grounds (Ganter and Cooke 1996, Morrison and Hobson 2004).

The King Eider (*Somateria spectabilis*) is a large sea duck that breeds in arctic tundra ecosystems around the world and spends 10 months of the year at sea (Suydam 2000). Outside the breeding season, it forages on marine benthic invertebrates by diving, whereas on its breeding grounds it consumes mostly small invertebrates from fresh water by dabbling (Lamothe 1973, Holcroft-Weerstra and Dickson 1997, Suydam 2000). In northern Alaska, King Eiders arrive on tundra breeding grounds approximately 2 weeks prior to clutch initiation (Phillips and Powell 2006, Oppel et al. 2008, Oppel and Powell 2010). They forage in small lakes and tundra ponds, and stable-isotope analysis of eggs has indicated that birds rely on freshwater foods for egg production (Oppel et al. 2010). However, the amount of time spent searching for and consuming prey (hereafter referred to as foraging effort) during the pre-breeding period is poorly described (Holcroft-Weerstra and Dickson 1997), and the relative increase in foraging effort required to meet the energetic demands of breeding is unknown.

During the pre-breeding period the closely related Common Eider (*S. mollissima*) increases foraging effort by about 100–250% over that in other seasons (Gorman and Milne 1971, Christensen 2000, Guillemette 2001). Such a comparison is difficult for the King Eider, because upon arrival on the breeding grounds it switches from diving for marine invertebrates in deep waters to presumably much smaller prey in much shallower fresh water (Holcroft-Weerstra and Dickson 1997). Hence, any difference in foraging effort between the breeding and nonbreeding seasons is potentially confounded by the differences in the energetic return of different prey and in the energetic cost of foraging in different environments (Butler 2000). Estimating any increase in foraging effort in preparation for breeding thus requires an estimate of the baseline foraging effort required for maintenance. Because in the eiders females bear all the costs of egg formation and incubation, the foraging effort of males and females differs on the breeding grounds (Holcroft-Weerstra and Dickson 1997). If males maintain body mass during the pre-breeding period, one can assume that their foraging effort is sufficient for maintenance (Esler and Bond 2010). This foraging rate can thus provide a baseline against which an increase in females' foraging effort can be measured (Gorman and Milne 1971, Christensen 2000, Guillemette 2001).

In this study we first captured males throughout the pre-breeding period to examine whether they maintained body mass. We then quantified the behavior of both male and female King Eiders during the time between arrival on breeding grounds and the onset of incubation in order to estimate the proportion of time each sex allocates to foraging. Furthermore, we examine the diurnal pattern of foraging on the breeding grounds under continuous daylight. We present an assessment of invertebrate prey available in ponds where we observed King Eiders foraging. We use published data on the energy content of available prey and on energy expenditure by waterfowl to estimate intake rates King Eiders require to meet their energetic demands. This study thus provides crucial information on the increase in females' foraging effort on arctic breeding grounds in preparation for breeding.

METHODS

STUDY SITE

The study was conducted near the southeast shore of Teshekpuk Lake on the arctic coastal plain of Alaska (70.46° N, 153.16° W). The area is characterized by complexes of wetlands, flat to gently rolling tundra with numerous ponds, and lakes with both soft and hard bottoms. All large and deep lakes in the study area, including Teshekpuk Lake, are covered by ice until late June. King Eiders arrive in the study area in early June (Phillips and Powell 2006, Oppel et al. 2008), and most nests are initiated around 17 June (Bentzen et al. 2008a).

CAPTURES

From 2006 to 2008, using mist net arrays and decoys, we captured 39 male King Eiders on the breeding grounds during the pre-nesting period (8–16 June). We measured the body mass of each bird with Pesola spring scales accurate to 10 g.

FIELD OBSERVATIONS

We conducted behavioral observations from 8 to 22 June 2006, 8 to 15 June 2008, and on 8 June 2009 at randomly selected lakes, ponds, and wetlands in the study area. In 2009, field operations were disrupted by a brown bear (*Ursus arctos*), and we obtained only confirmatory qualitative data on eider foraging.

In the study area, King Eiders do not occur away from water bodies, and all behavioral observations were of birds on or adjacent to water. Satellite telemetry of several females has revealed that King Eiders do not commute between tundra nesting areas and marine staging areas after arrival on their breeding grounds (Phillips and Powell 2006, Phillips et al. 2007, Oppel et al. 2008). Because large lakes were still ice-covered during the study period, the smaller lakes, ponds, and wetland complexes we observed were the only foraging areas available to King Eiders. In the study area, the sun does not set in June, and in 2008 we observed King Eiders throughout the day (00:00–24:00), with a similar number of observations made during each 2-hr period of the day (Fig. 1). Sampling effort was spread evenly throughout the pre-breeding season in both 2006 and 2008.

Following the method described by Christensen (2000), we obtained activity budgets of King Eiders by instantaneous focal-animal sampling. Briefly, we observed a focal individual

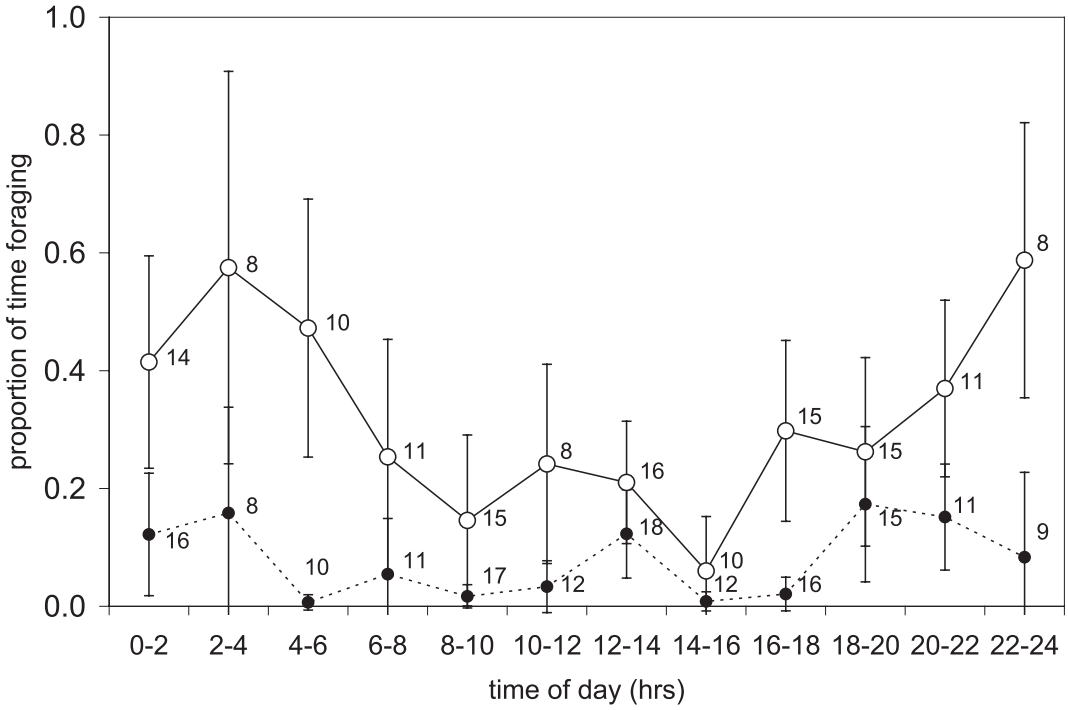

FIGURE 1. Mean (± 95% confidence intervals) proportion of time spent foraging by female (white, solid line) and male (black, dotted line) King Eiders on their breeding grounds in northern Alaska during the pre-breeding period in June 2008. Numbers next to symbols indicate sample size of 15-min observation periods.

for a given period and recorded its behavior at times separated by fixed intervals. We then calculated activity budgets by the frequency of instantaneously recorded behaviors over the period the focal individual was observed (Christensen 2000), and we use the observation period as the sample unit throughout the remainder of the paper.

In 2006, the length of observation periods was undefined, and we recorded the behavioral state of each focal individual every 5 min until it disappeared from view. In 2008, we recorded the behavior of each focal individual once a minute for a 15-min period or until the animal disappeared from view (11% of observation periods were 8–14 min). In 2009, we employed both approaches simultaneously and verified that the frequency of behaviors was equal whether recorded at intervals of 1 or 5 min. We present results from this analysis to justify our pooling of data from 2006 and 2008.

After each observation period we chose new individuals or initiated new observations in a different area to reduce the probability of repeatedly sampling the same birds. Sampling effort was spread throughout the entire study area (40 km^2), but because none of the birds was individually marked we cannot exclude the possibility that we may have sampled some individuals on more than one occasion. On the basis of the number of nests found in this area annually (48 ± 10, S. Oppel, R. Bentzen, A. N. Powell, unpubl. data) and a nest-detection rate far below 100% (Pagano and Arnold 2009), we estimate that about 200 individual King Eiders were available for sampling in the study area in mid June.

We observed birds with 30× spotting telescopes from distances >200 m in order to minimize behavioral bias due to the presence of observers. We recorded behavior in four activity classes: loafing (including resting, sleeping, preening, comfort behavior, and being alert), foraging (head-dipping, up-ending, diving), locomotion (swimming, walking, flying), and reproductive behavior (nest preparation, courtship, copulation, and aggressive interactions with conspecifics) (Goudie and Ankney 1986, Holcroft-Weerstra and Dickson 1997, Christensen 2000).

Our comparison of males' and females' time budgets assumes equal detectability of both sexes on the breeding grounds. Because King Eiders maintain a strong pair bond during the pre-breeding period, we generally observed pairs together and only a few males without female partners. Although while prospecting for nest sites females could temporarily become hard to observe, these periods of low detectability were usually very brief and characterized by males being in a state of increased alertness on a nearby pond. Hence, we are confident that any differences in foraging activity we recorded were not due to different detectability of the two sexes. All field methods had approval of the University of Alaska Fairbanks Institutional Animal Care and Use Committee under protocol 05–29.

PREY COLLECTION AND BIOMASS ESTIMATION

We sampled invertebrates in several shallow ponds and lake margins of the core study area in June 2006 and 2009. We surveyed larger invertebrates within 2 m of shorelines (water depths <50 cm) by sweeping through emergent vegetation and sieving surficial sediments with a 1.0-mm-mesh dip net in ponds and lakes of the study area where we observed King Eiders foraging. In addition to these qualitative collections, on 8 June 2009 we made a quantitative assessment of the abundance and size distribution of invertebrates near the shore (depth 40–50 cm) of a pond where we had observed two pairs of King Eiders foraging during the previous night. Because the sediment of ponds is an incoherent layer of flocculent organic material floating above frozen ground, quantitative core samples were not feasible. We therefore scooped eight randomly chosen patches of sediment (~194 cm^2 each) within an area of ~10 m^2 to a depth of 10 cm with a rectangular net, representing approximately 0.15 m^2 of pond sediment. We sieved the samples with a 0.5-mm-mesh screen, reducing the volume of the flocculent organic sediments by <50%. All benthic invertebrates >1 mm length were extracted from this quantitative sample by sucrose flotation (Butler 1982), preserved with 5% formalin, and identified to lowest practical taxonomic level (typically to genus). We photographed several individuals representative of each taxon and size class under a dissecting microscope and measured their body lengths on the digital images with the software ImageJ. We estimated the dry mass of each category of prey with appropriate length–weight regressions (Benke et al. 1999).

STATISTICAL ANALYSIS

To explore whether males' foraging effort was sufficient to maintain body mass, we analyzed the trend in body mass of males over the pre-breeding period with a linear regression.

To quantify foraging effort, we calculated the proportion of each behavior for every individual within each observation period and used those observation periods as sampling units (Christensen 2000). Observation periods were 15–160 min (mean 65 ± 30 min) in 2006 and 15 min in 2008. We averaged the frequency of each behavior across individuals for each sex and tested for significant differences between behavioral categories and sexes with nonparametric Wilcoxon tests.

To describe diurnal activity patterns in 2008, we averaged each behavior's frequency across individuals from each sex for every 2-hr period of the day starting and ending at midnight. All analyses were run in R 2.8.0, and we present results as mean and 95% confidence intervals.

ESTIMATION OF INTAKE RATES

We explored whether the foraging effort recorded in our study could explain the known pattern of nutrient allocation to eggs in the King Eider (Oppel et al. 2010) by estimating intake rates based on energetic balance. For each taxon of prey, we used energy content per dry mass from published studies (Brittain and Lillehammer 1978, Penczak et al. 1984, Custer et al. 1986) to estimate intake rates required to maintain energy balance.

TABLE 1. Energetic costs of main activities experimentally determined for several species of waterfowl.

Activity	Energetic cost (W kg^{-1})	Reference
Up-ending	9.4	Nolet et al. 2006
Head-dipping	11.8	Nolet et al. 2006
Resting	5.9	Richman and Lovvorn 2008
Swimming	17.7	Butler 2000, Prange and Schmidt-Nielsen 1970, Woakes and Butler 1983
Flying	75.0	Pelletier et al. 2008

We estimated males' daily energy expenditure on breeding grounds by multiplying activity budgets from our observations by the experimentally determined energy expenditure of White-winged Scoters (*Melanitta fusca*) resting on 9° C water (Richman and Lovvorn 2008), foraging costs of Bewick's Swans (*Cygnus columbianus bewickii*) head-dipping or up-ending in small ponds (Nolet et al. 2006), swimming costs of diving ducks (Prange and Schmidt-Nielsen 1970, Woakes and Butler 1983, Butler 2000), and flying costs of free-ranging Common Eiders in Denmark (Pelletier et al. 2008) (Table 1).

Because the energetic cost of egg formation is partly met by reducing body-maintenance costs (Nilsson and Raberg 2001, Vezina and Williams 2002, Williams 2005), we used an estimate of total daily energy expenditure during egg formation for the Common Eider (Parker and Holm 1990) as surrogate for the likely energy-intake requirements of female King Eiders. In addition, we estimated the minimum daily energy expenditure of nonbreeding females by the same approach described above for males (Table 1).

For both males and females, we estimated how much invertebrate biomass an adult eider needed to consume to ingest the required energy per day, assuming an assimilation efficiency for invertebrate prey of 85% (Reinecke and Owen 1980, Hilton et al. 2000, Richman and Lovvorn 2003, 2004). Finally, from our observations of the average daily foraging effort by each sex, we converted those estimates to intake rates (in g dry mass min^{-1}).

RESULTS

We recorded King Eider activity for a total of 9825 min over 146 observation periods in 2006 and for 4294 min over 296 observation periods in 2008. In 2009 we observed two pairs for 450 min during 8 observation periods and recorded their behaviors at both 1-min and 5-min intervals. The frequencies of the three most common behavior categories for each sex did not differ by length of observation interval, but very uncommon

TABLE 2. Relative frequency (mean ± standard deviation) of behaviors of male and female King Eiders on breeding grounds in Alaska during the pre-breeding periods in June 2006 and 2008. Observation periods in 2006 were on average four times as long as in 2008.

	Female[a]		Male[b]	
Behavior	Mean	SD	Mean	SD
2006				
Loafing (rest, alert, comfort)	0.46	0.30	0.59	0.30
Foraging	0.28	0.27	0.11	0.17
Locomotion	0.19	0.19	0.24	0.20
Reproduction (nesting, courtship, aggression)	0.06	0.17	0.04	0.12
2008				
Loafing (rest, alert, comfort)	0.56	0.35	0.74	0.26
Foraging	0.31	0.33	0.08	0.16
Locomotion	0.09	0.12	0.11	0.14
Reproduction (nesting, courtship, aggression)	0.04	0.08	0.07	0.13

[a] $n = 62$ in 2006, 141 in 2008.
[b] $n = 84$ in 2006, 155 in 2008.

behaviors (e.g., flying, aggressive interactions) were underrepresented during the 5-min intervals. As these behaviors are negligible for our purpose of analyzing foraging effort, the methods we employed in 2006 and 2008 can be considered equivalent, and we pooled data from both these years.

On average, both male and female King Eiders foraged for less than one-third of the time and spent the majority of the day loafing (Table 2). Male King Eiders weighed on average 1660 ± 130 g, and the estimated change in body mass between males captured in early June and males captured 8 days later was –3.8 ± 10.4 g day^{-1} (mass = –3.80 × time + 1710 g, $n = 39$, $P = 0.72$). We therefore assumed that males' foraging effort was sufficient for energy balance and thus useful as a baseline estimate against which increase in females' foraging effort could be measured.

Females foraged three times more than males ($P < 0.001$, $n = 442$), spending on average 7.2 hr day^{-1} (95% CI: 6.0–8.4 hr day^{-1}) foraging, while males spent only 2.3 hr day^{-1} (95% CI: 1.5–2.8 hr day^{-1}) foraging. Conversely, males spent more time loafing ($P < 0.001$, $n = 442$). Most loafing males were guarding their partner while the female was foraging. Both locomotion and reproductive behavior were relatively uncommon (Table 2), and the proportion of time males and females spent on those activities did not differ ($P = 0.08$ for locomotion, $P = 0.13$ for reproductive behavior).

In 2008 we observed a diurnal pattern in the foraging behavior of female King Eiders, with foraging more frequent during the "night" hours (20:00–06:00) and less frequent during the middle of the day (Fig. 1). For males the pattern was similar but less pronounced (Fig. 1). We were not able to explore diurnal patterns in 2006 because no data were recorded between 22:00 and 06:00.

Foraging behavior consisted mostly of birds swimming in shallow water with heads dipped under water. We also frequently observed up-ending, but we recorded diving on only four occasions. No prey handling, manipulation, or swallowing of food was observable, and the items consumed appear to have been very small. On one occasion a female was observed with a small fish in her bill, but the fish was dropped and not consumed. Some females emerged from head-dipping with aquatic vegetation attached to the bill, but it was impossible to discern whether they were foraging on vegetation or whether uptake was accidental. The birds foraged either in shallow ponds (<70 cm deep) or very near (<5 m) the shoreline of deeper ponds or lakes, and in most locations eiders were able to reach the sediment of water bodies by up-ending.

We found very few invertebrates in the water column, suggesting that King Eiders retrieve prey mostly from sediments. The most common benthic invertebrates we found were dipteran larvae of the family Chironomidae. Most chironomid larvae were <5 mm long and <0.1 mg dry mass, but late-instar larvae of larger species exceeded 10 mm length and approached 1 mg dry mass. Other large invertebrates collected included oligochaete worms, larvae of other dipterans (Muscidae, Tipulidae), caddisfly and stonefly larvae, and snails (Table 3).

The quantitative sample contained at least 13 species of potential prey but lacked some large taxa such as caddisflies, stoneflies, and snails. We estimated total prey biomass from this quantitative sample to be 350 mg dry mass m^{-2}. Oligochaete worms and larger chironomid larvae (>0.16 mg dry mass) accounted for only 17% of individuals but 88% of total invertebrate biomass.

We estimated the mean energy content of potential food items available to King Eiders in our study area as 21.8 kJ g^{-1} dry mass by averaging values in the literature for the Chironomidae, Tipulidae, Muscidae (Custer et al. 1986), Trichoptera, Plecoptera, and Oligochaeta (Brittain and Lillehammer 1978, Penczak et al. 1984). We used this mean energy content to estimate the King Eider's intake rates of invertebrate biomass on the basis of their activity budgets and published estimates of energy expenditure during those activities.

We estimated the daily energy expenditure of males to be 1372 kJ, corresponding to a required dry-mass intake of 74 g day^{-1} to maintain energy balance (Table 4). Given a foraging effort of 2.3 hr day^{-1}, males require an intake rate of 0.54 g of dry mass per minute of foraging. We estimated the daily energy expenditure of females to range from 1471 kJ day^{-1} for females not producing eggs (Table 4) to 2528 kJ day^{-1} for females producing eggs (Parker and Holm 1990). Females thus required between 80 and 137 g of dry mass to meet energetic demands. During 7.2 hr of foraging per day, a female would thus have to maintain an intake rate ranging from 0.18 to 0.32 g dry mass min^{-1}.

TABLE 3. Aquatic invertebrates found in the muddy substrate of ponds and lakes on the arctic coastal plain of Alaska where King Eiders were observed foraging during the pre-breeding period in early June 2009.

Order or class	Family	Subfamily or tribe	Genus	Size[a]
Diptera	Chironomidae	Tanypodinae	*Procladius*	large
			Conchapelopia	
		Chironomini	*Chironomus*	
			Cladopelma	small
			Cryptochironomus	large
			Dicrotendipes	large
			Stictochironomus	
		Tanytarsini	*Cladotanytarsus*	small
			Paratanytarsus	small
			Tanytarsus	small
		Orthocladiinae	*Cricotopus*	small
			Parakeifferiella	small
			Corynoneura	small
			unidentified	
	Tipulidae		*Tipula*	
	Muscidae		*Limnophora*	large
Trichoptera	Limnephilidae		*Asynarchus*	
Plecoptera	Nemouridae		*Nemoura*	
Oligochaeta	Tubificidae		unidentified	large
	Enchytraeidae		*Propappus*	large
Acari	Hydrachnidia		*Lebertia*	
Gastropoda			*Physa*	

[a]Large, some individuals in the quantitative sample exceeded 6 mm in length or 0.16 mg in estimated dry weight; small, no individual in this sample exceeded these measurements.

TABLE 4. Minimum daily energy expenditure of King Eiders during the pre-breeding period in northern Alaska, estimated from time budgets observed in this study (Table 2) and experimentally determined costs for main activities (Table 1). Foraging effort is the sum of up-ending and head-dipping activities.

Sex	Activity	Time spent (hr day^{-1})	Energetic cost (kJ hr^{-1})	Daily energy cost (kJ day^{-1})
Male	up-ending	2.0	57.5	115.0
	head-dipping	0.3	72.3	18.1
	resting	16.8	36.2	607.6
	swimming	4.8	108.5	520.8
	flying	0.2	459.0	110.2
	total			1371.7
Female	up-ending	4.8	57.5	276.0
	head-dipping	2.4	72.3	173.5
	resting	12.2	36.2	442.7
	swimming	4.3	108.5	468.8
	flying	0.2	459.0	110.2
	total[a]			1471.1

[a]For breeding females, the actual daily energy expenditure is substantially higher because of the costs of egg formation. Because egg-formation costs can be partially compensated for by reducing other metabolic costs, they could not be added to the energy budgets in this table. See text for details.

DISCUSSION

In northern Alaska, pre-breeding female King Eiders spent on average 30% of their time or 7.2 hr day^{-1} foraging in tundra lakes and ponds. Males accompanying those females foraged only for 2.3 hr day^{-1}, but our capture data indicate that males did not lose body mass during the pre-breeding period. Hence, if males' foraging reflects the minimum effort required for energy balance (Gorman and Milne 1971, Guillemette 2001), then females appear to triple their foraging effort in preparation for breeding. This increase in foraging effort may be sufficient for female King Eiders to meet the energetic demands of egg formation (Vezina and Williams 2002, Williams 2005, Nager 2006).

Foraging time alone is an insufficient measure of nutrient intake, as it does not take foraging efficiency or prey type and density into account. Most prey items available in water bodies of the study area were small relative to the King Eider's marine food resources (Merkel et al. 2007), but larger worms and insect larvae constituted the bulk of invertebrate biomass we measured in tundra ponds. Several species of waterfowl are known to forage on chironomid larvae almost exclusively (Phillips 1991, Krapu and Reinecke 1992, Green et al. 1999), and the high protein content of insect larvae renders them a food source sufficient to meet the protein requirements of egg

production (Krapu and Swanson 1975, Thompson and Drobney 1997). Despite the small size of potential prey items such as chironomid larvae, they may be energetically profitable because of the low cost of foraging. While diving to capture benthic prey at sea requires considerable amounts of energy (Butler 2000, Richman and Lovvorn 2008), the modes of foraging that we observed (head dipping and up-ending) require less than half as much energy (Nolet et al. 2006).

According to our model, King Eiders must consume between 0.2 and 0.6 g of dry mass per minute of foraging, corresponding to 1.0–2.5 g of fresh invertebrate biomass (Leuven et al. 1985). These intake rates are within the range of intake rates estimated for a variety of diving ducks feeding on benthic bivalves obtained by diving: Guillemette et al. (1992) estimated wild Common Eiders to ingest 4.6 g of wet mussel mass during a 43-sec dive, de Leeuw (1999) found captive Tufted Ducks (*Aythya fuligula*) and Greater Scaup (*A. marila*) to ingest 16.2–27.6 g fresh mussel mass per minute, and Richman and Lovvorn (2003) reported that captive White-winged Scoters were able to ingest between 0.39 and 4.68 g of ash-free dry clam mass per minute. However, in all the experimental studies mentioned above, and in similar studies of dabbling ducks (Fritz et al. 2001, Arzel et al. 2007), prey densities were much higher (>10 g m^{-2}) than we recorded in our study area (0.35 g dry mass m^{-2}). We are unaware of any studies examining the sediment-filtering efficiency of eiders, but our analysis suggests that it is realistic for King Eiders to acquire a large proportion of the nutrients required for egg formation directly on breeding grounds (Lawson 2006, Oppel et al. 2010).

There is currently no information available on the prey species King Eiders actually digest on their breeding grounds. Stable-isotope analysis indicates that a wide variety of invertebrates may be consumed, but because of the isotopic variation among invertebrates the abundance of different prey items in the King Eider's diet could not be estimated reliably (Oppel et al. 2009, 2010). The guts of collected birds contained not only invertebrates but also vegetation (Lamothe 1973, Bergman et al. 1977). If part of the foraging effort is spent on ingesting vegetation, then our estimated intake rates are biased low. We speculate that intake of vegetation may be incidental and that most vegetative matter is not assimilated. More research is required to determine the exact composition of the King Eider's diet on its breeding grounds.

As daylight was not a limiting factor, foraging occurred around the clock but slightly more frequently around midnight than noon. In our study area temperatures and light intensity during June are generally lower between 22:00 and 07:00 than during the remainder of the day. The diurnal pattern of foraging may result from different prey availabilities (Holcroft-Weerstra and Dickson 1997) or from small differences in temperature making it energetically more efficient to forage during the colder part of the day (de Leeuw et al. 1998, Kaseloo and Lovvorn 2003).

In summary, our study shows that to prepare for egg formation and incubation, female King Eiders triple their foraging effort on breeding grounds between arrival and the start of incubation. As most available prey items are small and should not pose any digestive constraints (Guillemette 1994), and daylight is not limiting, a further increase of foraging effort appears possible. Thus, lower density or altered prey availability in years with unfavorable environmental conditions may not affect the ability of King Eiders to breed but may require an increase of females' foraging effort. While food from fresh water on the tundra is an important resource at all stages of the breeding season, female King Eiders still arrive with and utilize body reserves during incubation (Kellett and Alisauskas 2000, Bentzen et al. 2008b). Given the low densities of prey in tundra ponds it appears unlikely that high intake rates on the breeding grounds could compensate for birds arriving in poor body condition.

ACKNOWLEDGMENTS

This study was funded by the U.S. Geological Survey's Outer Continental Shelf Program. The Alaska Fish and Wildlife Fund, through the U.S. National Fish and Wildlife Foundation, supported the sampling of invertebrates in 2009. We thank the North Slope Borough and R. Suydam for logistical support during field work. P. Petterson Sartz, E. Goldsmith, J. Heathcote, J. Rogalla, and J. Lambrecht assisted in behavioral observations. We appreciate the comments of J. Lovvorn, P. Barboza, D. L. Dickson, E. C. Murphy, R. Elner, and two anonymous reviewers on an earlier draft of the manuscript. Mention of trade names or commercial products is for descriptive purposes only and does not imply endorsement by the U. S. government.

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AMBIO (2011) 40:589–599
DOI 10.1007/s13280-011-0165-1

Changes in Tundra Pond Limnology: Re-sampling Alaskan Ponds After 40 Years

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Abstract The arctic tundra ponds at the International Biological Program (IBP) site in Barrow, AK, were studied extensively in the 1970s; however, very little aquatic research has been conducted there for over three decades. Due to the rapid climate changes already occurring in northern Alaska, identifying any changes in the ponds' structure and function over the past 30–40 years can help identify any potential climate-related impacts. Current research on the IBP ponds has revealed significant changes in the physical, chemical, and biological characteristics of these ponds over time. These changes include increased water temperatures, increased water column nutrient concentrations, the presence of at least one new chironomid species, and increased macrophyte cover. However, we have also observed significant annual variation in many measured variables and caution that this variation must be taken into account when attempting to make statements about longer-term change. The Barrow IBP tundra ponds represent one of the very few locations in the Arctic where long-term data are available on freshwater ecosystem structure and function. Continued monitoring and protection of these invaluable sites is required to help understand the implications of climate change on freshwater ecosystems in the Arctic.

Keywords Arctic tundra ponds · Climate change · Nutrients · Algae · Plant communities · Species change · Temperature

INTRODUCTION

The Arctic region is experiencing a period of unprecedented warming (Callaghan et al. 2004), and tremendous changes have been recorded in Arctic freshwater ecosystems in response to global climate change. In the paleolimnological record, Smol et al. (2005) and Douglas et al. (1994) observed dramatic changes in diatom communities in high Arctic lakes and ponds over the past 150 years. Decreased ice cover, due to environmental warming, has resulted in longer growing seasons for algae and other organisms, and has been linked to increased primary production and changes in algal and invertebrate communities (Smol et al. 2005; Keatley et al. 2008). Spectral reflectance measurements on sediment cores also suggest that climate warming over the past 150 years has led to increased primary production in Arctic lakes (Michelutti et al. 2005). Evidence from several locations suggests that warming permafrost may be releasing nutrients and dissolved organic carbon (DOC) into Arctic freshwater ecosystems (Hobbie et al. 1999; Frey and Smith 2005; Schindler and Smol 2006). Despite these compelling trends, there is generally a scarcity of long-term data sets in the Arctic, especially in freshwater ecosystems (Smol and Douglas 2007b), and the effects of warming and permafrost thaw on Arctic freshwater ecosystems remain poorly understood.

The village of Barrow, AK, is the northernmost settlement in the United States (Fig. 1) and has been home to an active scientific research program since the 1940s. The region is underlain by continuous permafrost, with a maximum seasonal thaw (active layer) depth ranging from 30 to 90 cm in thickness (Hinkel and Nelson 2003). The coastal plain of the Alaskan North Slope has changed substantially over the past 40 years. Temperature and length of growing season have increased (Callaghan et al. 2004). Ponds in the region appear to have greater plant cover than recorded during in the 1970s (Stow et al. 2004). While there have been no reported losses of lakes and ponds on the Arctic coastal plain (Riordan et al. 2006),

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water bodies in areas of discontinuous permafrost are declining in area and abundance (Smith et al. 2005; Riordan et al. 2006). Furthermore, the human population, and its consequent anthropogenic sources of pollutants, has been steadily increasing in the region, and nutrient and chemical pollution in Arctic ecosystems, from both local and distant sources, is an emerging concern (Schindler and Smol 2006).

Despite the fact that about 22% of the land area on the Arctic Coastal Plain is covered with lakes, and more than 65% is marked by former lake basins filled with ponds (Hinkel et al. 2003; Frohn et al. 2005), relatively little limnological research has been conducted at Barrow since the late 1970s. During the 1970s, however, there was a substantial emphasis on limnology in the Barrow area and research performed at that time was paramount in pioneering arctic limnology and arctic ecological research in general. In 1971, the US National Science Foundation (NSF) funded the International Biological Program (IBP)—Tundra Biome project near the village of Barrow. The aquatic portion of that project culminated in a volume titled "The Limnology of Tundra Ponds" (Hobbie 1980). This report summarized the numerous publications of many scientists who cooperated to understand the ecology of ponds and a few lakes near Barrow, with a focus on energy flow and factors controlling productivity. With their intensive historical data, the IBP ponds represent a valuable, and virtually untapped, resource for studying ecological change on a decadal time scale.

The IBP ponds are small (30 × 40 m), shallow (<0.5 m deep) ponds occupying low-centered ice wedge polygons and surrounded by wet tundra within a large thaw-lake basin. Water flows between the ponds for only a few days each spring during snow melt, with no above- or below-ground flow for the rest of the summer, except in the rare event of exceptionally heavy rains. During the summer, most water lost from the ponds through evaporation is balanced by precipitation. During the IBP project, several ponds in the center of a former lake basin were studied on a regular basis, while additional ponds were visited or manipulated on occasion (Hobbie 1980) (Fig. 2). Researchers in the 1970s found that both planktonic and benthic algae in the IBP tundra ponds had temperature optima that were higher than ambient temperatures, indicating their potential to increase growth rates under warmer conditions (Stanley and Daley 1976; Alexander et al. 1980). Researchers also found that pond algal growth and photosynthesis were limited by phosphorus. When phosphorus was added to the ponds, nitrogen became limiting and enhanced the growth of nitrogen-fixing blue-green algae in the sediment (Alexander et al. 1980). Phytoplankton biomass and primary production were also controlled by zooplankton grazing, while benthic algae were likely kept low by bioturbation of animals (Alexander et al. 1980). The consumers in these ponds were primarily cladocerans, copepods, and anostracans in the water column (Stross et al. 1980), and a diverse assemblage of chironomid larvae in the sediments (Butler et al. 1980).

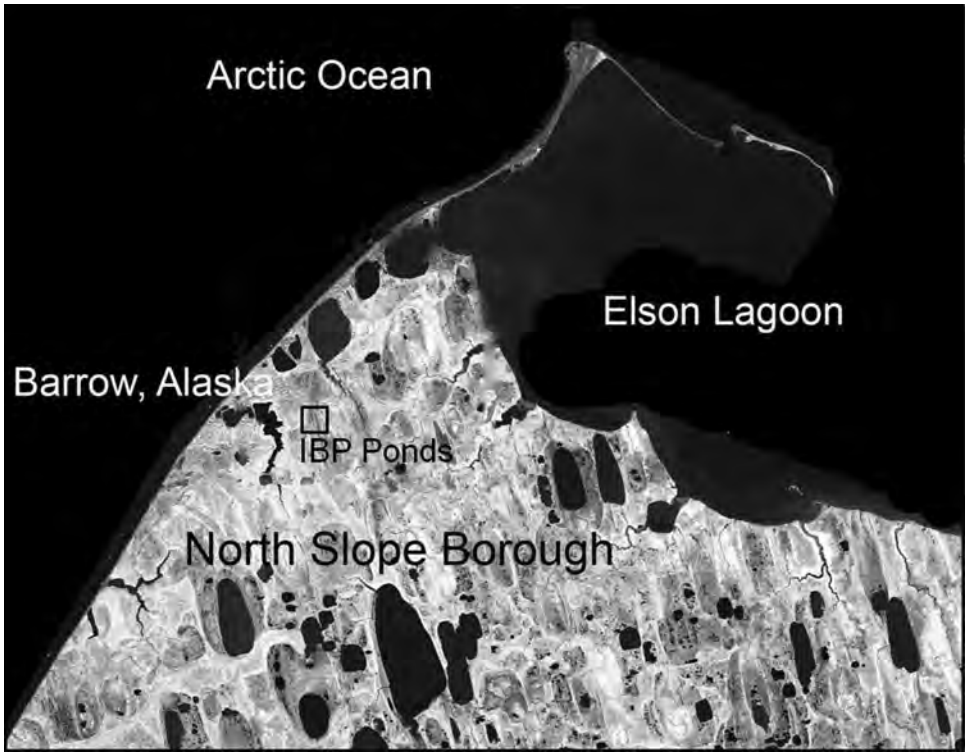

Fig. 1 Location of IBP tundra ponds site near Barrow, Alaska (71.29N, 156.79W)

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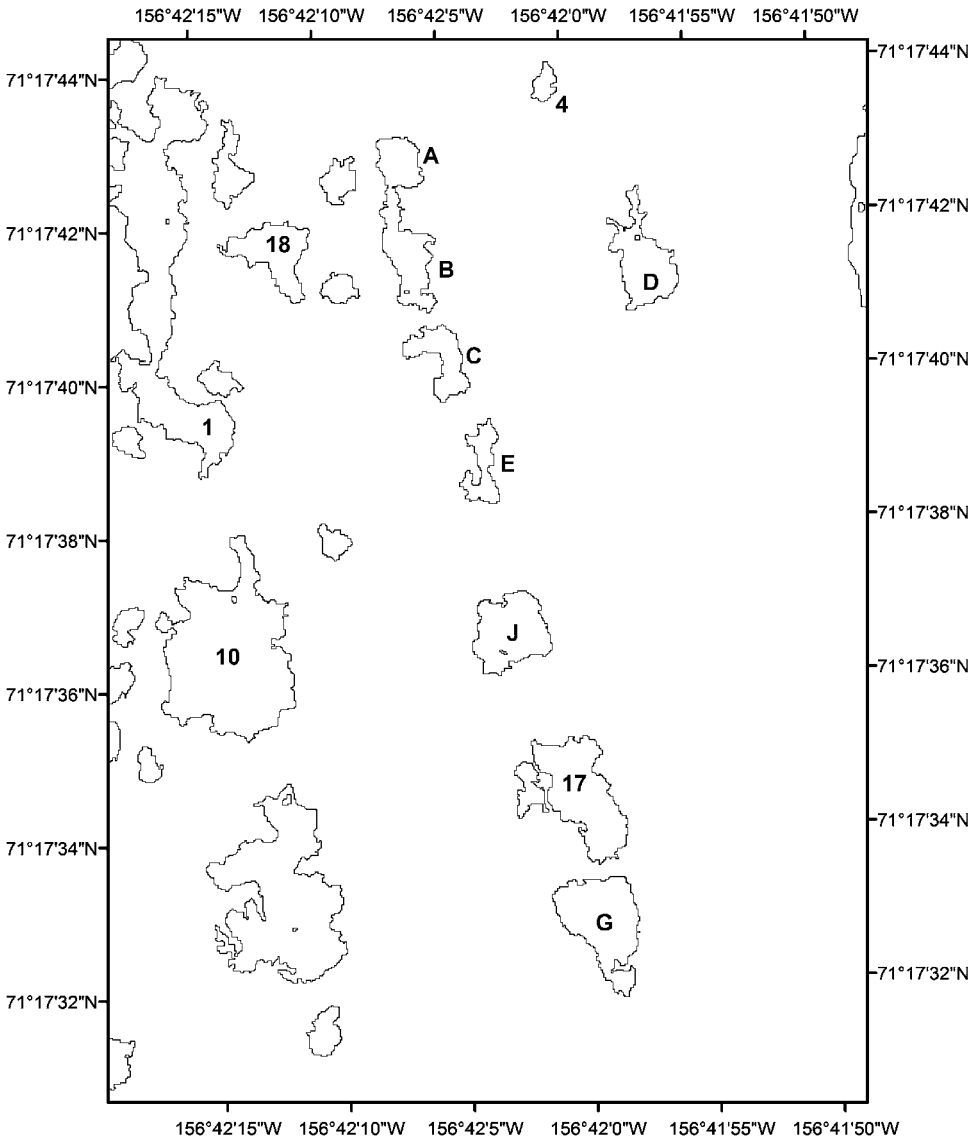

Fig. 2 IBP tundra ponds in Barrow, Alaska. *Numbers* and *letters* correspond to sites names assigned to the ponds in the 1970s; several of these ponds were re-visited in this study

Recently, air temperatures in the Barrow region have increased by 0.7°C per decade (Hobbie et al. 1999), and this has likely led to increased water temperatures. However, establishing a direct relationship between air and water temperatures is complicated by wind, depth, ice cover, and other physical processes that determine water temperatures in water bodies (Livingstone and Lotter 1998; Livingstone and Dokulil 2001). Warmer temperatures may impact arctic ponds through a variety of factors, including reduced pond area (Smol and Douglas 2007a), increased primary production (Michelutti et al. 2005), and increased nutrient and DOC levels (Hobbie et al. 1999, Schindler and Smol 2006). The IBP pond studies from the 1970s provide a baseline of temperature data, against which more recently acquired data can be compared. Despite a large data gap between the IBP study of the early 1970s, and more recent data collected in the twenty-first century, these data represent a valuable starting point for examining changes in freshwater temperatures in the Arctic.

This article represents one of the first analyses of the physical, chemical, and biological characteristics of the Barrow IBP tundra ponds since the 1970s. Given the prevalence of tundra ponds on the Arctic landscape, documenting their response to warming is important to understanding regional carbon and energy balance, energy flow, and biodiversity. The IBP ponds and their historic data represent a valuable and untapped resource for studying the impact of global change on aquatic environments at northern latitudes.

The goals of this study are to present an initial look at how the physical, chemical, and biological characteristics of the Barrow IBP tundra ponds have changed since the 1970s. In particular, we present data on water temperature, changes in nutrient chemistry, phytoplankton biomass, and

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some initial observations of macroinvertebrate community change.

MATERIALS AND METHODS

Water Temperature

Water temperatures were monitored in IBP Pond C during 1971, 1972, and 1973, from shortly after pond thaw through the third week of August each year. A telethermometer placed on the pond sediment at approximately 20–30 cm water depth recorded sediment-surface temperatures hourly on a potentiometric recorder (Stanley 1974). During 2007, 2008, and 2009, Hobo Pro® waterproof temperature loggers collected hourly temperatures from the same location in Pond C, year-round beginning on 13 June 2007. Daily temperature averages, maxima, and standard deviations were summarized into weekly averages for each year, which were then sorted and averaged by "early" years (i.e., 1971–1973) and "late" years (i.e., 2007–2009). We present only data from weeks for which there were paired data for both the early- and late-years, which was the 11-week period beginning in week 25 of the year and extending through week 35, roughly corresponding to mid-June through mid-August.

In order to test for differences in the pond's temperatures in the 1971–1973 versus 2007–2009, we regressed the weekly response variables for the late years versus those of the early years, using as a null hypothesis both an intercept equal to zero and a slope equal to unity. We also generated time-series graphs of these data and fit a second-order polynomial line through the temperature by week data to account for the seasonal amplitude of temperatures during the season in order to visualize seasonal differences between the early and the late years. We used an F test for equality of variance between residuals from the polynomial model, and residuals from a null model that the best estimate for temperatures was the simple average over the ice-free season. This test is analogous to the F statistic generated automatically by software packages as output for a linear regression. We did the calculations manually since we used a piece-wise nonlinear function (i.e., polynomial trends were fit separately to the EARLY and LATE periods) to model temperature against time.

Water Chemistry and Algal Biomass

While many nutrient chemistry and algal data were collected from the IBP tundra ponds in the early 1970s, for the purposes of this study we are comparing 3 years of data collected from IBP Ponds B, C, and E (Fig. 2) during the months of August 1970, 1971, and 1972, to 3 years of data collected from the same ponds in August 2008, 2009, and 2010. During the 1970s, a total of 9–12 samples were collected per pond, while between 6 and 7 samples were collected per pond in 2008–2010.

Nutrient chemistry of water was analyzed using standard methods (American Public Health Association 1998) that best reflected methods utilized during the IBP (Hobbie 1980). Nitrate-nitrogen was determined by cadmium reduction; ammonia by the phenate method; total phosphorus by ascorbic acid method following persulfate digestion; soluble reactive phosphorus by the ascorbic acid method; and, silica by the heteropoly blue method. Phytoplankton chlorophyll *a* was measured after extraction in 90% acetone and concentrations estimated according to Strickland and Parsons (1972). Concentrations were compared using a t test, with data log-transformed to meet the assumption of normality.

Macroinvertebrates

Macroinvertebrate studies during the IBP years lacked taxonomic resolution, but more intensive work on benthos in these same ponds was conducted in 1975–1977 (Butler 1980a, b, 1982a, b; Butler et al. 1980). Butler et al. (1980) provided a tentative list of macroinvertebrate taxa known from the IBP ponds, as of 1977. That faunal list was based on qualitative and quantitative sampling of larger (>1 mm length) aquatic invertebrates, mostly in Ponds E, J, and G (Fig. 2). Emergence of aquatic insects was monitored continuously for several weeks in Pond J, providing adult and pupal material that permitted species-level identification of many insects, including the numerically dominant Chironomidae. During 2007–2010, aquatic macroinvertebrates were again surveyed both quantitatively and qualitatively. Insect emergence was monitored in 2009–2010 to assess the phenology of insect emergence. Instead of the quantitative traps used in 1975–1977, recent emergence monitoring involved standardized dipnet sweeps along the leeward shore of Ponds C and J at 3-day intervals, again providing adult and pupal insect specimens. While the collection methods between the two study periods were slightly different, and approximately four times as many organisms were collected in 2009–2010 than during the studies by Butler et al. (1980), these data still represent an invaluable opportunity to compare species presence–absence and relative abundances. In particular, abundance of all chironomid taxa comprising >0.5% of specimens collected in both 1975–1977 and 2009–2010 was determined and used to rank the taxa from most (1) to least (20) abundant.

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RESULTS

If temperatures in Pond C were comparable between the two study periods, weekly data from "late" years (2007–2009) should show a 1:1 relationship with corresponding values from "early" years (1971–1973). We regressed weekly summaries of daily mean and maximum temperatures for the late years against corresponding values for the early years (Fig. 3). Slopes were lower than unity and intercepts greater than zero (based on 95% confidence intervals as a measure of significance). The occurrence of higher mean and maximum temperatures during the late years (2007–2009) relative to the early years (1971–1973) was most pronounced during the beginning (weeks 25 and 26) and end (weeks 31–35) of the open-water season (Fig. 3), whereas mid-summer weeks (notably 27, 28, and 30) plotted closer to the 1:1 line (Fig. 3a, b). Week 29 reflected unexpectedly cool weather during mid-July of 1971 and 1973 (Hobbie 1980).

A second-order polynomial trend line was fit through both temperature summary variables, separately for the early- and late-year data sets, to illustrate the main trends in these time series (Fig. 3d, e). A polynomial model accounted for significantly more variance than a seasonal average for all of the temperature measures, including the daily average ($F_{21,21} = 0.344$, $p = 0.018$), the daily maximum ($F_{21,21} = 0.315$, $p = 0.011$), and the daily standard deviation ($F_{21,21} = 0.259$, $p = 0.003$). These graphs support the statistical analysis of early versus late year summaries (linear regressions), in that trends in both average and maximum pond temperatures are most different during the earliest (weeks 25 and 26) and latest (weeks 34 and 35) parts of the season but tend to become more similar during the middle of the growing season (Fig. 3d, e). We also found that weekly averages of the daily maximum temperatures corresponded well with weekly averages of the daily mean temperatures, indicating one is a good predictor of the other. Weekly average of the daily maximum temperatures increased at approximately 86% of the rate in the daily mean temperature ($y = 1.21 + 0.86x$; $R^2 = 0.967$).

The variability in daily temperatures as measured by the standard deviation was higher during the beginning (weeks 25 and 26) and end (weeks 34 and 35) of the season for the 2007–2009 data as compared to 1971–1973 but tended to be lower during the middle of the thaw season (weeks 27–30) (Fig. 3c, f).

Data indicate that the IBP ponds in 2008–2010 had significantly higher ammonia, nitrate, and soluble reactive phosphorus concentrations (t tests, $p < 0.01$), as well as marginally higher phytoplankton biomass ($p < 0.10$) than the same ponds in the early 1970s (Fig. 4). There were no

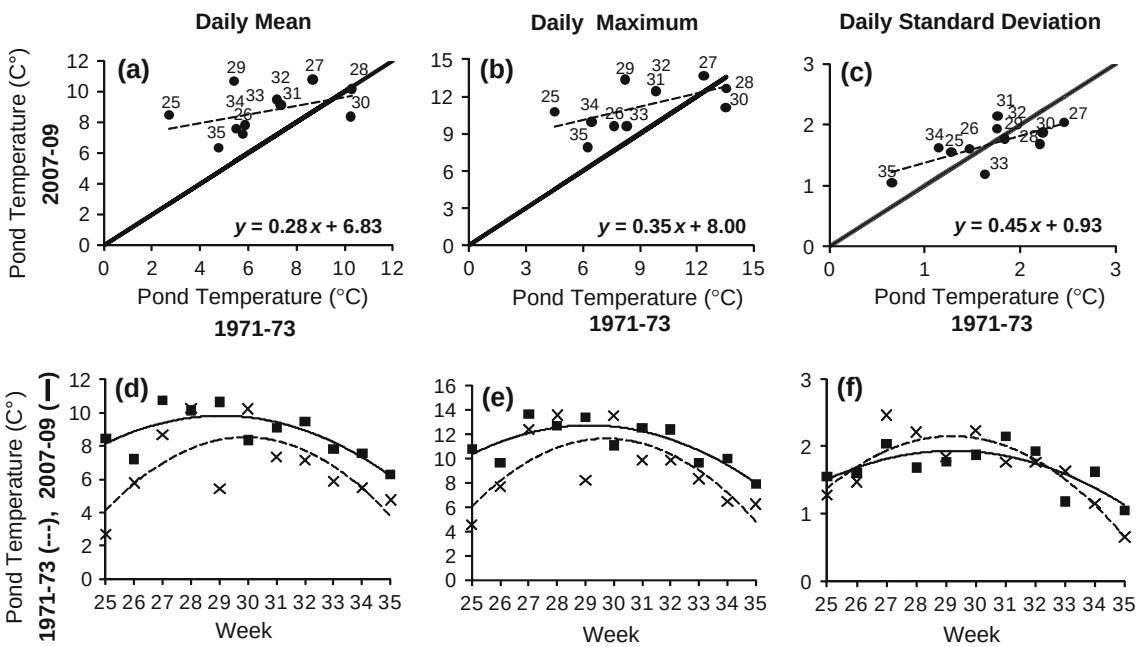

Fig. 3 Comparison of IBP Pond B and/or C temperatures summarized by week of the year. For plots **a–c**, the numbers associated with points indicate the week of the year, the *dark black line* indicates the 1:1 relationships, and the *dashed line* indicates the best fit line from least squares regression with the equation given inset. For plots **d–f**, *lines* represent a fit for a second-order polynomial function justified by our assumption of seasonal rise and decline of average annual temperatures. For model fits, the coefficient of determinations ranged from 0.56 to 0

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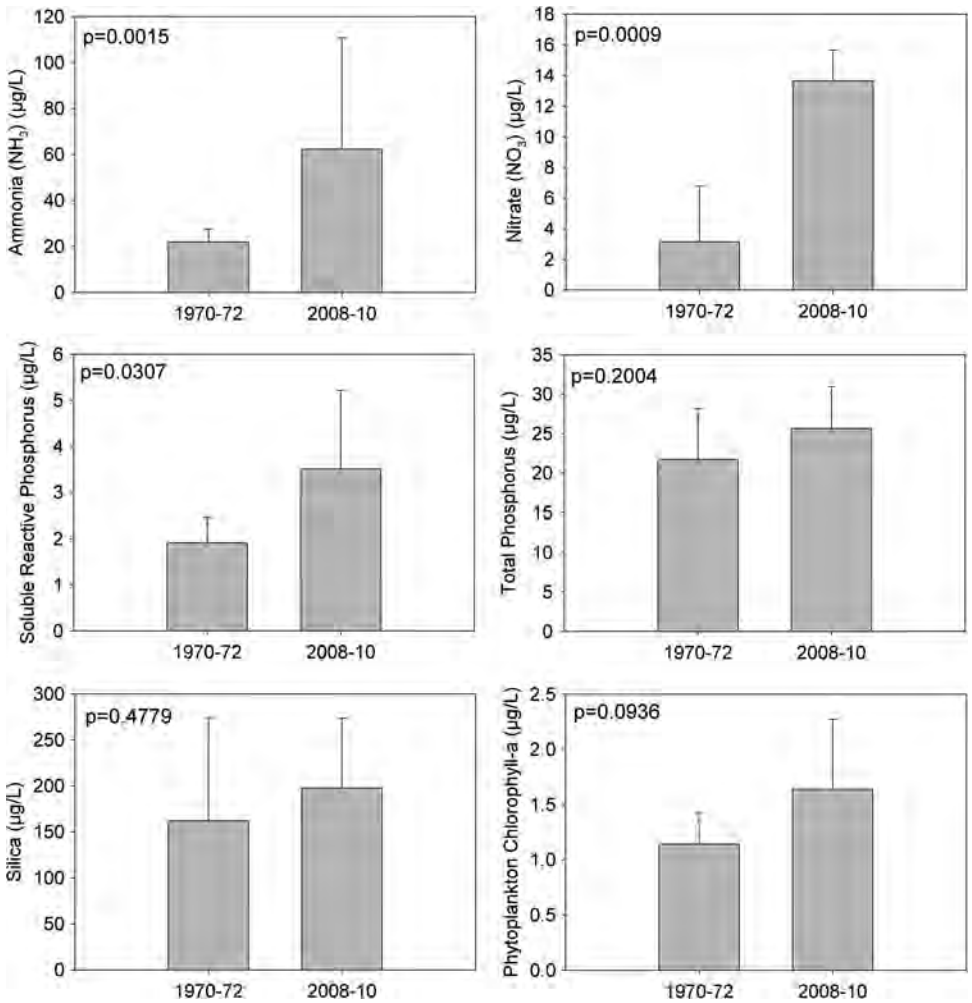

Fig. 4 Comparison of nutrients and phytoplankton algal biomass at IBP ponds in August 1970–1972 as compared to August 2008–2010. Means (±1SD) are from IBP Ponds B, C, and E. Data: Ponds B, C, E in August, only ponds sampled completely at least 2 years per study period

significant differences in total phosphorus or silica concentrations.

Macroinvertebrate communities in the IBP ponds have changed little over the past four decades. All the larger benthic macroinvertebrates reported by Butler et al. (1980) were still common in recent samples, including two trichopteran species: a limnephilid (*Asynarchus* sp.) and a brachycentrid (*Micrasema scissum*) reported but erroneously omitted from a table in that report. Of 27 insect genera found during sampling in the 1970s, 22 genera belonged to the dipteran family Chironomidae. The six highest-ranked chironomid taxa comprised 82 and 86% of total specimens collected in the early and recent studies, respectively, and five of these top taxa were identical in both data sets (Table 1). *Paratanytarsus penicillatus* was the most abundant chironomid in both surveys (>30% relative abundance), followed by two *Tanytarsus* species, and tiny midges in the genus *Corynoneura* that probably represent several species. In general, chironomids with high abundance rankings in the 1970s data were also abundant in the recent samples, although the largest changes in relative abundance occurred in the most common taxa with *Tanytarsus aquavolans* declining by 10% and *Tanytarsus nearticus* increasing by 17%. *Procladius vesus*, which was common in the 1970s, had the largest decline in rank abundance, from 5th most abundant in the 1970s to 20th in 2009–2010.

Rarer macroinvertebrate taxa (<0.5% of specimens collected) tended to remain rare, although some changed substantially in relative rank. Three such rare taxa, *Chironomus riparius*, *Cricotopus* sp3, and *Limnophyes* sp., increased substantially between the earlier and later study periods, while three of the more abundant species in the 1970s collections (*Procladius vesus*, *Cricotopus tibialis*, and *Cryptochironomus* sp.) were still present but rarer (<0.5%) in the 2009–2010 samples. *Dicrotendipes* sp., present but rare in the 1970s, was not found in 2009–2010. Two new taxa appeared in the Barrow ponds recently: a second, larger *Paratanytarus* species was found at low density in 2010, while a new tanypod species in the genus *Conchapelopia* appeared in both Ponds C and J, as well as other ponds in the Barrow area, in 2009 and in 2010.

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Table 1 Benthic macroinvertebrates collected from tundra ponds near Barrow, AK during 1975–1977 and 2007–2009; taxonomy updated from Table 7-1 in Butler et al. (1980). *P* taxon present, *A* taxon not found. Relative and ranked percent abundances are given for chironomid taxa comprising >0.5% of specimens collected in each data set, based on 2043 adults from emergence trapping (1976–1977, Pond J) and 8660 pupal exuviae from PE sweeps (2009–2010, Ponds C&J)

		Taxon	1976–1977	2009–2010
Turbellaria		Unidentified	P	P
Annelida	Oligochaeta			
	Naididae	*Tubifex* sp.	P	P
	Propappidae	*Propappus* sp.	P	P
Hydracarina	Lebertiidae	*Lebertia* sp.	P	P
Gastropoda	Physidae	*Physa* sp.	P	P
Insecta	Plecoptera	*Nemoura arctica*	P	P
	Trichoptera			
	Brachycentridae	*Micrasema scissum*	P	P
	Limnephilidae	*Asynarchus* sp.	P	P
	Coleoptera			
	Dytiscidae	*Agabus* sp.	P	P
		Hydroporus sp.	P	P
	Diptera			
	Chironomidae		Ranked occurrence	
	Podonominae	*Trichotanypus alaskensis*	9 (2.3%)	10 (1.1%)
	Tanypodinae			
	Macropelopini	*Derotanypus aclines*	P	P
		Derotanypus alaskensis	15 (0.7%)	16 (0.6%)
		Procladius prolongatus	14 (1.2%)	15 (0.7%)
		Procladius vesus	5 (4.6%)	P
	Pentaneurini	*Conchapelopia* sp.	A	13(0.9%)
	Chironominae			
	Chironomini	*Chironomus prior*	12 (1.2%)	12 (0.9%)
		Chironomus tardus	7 (3.7%)	14 (0.8%)
		Chironomus riparius	P	9 (1.3%)
		Chironomus sp4	P	P
		Cryptochironomus sp.	11 (1.3%)	P
		Dicrotendipes sp.	P	A
		Stictochironomus sp.	17 (0.5%)	P
	Tanytarsini	*Cladotanytarsus* sp.	8 (2.9%)	17 (0.6%)
		Constempellina sp.	6 (4.4%)	6 (7.6%)
		Paratanytarsus penicillatus	1 (30.3%)	1 (30.9%)
		Paratanytarsus sp2	A	P
		Tanytarsus aquavolans	3 (10.1%)	2 (21.1%)
		Tanytarsus nearcticus	2 (25.6%)	4 (8.7%)
	Orthocladiinae			
	Orthocladini	*Cricotopus tibialis*	10 (1.4%)	18 (0.4%)
		Cricotopus nr *perniger*	16 (0.5%)	7 (2.3%)
		Cricotopus sp3	P	11 (1.1%)
		Psectrocladius spp.	13 (1.2%)	5 (7.7%)
		Orthocladius spp.	P	P
	Metriocnemini	*Bryophenocladius* sp.	P	P
		Corynoneura spp.	4 (7.4%)	3 (10.5%)
		Lapposmittia sp.	P	P
		Limnophyes sp.	P	8 (1.4%)
		Mesosmittia sp.	P	P
		Metriocnemus spp.	P	P
		Parakiefferiella spp.	P	P

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Differences in the rank abundance or the presence/absence of rarer taxa may reflect increased sampling effort during 2007–2010, when over 8660 specimens were collected versus 2043 specimens in 1976–1977.

DISCUSSION

In summary, these data suggest that the IBP sites have undergone a change in their physical, chemical, and biological characteristics since the 1970s. While these data represent only a snapshot of the conditions found in the early 1970s and 2007–2010, each analysis was performed on at least 3 years of data, thus minimizing the impacts of any potential outliers. In particular, we observed a change in thermal regime, with higher daily mean and maximum pond temperatures relative to available earlier data. These findings are in agreement with much of the work drawing more indirect conclusions based on paleolimnological data (Michelutti et al. 2005; Smol and Douglas 2007b) and are consistent with overall global findings of climate change, and in particular, the arctic amplification. The data also indicate an effect of warming on seasonality, with the greatest differences in warming observed early and late in the season. This supports suggestions by Rouse et al. (1997) that a warming Arctic may lead to lengthened growing seasons and reduced ice cover in aquatic ecosystems. In Barrow, snow melt is occurring earlier than it was in the mid-1960s (Stone et al. 2002). Since many ecological rates are exponentially dependent upon temperature, even small changes in temperatures and growing season can impact ecological processes dramatically.

We also found that the IBP ponds have also become more nutrient-rich since the 1970s, indicating probable temperature-related changes to this ecosystem over the past 40 years. Several studies have indicated that warming permafrost may be releasing nutrients and DOC into Arctic freshwater ecosystems (Wrona et al. 2006). For example, at Toolik Lake, AK, elevated phosphorus in a stream was linked to the mining of gravel for road construction resulting in an abrupt deepening of the active (thawed) layer of soil and increased weathering (Hobbie et al. 1999). And, with degradation of near-surface permafrost, arctic riverine watersheds are exporting more organic and inorganic compounds into the Arctic Ocean (Frey and McClelland 2009).

Increases in nitrogen concentrations in the tundra ponds may also be a result of atmospheric deposition. Nitrogen deposition from the atmosphere has likely doubled in the Arctic since the 1950s (Mayewski et al. 1986; Goto-Azuma and Koerner 2001), and long-range transport of these pollutants has been recorded in Barrow (Jaffe et al. 1991). This deposition of nitrogen may have important implications for aquatic and terrestrial ecosystem structure and function (Baron et al. 2000), including primary production.

The coincident observed increases in pond temperatures and nutrient concentrations at the IBP ponds are likely contributing to increases in algal primary production. Experimental studies at the IBP ponds in the 1970s support these trends, as researchers suggested that an increase in ambient temperatures (Stanley and Daley 1976) or phosphorus availability (Alexander et al. 1980) could lead to increased algal biomass and production. Nutrients and DOC released from thawing permafrost (Frey and Smith 2005) can drive both autotrophic production and heterotrophic bacterial production. Indeed, we did see a marginal increase in phytoplankton biomass coincident with this increase in nutrients. The implications of these changes to the regional carbon balance are uncertain. If increased algal biomass is not coincident with increases in respiration, then net ecosystem production may tend toward the positive, and thus the ponds may store carbon. However, net heterotrophy has also been observed in nutrient-poor aquatic ecosystems (Algesten et al. 2004; Cole et al. 2007), particularly in small, shallow lakes, and this may lead to carbon efflux from the system, despite an increase in autotrophic production. Given both seasonal and year-to-year variation in limnological variables, a more thorough study is required to support these trends and fully understand their significance.

Aquatic macrophyte biomass also appears to have increased in the Barrow ponds. The aquatic plants *Carex aquatilis* and *Arctophila fulva* dominated primary production in the IBP ponds in the 1970s (Alexander et al. 1980) where they were more productive than in terrestrial sites. Repeat photography has provided anecdotal evidence that dominant species of aquatic vegetation such as *Carex aquatilis* have increased in biomass since the 1970s (Fig. 5). Related studies at sites surrounding the Barrow IBP tundra ponds have also found an increase in graminoid cover in wet tundra areas (Tweedie, unpubl. data). Experiments have indicated that phosphorus limitation plays a more important role than temperature in limiting macrophyte biomass and production in wet sedge tundra (Shaver et al. 1998). However, the causes and consequences of increased macrophyte biomass at the IBP ponds are unclear and require study to provide a more complete understanding of climate-related changes in primary production in aquatic ecosystems in the Arctic.

The macroinvertebrate fauna of the IBP ponds at Barrow has remained relatively stable despite the warming observed to date; however, comparisons to macroinvertebrate communities found in warmer tundra ponds not far inland on the Arctic Coastal Plain suggests that substantial change could occur with increased warming. Cold stenothermic insects like the stonefly *Nemoura arctica* and the podonomid midge

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Fig. 5 Photo of IBP Pond B in 1973 (*top*) and 2010 (*bottom*). Metal poles in the bottom photo remain from the 1970s; however, the wooden structures are not in the same location. Note the increased development on the horizon in 2010 and the increased cover by *Carex aquatilis*, notably in the upper right section of the pond. Photos by John Hobbie (1973) and Vanessa Lougheed (2010)

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Trichotanypus alaskensis are still abundant components of the Barrow pond community. These species are absent, however, from ponds at Olak (50 km inland, southeast of Teshekpuk Lake) and near Atqasuk, AK (100 km south of Barrow) (Butler, unpubl. data), where maximum temperatures are higher than in the IBP ponds. This suggests that further warming at Barrow may lead to elimination of these and other taxa through oxygen stress at higher temperatures. Conversely, the predatory midge *Conchapelopia* appears to be a new and relatively abundant addition to the pond fauna at Barrow. This midge has recently been collected from ponds at Atqasuk and Olak, where the pond invertebrate community at the species level differs substantially from that seen at Barrow. Atqasuk ponds host additional predatory invertebrates such as phryganeid caddisflies and larger dytiscid beetles, species that may invade coastal tundra ponds under future climatic scenarios. Further warming of coastal tundra ponds may thus alter the invertebrate community both directly, via elimination of stenothermic taxa and by thermal enhancement of larval insect growth rates, as well as indirectly through altered food-web interactions. The importance of this invertebrate fauna as a food resource for arctic-breeding birds, including passerines, shorebirds, and threatened species like Spectacled and Stellar's Eiders, may also be altered as arctic warming progresses.

While the IBP ponds represent a valuable source of historic data, the site is currently threatened by expansion of the village of Barrow, AK. The IBP ponds, once relatively isolated in the landscape, are now being encroached upon by housing development associated with local population growth at Barrow (Fig. 5). Greater protection and continued monitoring of these invaluable sites will enhance efforts to understand the implications of climate change on Arctic freshwater ecosystems.

Acknowledgments This project was funded in part by grants from the National Science Foundation Polar Programs (NSF-ARC-0909502) to VLL, and the National Fish & Wildlife Foundation, Alaska Fish & Wildlife Fund, to MGB. Special thanks to Craig Tweedie, Gilda Victorino, Francisco Reyes, Christian Andresen, Gabriela Contreras, Christina Hernandez, and Shane Braegelman for field and lab assistance. We thank the Barrow Area Science Consortium (BASC) for logistics support at Barrow. Historic reports and data were provided by Vera Alexander and Dick Prentki.

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