



Arctic LCC Project Summary

1. PROJECT INFORMATION

Title:	Changing Seasonality of Invertebrate Food Resources across the Arctic Coastal Plain
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Key words	insect emergence, tundra ponds, phenology, climate change, arctic warming, Chironomidae, thermal time, Cox proportional hazard model

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ABSTRACT

We assessed change in the seasonal timing of insect emergence from tundra ponds near Barrow, Alaska over a four-decade timespan, and explored factors that regulate this significant ecological phenomenon. The early-summer pulse of adult insects emerging from myriad tundra ponds on the Arctic Coastal Plain is an annual event historically coincident with resource demand by tundra-nesting avian consumers. Asymmetrical changes in the seasonal timing of prey availability and consumer needs may impact arctic-breeding shorebirds, eiders, and passerines. We have found evidence of change in the thermal behavior of these arctic wetlands, along with a shift in the phenology of emerging pond insects. Relative to the 1970s, tundra ponds at Barrow now thaw about one week earlier, average 2°C warmer, and show a 30% increase in growing degree days. Analyzing insect emergence data collected during 2009-2012 relative to similar data from the 1970s, we document a significant shift in the timing of insect emergence over this four-decade span. Composition of the invertebrate community has changed little over the decades, with the same species of chironomid midges dominating numbers and biomass in these ponds. Treating midge emergence as a ‘time-to-event phenomenon’, we used proportional hazard models to test for differences in the seasonal timing of adult insect emergence between our historic and recent data sets. For all species pooled, we found a significant increase in the daily likelihood of adult emergence during 2009-2011 relative to the 1970s, reflecting a shift toward emergence at earlier dates in the recent years. Analyzing individual species, we detected significant shifts toward earlier seasonal emergence in recent years for 14 out of 16 abundant taxa. We explored mechanisms potentially regulating emergence timing at the species level, toward development of models for predicting insect response to further climate change in this landscape. Date of pond thaw each spring explains much of the variation in overall emergence timing, and individual midge species show fairly consistent positions in the temporal sequence within any pond or year. Examining pre-emergence development of midge populations relative to hourly pond temperatures, we found that models based on an exponential rate response were more suitable than traditional “thermal-time” models that assume a linear response of developmental rate to temperature. We identify key biological and environmental variables needed to predict how the seasonal timing of insect emergence may respond to further warming of this arctic habitat.

2. PROJECT OVERVIEW

a. Briefly (4-5 sentences) describe both the research purpose and the underlying need for this research.

This research program has two dimensions, both bearing on food web support for avian species breeding on the tundra of Alaska's Arctic Coastal Plain (ACP). Our goals are (1) to better understand how climate regulates the seasonal timing of adult insect emergence from tundra ponds, and (2) to characterize existing variation in the abundance, biomass, and size structure of pond invertebrate communities at coastal (Barrow) versus inland (Atkasuk) sites on the ACP. ALCC supported work during 2011-12 focused primarily on insect emergence phenologies (Dimension 1), given ALCC interest in a potential mismatch between the timing of adult insect availability and the seasonal resource needs of tundra-breeding birds. Our efforts included continued monitoring of pond temperatures and insect emergence, experiments to improve our understanding of how insect emergence timing responds to water temperature, and methods development in support of avian food monitoring by the Arctic Shorebird Demographic Network (ASDN).

b. List the objective(s) of the project, exactly as described in your Statement of Work.

The primary objective of ALCC-supported work in 2011-2012 was to provide information helpful in predicting the seasonal timing of adult insect emergence from tundra ponds. Related work by D. Rinella, in conjunction with the ASDN, targets development of models for predicting the seasonality of emerging insect biomass under different climate scenarios. We have also continued with NFWF-supported work on the composition and size structure of aquatic communities under different thermal regimes, and temperature effects on life-history events relevant to the timing of insect emergence.

3. PROJECT SUMMARY

The work described here is part of a broader research program underway since 2009, supported by grants from the Alaska Fish & Wildlife Fund/National Fish & Wildlife Foundation, as well as the Arctic Landscape Conservation Cooperative. ALCC provided funding during 2011-12. Here we report on the portion of this work focused on understanding the seasonal timing of insect emergence in tundra ponds at Barrow, AK. We have analyzed data collected during 2009-2012 relative to similar data from the 1970s. We document a significant shift in the timing of chironomid (midge) emergence over this four-decade span. This change coincides with a one-week advance in the mean date of spring thaw and a 2°C increase in summer pond temperatures over the same time period. The changes we report are evident in the midge community as a whole, and for most individual species we have assessed. We look at how this altered phenology may be explained in terms of presumed relationships between larval and pupal development and the tundra pond thermal environment. Our findings clarify directions for further research leading to predictive models of insect community response in a changing thermal environment, summarized in **Section 5** at the end of this report.

Background and Introduction

Insect emergence in most ponds at Barrow, Alaska is comprised of a dozen or more relatively abundant chironomid midge species, with non-chironomid insects like beetles, stoneflies, and caddis flies quantitatively rare, although substantially larger (Butler et al. 1980, Lougheed et al. 2011). Though small in size, chironomids are ubiquitous and abundant, and are consumed by all insectivorous tundra-breeding birds. Emergence of adult midges makes these insects available to most shorebirds, passerines, and ducklings, including species unable to access the aquatic larvae in pond sediments. Thus we are

interested in the timing of insect emergence in relation to avian demand for prey resources. We seek to understand how this ecological event (midge emergence) is regulated, and how chironomid emergence phenologies may change with climatic warming.

Pond temperature data we collected during 2007-09 indicate warming of tundra ponds near Barrow relative to historical pond temperatures measured in the early 1970s (Lougheed et al. 2011, McEwen & Butler in review). Average water temperature over a ten-week period in late June, July, and August has increased by 2°C, with the greatest warming occurring at the beginning of summer (Fig. 1) – the time when insect larvae are maturing and pupating prior to adult emergence. In addition, the date of spring snow melt at Barrow has been trending earlier since 1941, but at an increasing rate since 1977 (Stone et al. 2005). Earlier and warmer summers may accelerate emergence of adult insects from tundra soils and ponds, potentially desynchronizing avian breeding periods from peak availability of important prey populations.

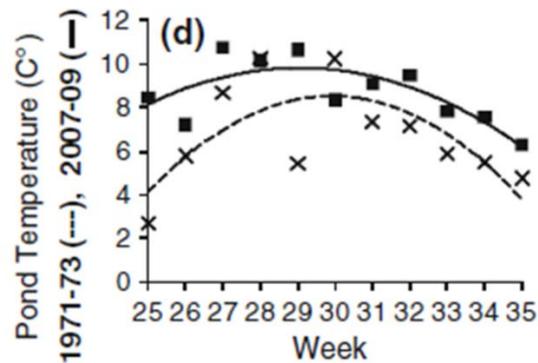


Figure 1. Comparison of mean daily temperatures in IBP Pond B and/or C during the recent decade vs. similar data collected during the IBP pond studies at Barrow nearly four decades earlier. Values are summarized by week of the year for ten weeks from mid-June through August. Lines represent fit of a second-order polynomial function to each data series. (Fig. 3d from Lougheed et al. 2011).

The seasonal pulse of overall insect emergence is an important aspect of prey availability for avian consumers. We don't yet know the relative importance of different members of the tundra invertebrate community to invertivorous birds, but aquatic insects are undoubtedly important and their emergence patterns may serve as a model for the terrestrial insect community. We can monitor the whole emerging insect community in multiple tundra ponds with fairly simple methods to characterize the phenology of this overall event. By also studying the dynamics of some of the important prey populations within this community, we can better test for potential climate-related changes while we investigate how emergence timing is regulated.

Chironomid emergence from a given pond generally forms a seasonal pulse spanning a period of several weeks, as documented for Pond J at Barrow via daily sampling in 1977 (Fig. 2 - upper panel). This overall pattern is comprised of a series of very synchronous, species-specific pulses, as illustrated for seven of the chironomid species emerging from Pond J in 1977 (Fig. 2 – lower panel; data from Butler 1980). In this example the highly abundant species *Paratanytarsus penicillatus* dominates the overall community pattern. This illustrates how variation in species composition from pond to pond, or from year to year, can influence the overall pattern of emergence observed in any pond/year.

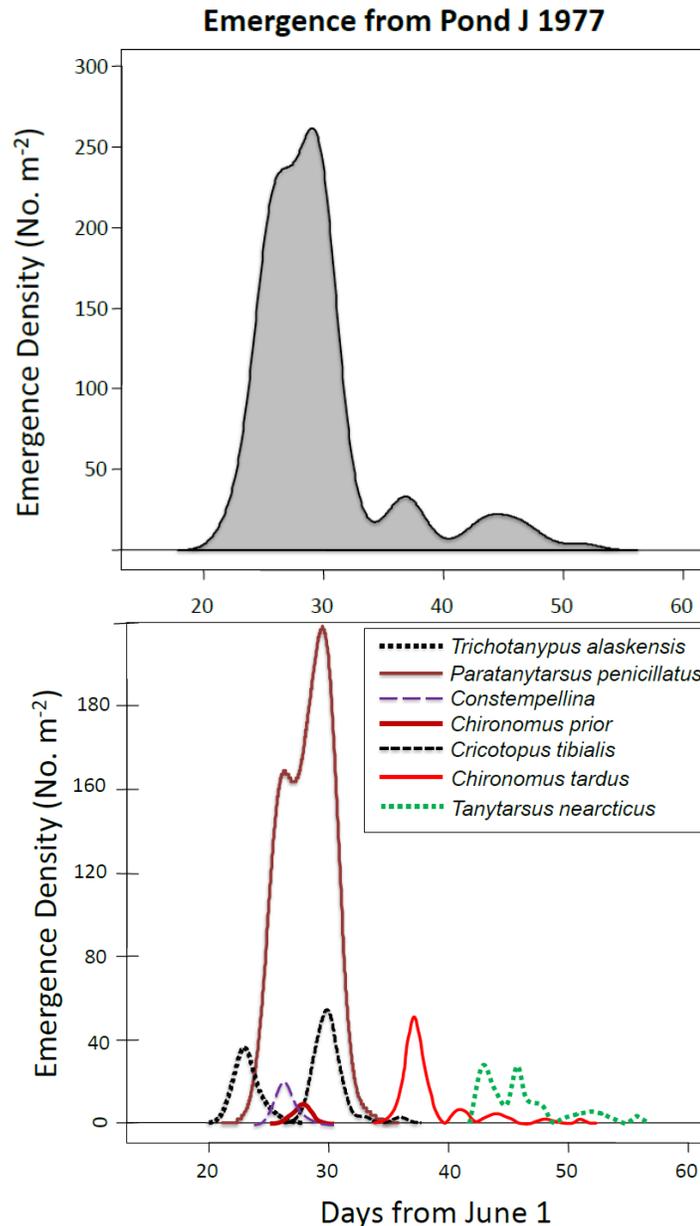


Figure 2. Seasonal emergence of Chironomidae from Pond J at Barrow during 1977. Upper panel shows total density of midges trapped; lower panel shows temporal distribution of the seven most-abundant contributing species.

ALCC funding during 2011-12 allowed us to further advance our understanding of how the seasonal timing of insect emergence in Barrow tundra ponds is regulated by climate. We continued our monitoring of pond temperatures at Barrow and the inland village of Atqasuk throughout 2011 and 2012. We monitored insect (primarily chironomid) emergence in eight Barrow ponds at 2-day (occasionally 3-day) intervals in 2011, from pond thaw in early June through mid-July. We simultaneously compared the standard dip-net sampling procedure we've used since 2009 (the method adopted by ASDN in 2011 for monitoring aquatic food resources) to the quantitative trapping method used by Butler (1980) to collect historic data on insect emergence phenologies during 1975-77. During a 12-day visit (21 June – 2 July) in 2012, we downloaded temperature loggers in Barrow & Atqasuk ponds and monitored emergence at Barrow during the period of peak insect emergence (through 2 July). Some additional emergence samples were collected into mid-July in 2012 with the assistance of students from the University of Texas at El Paso working on other studies. We also made a 3-day sampling trip to

Barrow in mid-October of 2012. During that visit we downloaded loggers to retrieve late summer temperatures from the 2012 season, and sampled larval populations for life history analyses.

Results

We now have recent chironomid emergence data for five years (2009-2012), and samples from 2013 are being processed. We can compare these recent observations to historic records of midge emergence phenology in Barrow tundra ponds from four years in the 1970s: unpublished 1972 data (collected by D. M. Bierle as part of the IBP Tundra Biome Project and provided to MGB by the late J.W. Sublette) and the 1975-77 data collected by MGB (Butler 1980a,b).

Influence of Thaw Date on Midge Emergence Timing:

Our first approach is to compare the onset and duration of the major pulse of midge emergence between the two decades (1970s vs. 2009-13). We limit this initial comparison to one specific tundra pond at Barrow (Pond J) that was sampled in all eight years (Fig. 3A). We illustrate the time span corresponding to the central 80% of cumulative chironomid emergence in Fig. 3B. Emergence of 2-3 early species is typically underway by the 10% emergence threshold, while only 1 or 2 species may contribute to the last 10% of the season. Figure 3A shows that both the onset and duration of midge emergence varies widely among years – in both the historic (1970s) and recent data sets.

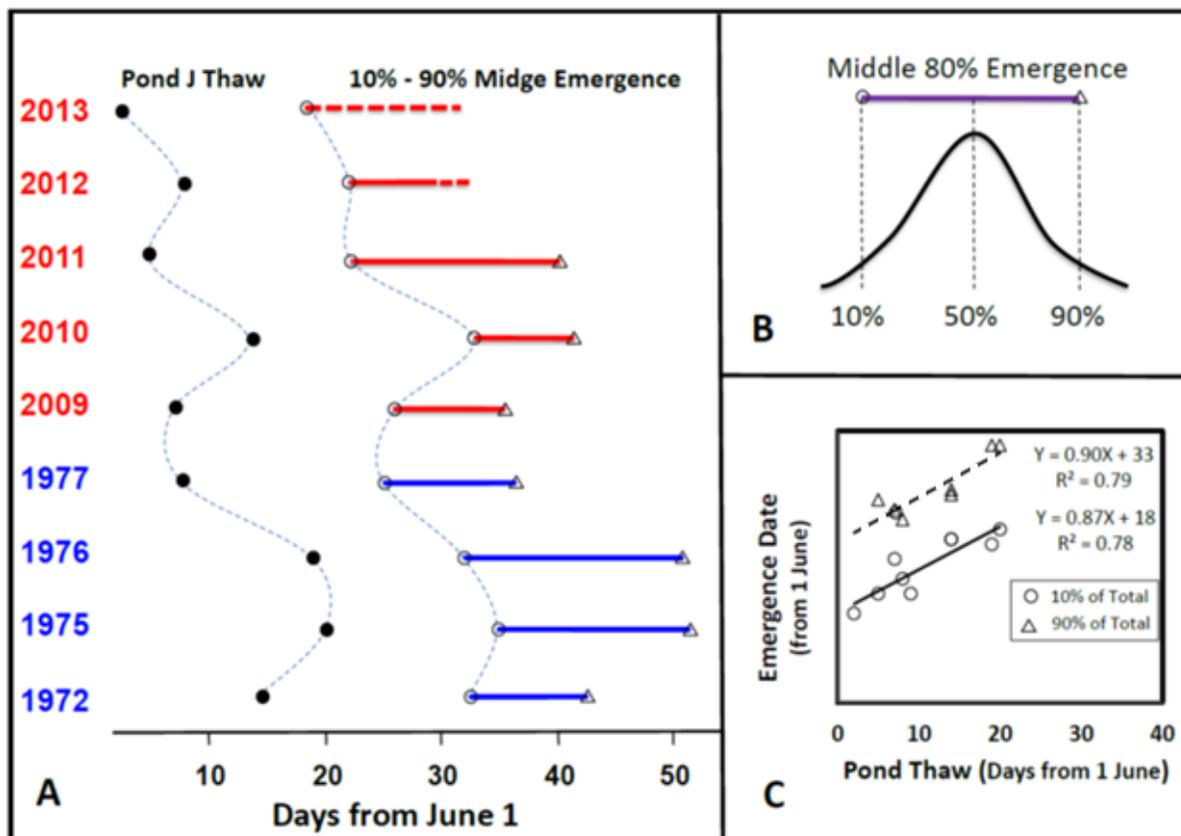


Figure 3. Seasonal timing of the middle 80% of total midge emergence from Pond J during four years in the 1970s and five years in the recent decade. A: Onset and span of this period relative to dates of thaw. B: Generalized illustration of cropping the initial and final 10% of the emergence pulse. C: Onset (10% point – circles, solid line) and end (90% point – triangles, dashed line) of main chironomid emergence pulse regressed against date of pond thaw. Late-season emergence data are unavailable for 2012; 2013 data are being processed.

We regressed both the beginning and the end of this 80% emergence pulse against the date of pond thaw each year (Fig. 3C). As a surrogate for actual pond thaw, we use snow-melt date at Barrow for each year (Stone et al. 2005, plus more recent data posted on the NOAA website <http://www.esrl.noaa.gov/gmd/grad/snomelt.html>), because direct observations of pond thaw are lacking for most years. For the five years 2008-2012, the correlation between snow-melt date and thaw date for Pond C (close by and similar to Pond J) was 0.94, making snow-melt date a useful index for addressing annual variation in thaw date for this single-pond analysis.

Both onset and end dates of the 80% emergence pulse in Pond J were highly, and equally, correlated with thaw date (Fig. 3C; $R^2 = 0.78$ and 0.79 , respectively). This suggests that most of the variation in the overall seasonal pulse of midge emergence from Pond J is due to variation in thaw date, which tracks snow-melt date. During late-thawing years at Barrow, emergence begins and ends later. In addition, we see there are both late and early thaws among the years sampled in each decade.

Superimposed on this pattern is additional potential variation due to pond-pond differences in thaw, differences in pond temperatures, and diversity in species composition. The timing of “spring thaw” in the region is likely the single best predictor of timing for the annual pulse of emerging insects. But much additional variance can result from landscape heterogeneity that causes ponds to thaw at different times, and to differ in their subsequent thermal regimes. Also, species-specific differences in life histories and physiological responses to temperature may mean that a warming climate may affect taxa in different ways. Such biological differences may produce different overall responses in communities of varying taxonomic composition. Changing environmental conditions may also lead to species replacements, which could compensate for (and potentially mask) actual biological changes.

Long-term Changes in Pond Thaw Date and Midge Emergence Timing:

If indeed thaw date is a robust predictor of overall midge emergence timing, the obvious question is “Has the timing of both pond thaw and insect emergence changed in Barrow ponds over the period in question?” Data on Barrow snow melt collected and analyzed by NOAA/ERSL scientists (R. Stone & colleagues cited above) indicate that the Barrow snow-melt date has been trending earlier for at least seven decades, with this measure of spring thaw advancing at an increasing rate since about 1977. Thus we ask whether we can detect any change in insect emergence timing with our Barrow data, a record spanning this four-decade period of rapid change in the arrival of spring. Given the variability inherent in both our biological data and in the climatic data, it is no simple task either to detect, or to rule out, such biological change.

We looked for evidence of earlier midge emergence between the two decades (1970s versus 2009-2012) by pooling all our data on emergence timing within each period. Insect emergence can be viewed as a time-to-event phenomenon, and thus can be modeled with survival analysis techniques (Bauer et al. 2008; Gienapp et al. 2005; Schaper et al. 2012). Figure 4 (upper panel) shows simple Kaplan-Meier survivorship curves for these two data sets, with both species and years pooled within each decade. At the point when 50% of annual emergence has been collected, there is a 4-day difference in the curves representing earlier (blue) and later (red) decades.

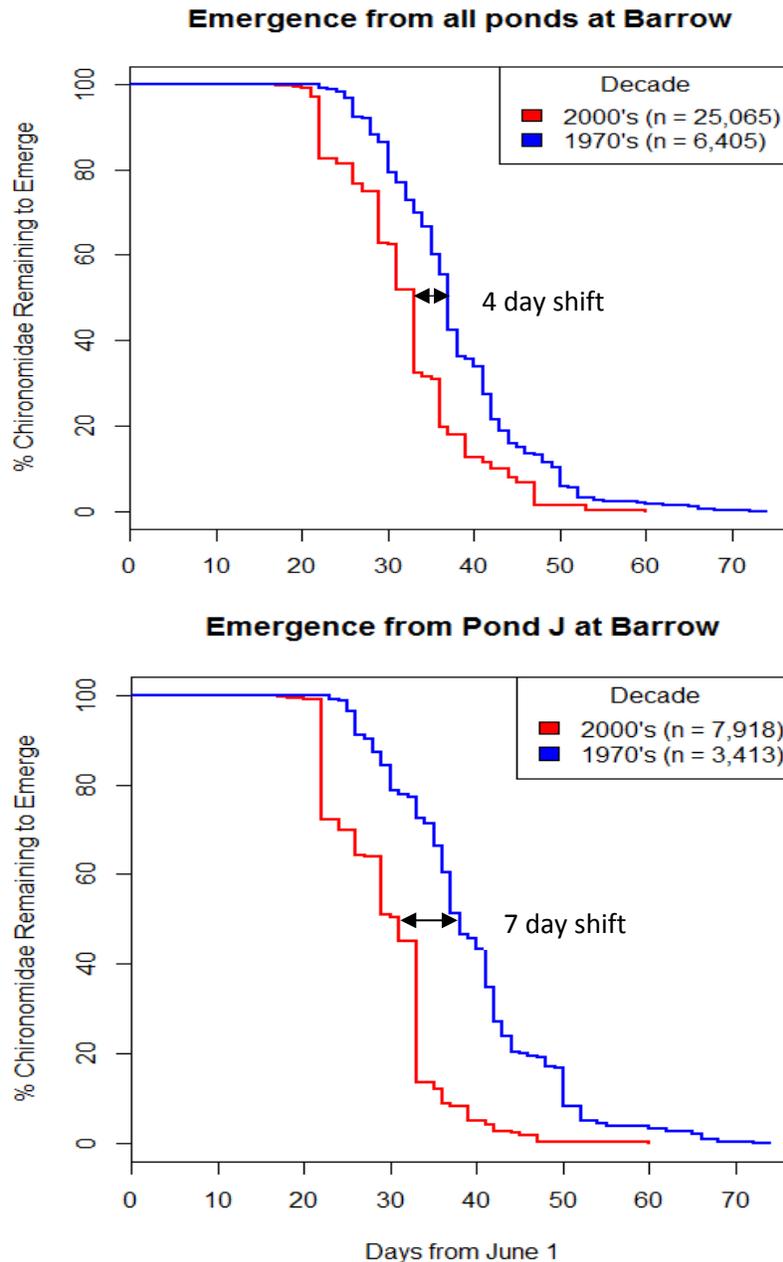


Figure 4. Survivorship curves illustrating observed insect emergence over time for all chironomid midges sampled in the two decades. Upper panel shows cumulative pooled emergence by date for all species from all ponds in each decade; lower panel shows midge emergence for Pond J only.

Our data sets were not collected from the exact same set of ponds in each decade, so differences in the nature of the ponds sampled (variations in time of thaw and subsequent thermal behavior) may influence this result, potentially masking (or inflating) the effect of “decade” on emergence timing in any one pond. We thus analyzed only the data from Pond J, which was sampled in all years in both decades (Fig. 4 - lower panel). Although sample sizes are lower, the Kaplan-Meier curves show greater separation, reflecting an even greater difference in overall emergence timing between the decades in this single pond (7 days different at mid-emergence).

Insect emergence is directly analogous to survivorship in a population, with the subjects having some probability of emerging (rather than dying) before the next census. An appropriate tool for analyzing

either phenomenon is a Cox proportional hazard (CPH) model. The model begins with an unspecified baseline hazard rate, where “hazard” is the instantaneous probability¹ of emerging before the next observation (analogous to the probability of death in survival analysis). Covariates representing additional information known about the system serve to adjust the baseline hazard rate (Therneau 2012) by informing the model if emergence is more likely or less likely to occur, or if no change in the hazard rate is expected given the additional information. Our models include the term ‘decade’ as a fixed effect, and if the model is significant we can see the relative magnitude of a difference between the two decades by looking at the model’s “effect size”. Effect size is essentially an “odds ratio”, a proportional comparison of the log-likelihood values representing emergence hazards modeled for the two distributions (two decades). An effect size of 1.0 would indicate *no difference* in hazard attributable to the fixed effect. In a mixed-effects CPH model, one or more covariates (such as ‘pond’) can be entered as random effects. Inclusion of a significant covariate can adjust the model for influence of that variable (*e.g.* pond identity) on emergence behavior that might otherwise skew the overall result.

Our most basic CPH model compares pooled species data from all ponds sampled in each decade; it produced a very highly significant difference in the daily likelihood of midge emergence between the two decades, with an effect size of 1.81 (Table 1). This means that in the 2009-12 data, the “daily risk” of a midge emerging was nearly twice as high as in the 1970s. That higher daily emergence risk reflects a shift toward significantly earlier emergence dates in the recent decade. Because our two data sets were not drawn from the exact same set of ponds in each decade, pond-specific differences (in thermal behavior or taxon composition) could skew the result of this basic model. Thus we ran a basic CPH model on data from Pond J alone, which was sampled in all study years in both decades. This basic model for Pond J also showed a significantly greater emergence hazard in the recent decade, with an effect size of 3.38 (Table 1).

Returning to the pooled species data from all ponds, we used a mixed-effects CPH model, again with ‘decade’ as a fixed effect but also specifying the variable ‘pond’ as a random effect. This model controls for the potential influence of pond-specific differences on the comparison of emergence hazard between the two decades. Our all-pond, all-species, mixed-effects model also produced a highly significant difference in emergence hazard, with an effect size of 3.61 (Table 1). Taken together, these three analyses of pooled species data indicate a clear shift toward earlier midge emergence dates in the recent decade that is not an artifact of pond-specific differences.

We also performed Cox proportional hazard analyses individually, for each of the 16 most-abundant midge species at Barrow that appeared in both of our data sets. Basic CPH models (pooling all emergence observations for a species within each decade while ignoring the covariate ‘pond’) produced highly significant differences in daily emergence hazard between the decades for 15 species (Table 1). All but one species tended to emerge *earlier* in recent years, with *Cricotopus tibialis* showing a slight shift toward *later* emergence (effect size of 0.54). Of the 14 midge taxa showing a *greater* emergence hazard in the 2009-2012 data, six species had effect sizes exceeding 2.0, indicating at least a doubling of the daily emergence probability in the recent decade. Because all species were not equally represented in all ponds, nor were all ponds sampled in both decades, we also ran mixed-effects models for all 16 species by including ‘pond’ as a random effect. These mixed-effects, single-species models produced results very similar to the basic CPH models (Table 1). Again, 14 midge species showed very highly significant increases in emergence hazard in the recent data set, and effect sizes exceeded 2.2 for ten of these species.

¹ This “instantaneous probability” is a *constant* for each population; a higher value implies an earlier likelihood of emergence - in the same way that a high probability of mortality for a population implies earlier deaths. Comparing these probabilities for a midge species in the two different decades indicates whether emergence timing has shifted.

Table 1. Output from Cox proportional hazards models used to contrast chironomid emergence phenologies in Barrow ponds between two decades. Basic CPH models include ‘decade’ (1970s vs. 2000s) as a fixed effect, pooling data from all years within each decade for all species from all ponds, for all species from Pond J only, and by individual species across all ponds and years. Mixed-effects CPH models include ‘pond’ as a random effect, while using data from all ponds (or Pond J only) sampled in all years.

Model	Basic CPH		Mixed Effect: Pond		N (1970s)	N (2000s)	N (total)
	Effect Size	p - value	Effect Size	p - value			
All ponds, all species:	1.81	<0.001	3.61	<0.001	6405	26177	32582
Pond J, all species:	3.38	0.04	-	-	3522	8045	11567
All ponds, by species:							
<i>C. prior</i>	6.32	<0.001	7.85	<0.001	85	1122	1207
<i>C. tardus</i>	1.53	<0.001	1.47	0.007	269	130	399
<i>Cladotanytarsus</i>	4.72	<0.001	13.4	<0.001	173	189	362
<i>Constempellina</i>	1.41	<0.001	1.9	<0.001	377	1918	2295
<i>Corynoneura</i> spp.	1.88	<0.001	3.51	<0.001	122	2237	2359
<i>C. tibialis</i> *	0.54**	<0.001	0.09**	<0.001	118	100	218
<i>C. perniger</i>	2.18	<0.001	1.68	0.066	70	426	496
<i>D. aclines</i>	2.88	<0.001	7.32	<0.001	22	44	66
<i>D. alaskensis</i>	2.32	<0.001	4.52	<0.001	76	79	155
<i>P. penicillatus</i> *	1.51	<0.001	2.53	<0.001	1334	7761	9095
<i>P. prolongatus</i> *	1.3	0.07	1.42	0.034	81	152	233
<i>P. vesus</i>	1.73	<0.001	2.37	<0.001	238	163	401
<i>Psectrocladius</i> sp1	1.24	<0.001	3.31	<0.001	517	1848	2365
<i>T. alaskensis</i>	1.44	<0.001	3.76	<0.001	942	1126	2068
<i>T. aquavolans</i> *	3.89	<0.001	4.43	<0.001	834	4841	5675
<i>T. nearcticus</i>	1.96	<0.001	1.44	<0.001	1015	1359	2374

*Species illustrated graphically in Figure 5.

**For *Cricotopus tibialis*, the significant effect sizes of 0.54 and 0.09 indicate small increases in the likelihood of *later* (not earlier) emergence in the recent decade.

Because the mixed-effects CPH models (those including ‘pond’ as a random effect) produced similar outcomes to our basic CPH models, we conclude that among-pond differences in emergence timing are small relative to the fixed effect of ‘decade’.

Four species-specific examples in Figure 5 illustrate graphically the range of outcomes represented statistically in Table 1. The chironomids *Paratanytarsus penicillatus* and *Tanytarsus aquavolans* (Fig. 5 - upper panels) are two common midge species showing clear shifts toward earlier emergence in recent years. Figure 5 also includes graphs of *Procladius prolongatus*, a species showing little detectable change between the decades, and *Cricotopus tibialis*. Emergence of *Cricotopus* began earlier and ended later in the recent decade and our CPH models (Table 1) indicate a slight shift toward later emergence (effect sizes <1). This result could reflect taxonomic error. A later-emerging *Cricotopus* seen in samples from the 2000’s may be a new species, not readily distinguished from *C. tibialis*, that was absent in the 1970’s.

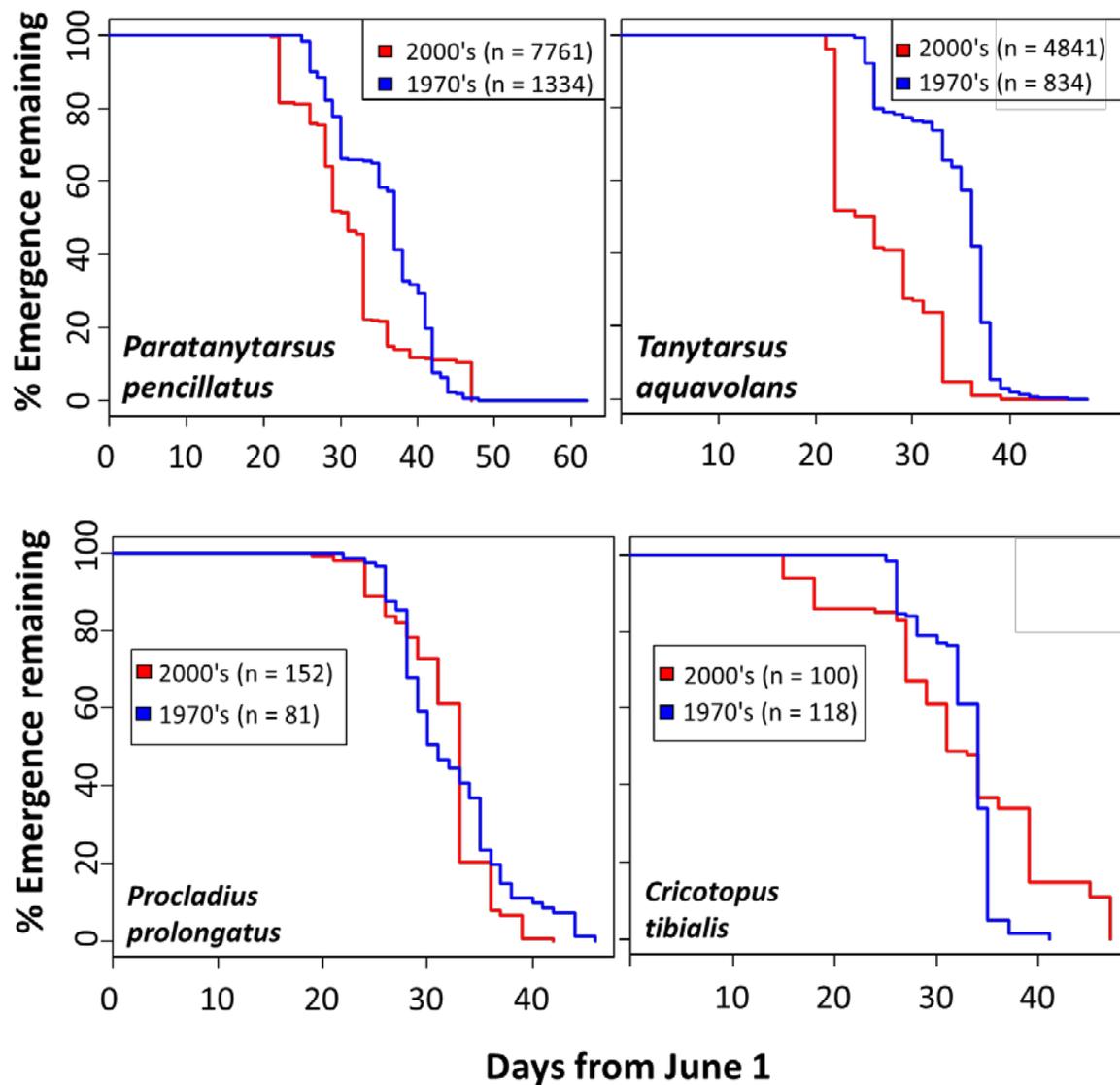


Figure 5. “Survivorship” curves illustrating emergence over time (from June 1) for four chironomid species from all ponds and years sampled in both decades. *Paratanytarsus pencillatus* and *Tanytarsus aquavolans* showed significantly higher daily emergence risk in the 2000’s relative to the 1970’s, whereas the daily hazard did not differ between the decades for *P. prolongatus*. *Cricotopus* emergence began earlier - but ended later - in the 2000’s, overall showing a slightly lower daily emergence risk (thus later emergence) in the recent decade.

We can illustrate these results more intuitively by plotting the annual sequence of species’ emergence in Pond J alone. In Figure 6A we see a consistent sequence of species’ emergence peaks (dates of 50% cumulative emergence) each year, from earliest-emerging to latest-emerging midge species. Thus there is a strong effect of species-identity on emergence timing, but the annual sequence is fairly consistent across years in both decades. There is also an obvious effect of thaw date, which varies widely among years and is responsible for much of the year-to-year variation in overall emergence phenology. This is illustrated in Figure 6B, where the time scale for each year is shifted to align annual thaw dates. This adjustment to the time scale provides a uniform starting point for biological activity each year; the improved alignment of species across years illustrates that thaw date can explain a major portion of the variance in date of emergence for the midge community. In a general way, this graphical adjustment is analogous to inclusion of ‘year’ as a random effect in a Cox proportional hazard model for Pond J. When

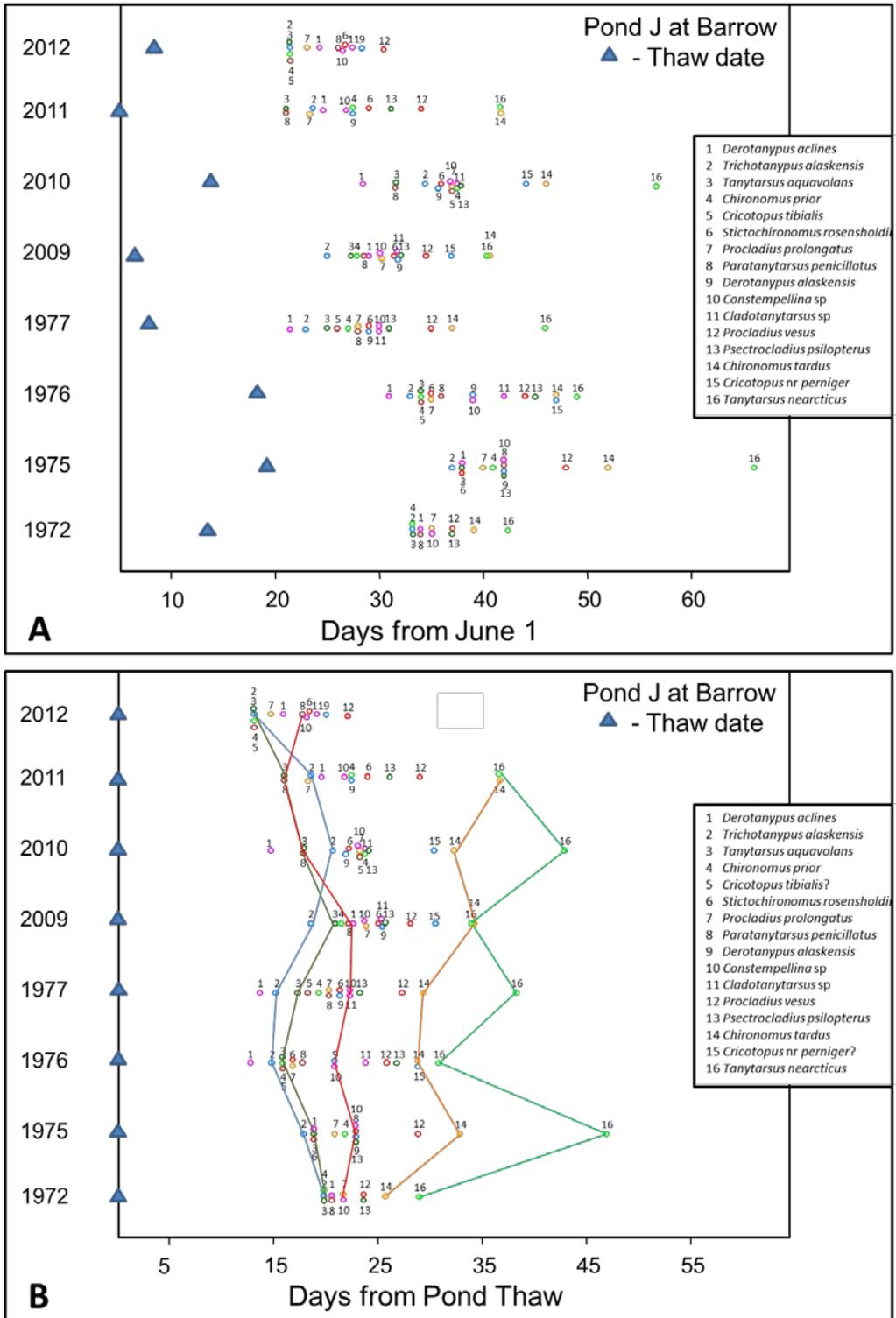


Figure 6. Peak chironomid emergence in Pond J at Barrow for four years in each of two decades (1970's & 2009-2012). (A) Time line based on calendar date, with presumed date of pond thaw (= Barrow snow melt date) indicated. Emergence records after 2 July 2012 not available. (B) Time lines for each year shifted to align estimated dates of pond thaw (see text). Lines connect five taxa that were abundant in all years, representing early, mid-season, and late-emerging midge species.

we ran such mixed-effect models (not presented here) the outcome was rarely significant. This is because among-year differences in thaw date contribute so strongly to the total variation in midge emergence timing. Essentially, decadal differences in thaw date may be driving much of the change we can detect in chironomid emergence phenologies.

More than just ‘thaw date’ differs from year to year however, even for a single pond such as Pond J. There are likely other drivers underlying insect emergence timing, such as differences in thermal conditions between pond thaw and the emergence of a given species. If Pond J experienced the same temperature regime every year, we would expect to see straight vertical lines connecting each species across years in Figure 6B. Deviations from vertical may indicate that in some years a species requires more days post-thaw, and other years fewer days, to complete larval and pupal development prior to emergence. Thus we have explored the role of pond temperature during the pre-emergence period in regulation midge emergence.

Applicability of the Thermal Time Model for Midge Emergence:

We’d expect *lower rates* of development in cooler ponds, with an insect needing *more time* to complete development than in warmer ponds where processes occur at a *faster rate*, requiring *less time*. This is the essence of the **thermal time model** (Trudgill et al. 2005), which holds that a **thermal constant** (in degree-hours above a threshold temperature) is needed to complete any given developmental process. We’ve tested the thermal time model (illustrated in Fig. 7) for its utility in explaining emergence timing.

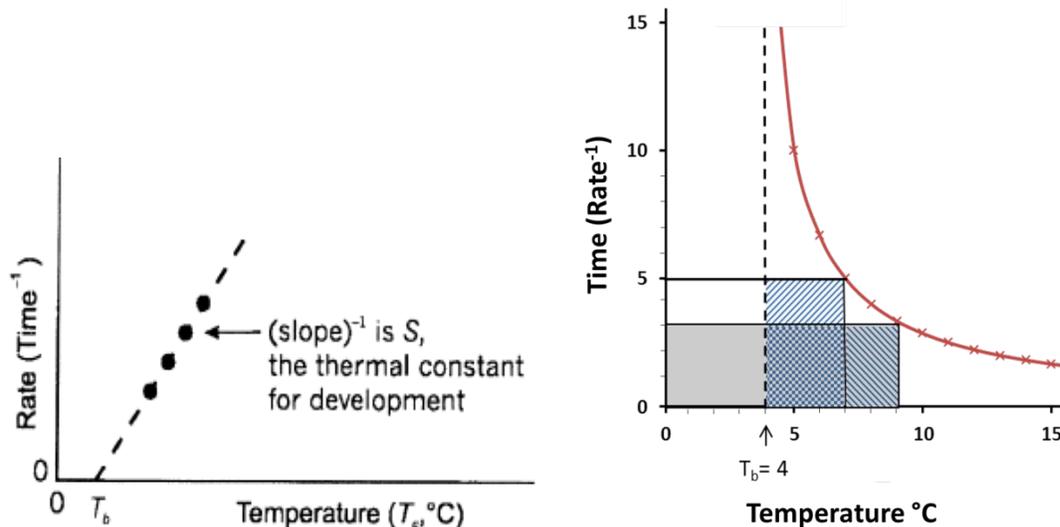


Figure 7. Hypothesized responses of insect development to temperature. Left: Linear response of developmental rate over a range of environmental temperatures (from Charnov and Gillooly, 2003). Right: Hyperbolic response of developmental time (= 1/rate). T_b is the developmental base temperature. The reciprocal of the slope of the rate relationship is S, the degree-hours above T_b required to complete development. In this illustration S = 15 thermal time units: 3°C x 5 time units (hatched portion of clear rectangle) or 5°C x 3 time units (hatched portion of gray rectangle).

How might “thermal time” concepts be applied here? We’ve seen that emergence of a Barrow pond chironomid is greatly influenced by (1) species identity, and (2) date of thaw in the year of emergence. A thermal-time model would predict the time of adult emergence as the end-point of a developmental process. The starting point for this pre-emergence development is a species-specific overwintering stage. [Note that many midge species in ponds at Barrow spend two or more years as larvae, but only remaining larval, then pupal, development in the year of emergence is relevant to the regulation of emergence timing.] Given a starting time (‘date of thaw’), a species-specific linear response of development rate to increasing temperature implies a “thermal constant” (S in Fig. 7 - some fixed number of degree-hours to complete development). Under the thermal-time model, any pond-to-pond

or year-to-year *variation in time* to emergence should be compensatory to *thermal variation*. We've tested predictions of this model with both field and experimental data.

Testing the thermal constancy of pupal development: While most chironomid larvae live inside tubes in the sediments, the larvae of some species range freely in the water column, foraging on substrate surfaces. *Trichotanyptus alaskensis* is an early-emerging midge species abundant in many Barrow ponds, and is well-suited to experimentation. Both larvae and pupae are active in the water column and are easily monitored in rearing experiments. We conducted multiple experiments in which we reared overwintering *T. alaskensis* larvae in incubators at differing constant or variable temperatures, or in ponds with varying natural thermal regimes. We checked these rearings daily for new pupae, which were segregated into daily cohorts of known pupal age. We logged hourly water temperatures and monitored the pupal rearings daily. Thermal time for pupal development (cumulative hourly temperatures from pupation to adult emergence, recorded to the nearest day) averaged 1519 degree-hours (= 63.3 degree-days) for pupal development. Variation around this mean was not related to mean rearing temperature or to the amplitude of daily temperature fluctuation, but spanned a very broad range (Fig. 8). Of additional concern is that extrapolation of this linear rate/temperature relationship indicates a developmental base temperature for pupation by *T. alaskensis* of -2.1°C . This unrealistic result calls into question the aptness of the "thermal time" concept here (see further discussion below).

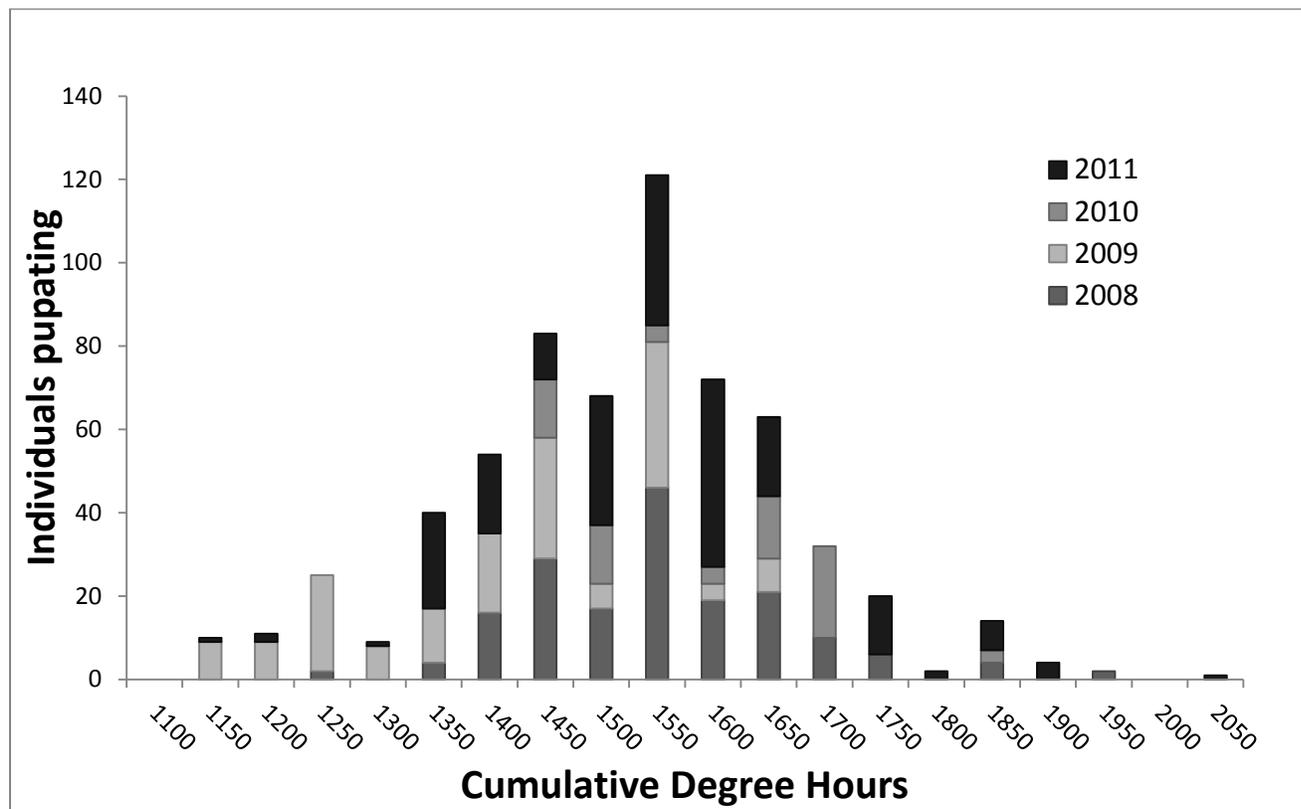


Figure 8. Distribution of degree hours required for pupation by *Trichotanyptus alaskensis* in lab and field rearing experiments conducted over four years. Assuming a linear model, the 'thermal time' required for pupation should be a 'thermal constant'.

Development rate versus temperature: A corollary to the model of thermal-time constancy is its inverse: the *rate* of development should be directly and positively related to the *mean temperature* (Fig. 7). We've assessed how the emergence timing of Barrow chironomids responds to variation in pond temperature over the time from pond thaw until peak emergence. We used a subset of common midge

species emerging from five ponds sampled during 2009-2011 (typically with over 100 specimens collected per pond each year). Summing hourly temperatures from ‘pond thaw’ until peak emergence (date of 50% cumulative total for each population), we plot the rate of pre-emergence development versus the average temperature experienced by the larvae and pupae of the species in each pond/year. In Figure 9 we show regressions for six of these abundant midge species. Each plot has 7-12 data points, depending on the number of ponds where the timing of peak emergence by a species was reliably documented in each of the three years. An exponential fit to these data was significant for five of the six species; linear fits were similar, with R^2 values marginally lower. For most other species our sample sizes are too low for a meaningful analysis.

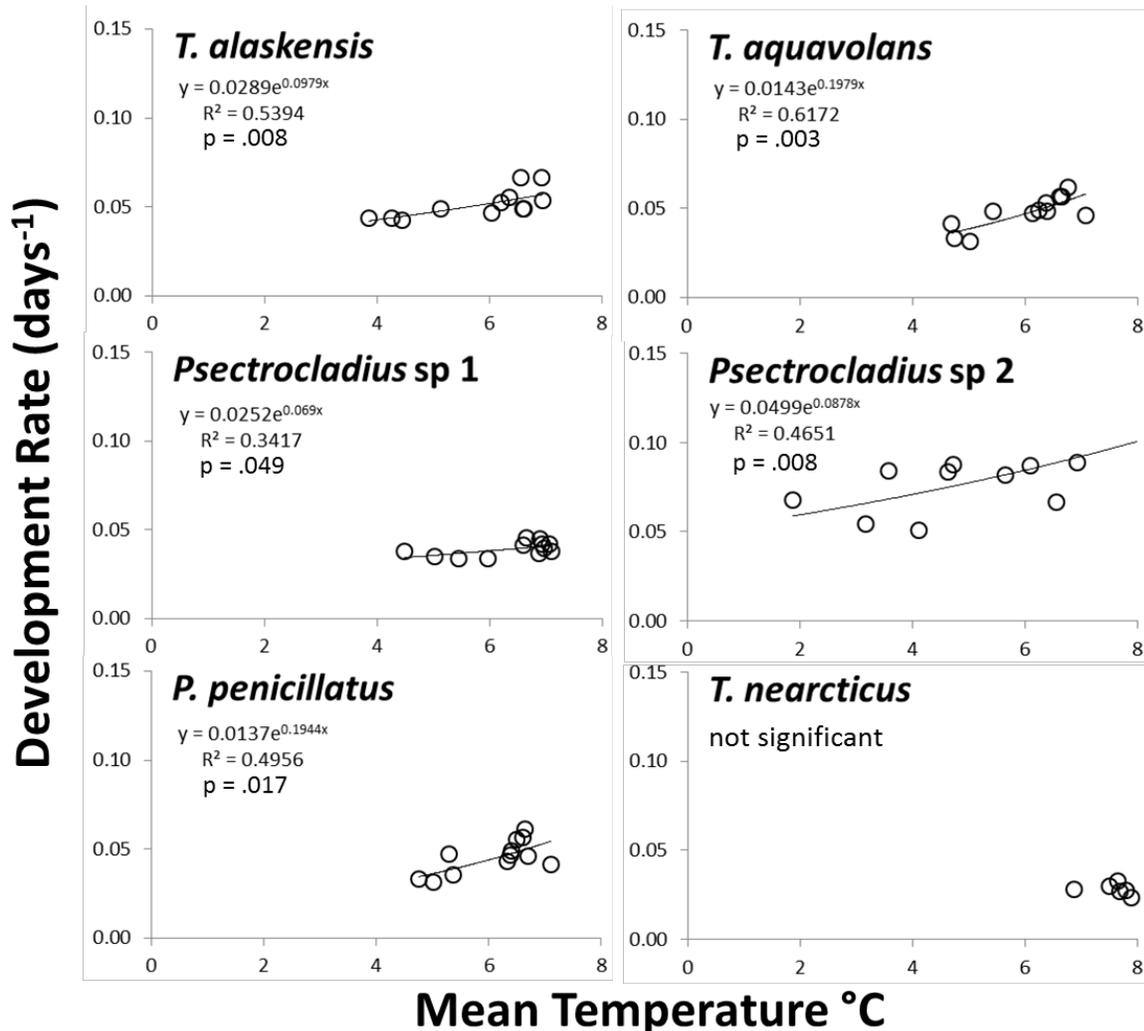


Figure 9. Pre-emergence development rate as a function of mean pond temperature for six abundant midge species. Development rate is the reciprocal of time between the annual snow-melt date at Barrow (a surrogate for actual pond thaw) and peak emergence for each species in five Barrow tundra ponds with hourly temperature recordings during 2009-2011.

We find these results quite intriguing, despite some recognized sources of imprecision in the data:

- 1) Our response variable: **developmental rate** is the reciprocal of **developmental time**, a time interval we defined as the number of days between **pond thaw** and the **date of 50% cumulative emergence** for a species. Initially, we used thaw dates taken from our pond-specific temperature loggers as the starting point for midge development in each pond, but found none of our regressions to be significant. Recognizing that spring “thaw” is a multi-day event in most

ponds, our single-point observations of sediment-surface temperatures in each pond could not apply accurately to all midge larvae whose emergence we subsequently recorded in that pond. Thus we subsequently used **Barrow snow melt date** as the presumed starting point for insect development in all ponds each year. An annual date of snow melt for the Barrow peninsula is determined by CMDL/NOAA, based tundra-surface albedo measurements:

<http://cmdl1.cmdl.noaa.gov:8000/www/albedo/>.

This approach, using a single, regional starting date for the onset of midge development, did produce significant regressions for five of the six species shown in Figure 9. Apparently, within-pond variation in thaw timing introduces more error into our estimate of the starting point for insect thermal-exposure (and thus to our calculation of mean temperature over the developmental period), than does among-pond variation in thaw for any year.

- 2) Our **50% cumulative emergence dates** are typically derived from a 2-day sampling interval. We used linear interpolation to estimate the median emergence date to the nearest day, and summed temperatures to noon on that date (the typical time of most emergence sampling). Daily sampling should provide higher precision in estimating these emergence mid-points for each midge population. We view these results as exploratory, and will seek additional statistical power by analyzing daily cohorts, increasing substantially the sample size for each species.

Although linear and exponential models had similar fits to our data on pre-emergence development versus temperature, there are good reasons to prefer the exponential alternative (Ratte 1985). A linear “thermal-time” model may be appropriate for insects living within a thermal range where the development rate response is nearly linear (Worner 1992, Charnov and Gillooly 2003). In such cases, the reciprocal of that constant rate (the ‘thermal constant’ S in Fig. 7) is useful in predicting how development will respond to temperature – if the developmental base temperature is known. Under the linear model, that base temperature (T_b - where the development rate equals zero) is the X-intercept of the relationship illustrated in Figure 7. Linear fits to our data produced T_b values essentially equal to 0°C for the two tanytarsine species. For the other three significant relationships in Fig. 9, T_b values for a linear fit were *negative* (the line crosses the Y axis at a positive value). Using a linear fit, we must conclude that *Trichotanypus alaskensis* could develop down to a T_b value of -4.3°C, while the two *Psectrocladius* species would develop at temperatures as low as -6°C or -8°C. Clearly that outcome is not possible. An exponential fit recognizes that developmental rates respond in a nonlinear way to temperature. This approach is clearly better justified for insects maturing at the low and variable temperatures these larvae and pupae experience in Barrow tundra ponds during June-July.

Coefficients from the five significant exponential relationships in Figure 9, based on field data, are used in Figure 10 to illustrate the relative shapes of these species-specific thermal response curves. The intercept and slope for each curve reflect that species’ base developmental rate, and its developmental rate response to increasing mean temperature, respectively. Also shown is the curve fitted to our experimental tests of pupation rate for *Trichotanypus alaskensis* (data shown as thermal time in Fig. 8).

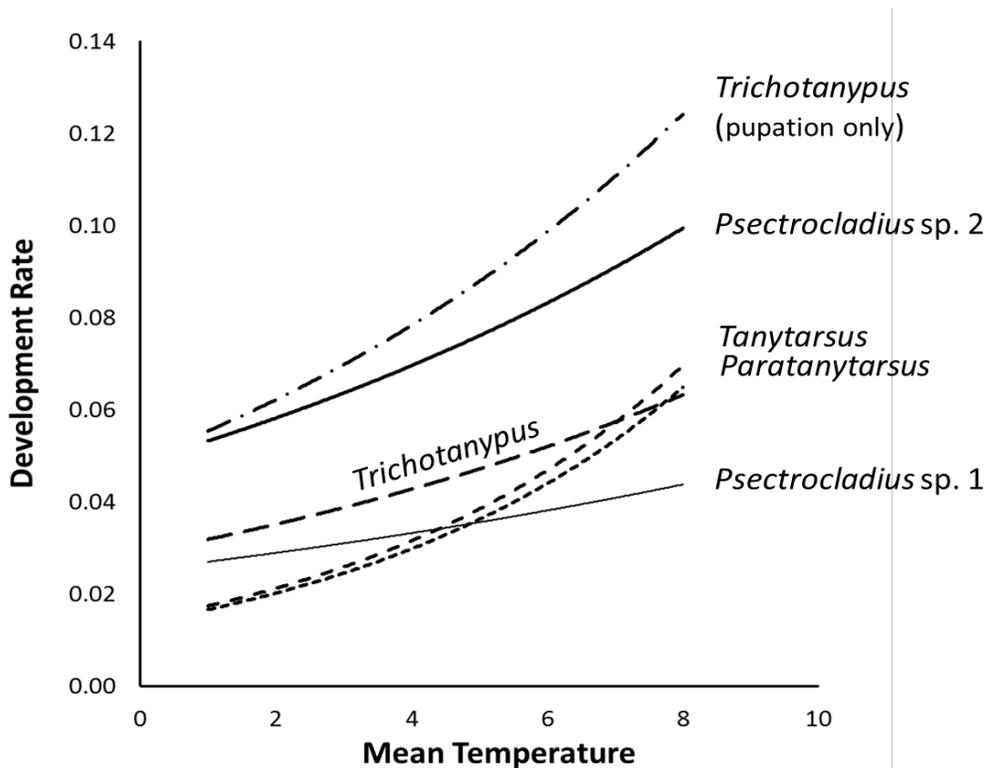


Figure 10. Pre-emergence development rates as a function of mean pond temperature for five midge species (from field-collected data shown in Fig. 9). Predicted rates of combined larval and pupal development are shown for mean temperatures between 1-8°C. Also shown is the thermal response of pupation rate by *Trichotanypus alaskensis* based on the duration of the pupal stage only.

It is premature to rigorously interpret between-species differences in the slopes or intercepts of these regressions, but we note two interesting patterns. First, development rates for the two tanytarsine species (*T. aquavolans* and *P. penicillatus*) appear to respond more strongly to temperature (higher slope coefficients) compared to the other three species. Both *Trichotanypus alaskensis* and the two *Psectrocladius* species belong to chironomid subfamilies generally considered as “cold-adapted” (Podonominae and Orthoclaadiinae, respectively), whereas the tribe Tanytarsini belongs to a more “warm-adapted” subfamily (Armitage et al. 1995). Greater slopes imply that development is more temperature sensitive for the tanytarsines, whereas more cold-adapted taxa may be less able to benefit from warmth, but better at completing development at low temperatures. The intercepts of these exponential curves show a similar dichotomy between the two midge groups, with the tanytarsines having much lower projected developmental rates at 0°C (rates of ~0.014 d⁻¹ vs. 0.025-0.050 d⁻¹). Exploring developmental response to temperature for a range of aquatic ectotherms (using linear models), Charnov and Gillooly (2003) documented an inverse relationship between the base temperature and the rate of response to increasing temperature.

Another interesting outcome from this analysis is the non-significant relationship for *Tanytarsus nearcticus*, the late-emerging midge that always marks the end of the chironomid emergence season at Barrow. We have only seven data points (populations) for this species due to low counts or incomplete late-July sampling in some ponds/years. Our available data span much lower ranges of both variables (mean temperature and development rate) than for the other five species. As a late-emerging species, *T. nearcticus* spends at least 6-8 weeks in the pond prior to appearance of adults; a mathematical consequence of this longer developmental period is that *daily rates* for pre-emergence development are very low for this species, and significant variation among populations is harder to detect with our

methods. Also, variation in mean daily water temperature (our explanatory variable) is lower, both among ponds and from year-to-year, when calculated over this longer portion of the Barrow summer. Figure 11 shows mean daily pond temperatures for 6-7 weeks following thaw for the seven pond-years producing data on *T. nearcticus* emergence.

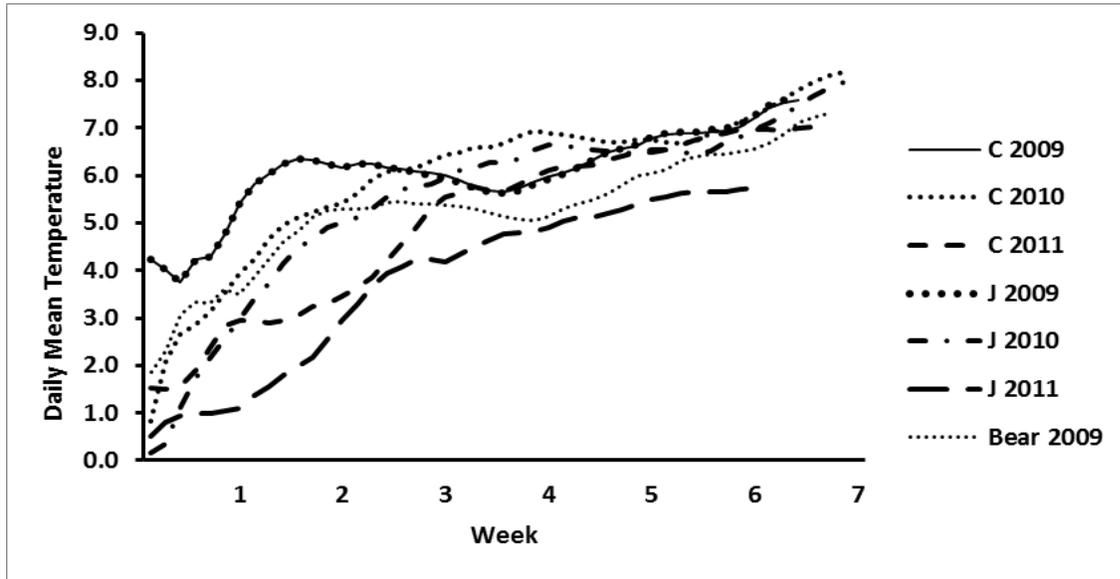


Figure 11. Average daily pond temperatures during early summer for seven pond-years generating data on emergence of *Tanytarsus nearcticus*. Variation in mean thermal exposure (both among ponds and between years) is high for the first three weeks, becoming more stable by late June and into July.

Pond temperatures vary more widely among ponds, and between years, in the early weeks of the summer. Populations of *Trichotanytus alaskensis* and *Psectrocladius* sp. 2, which complete development in those earliest weeks, experience greater variability in thermal conditions, as shown in Figure 9. This does not necessarily mean we shouldn't expect development rate to depend on temperature for later-emerging species like *T. nearcticus*, only that we are less able to detect such dependence without data from populations maturing over a greater range of temperatures. In addition, the seasonal phenology of late-emerging species like *T. nearcticus* and *Chironomus tardus* may be less-adequately characterized by a single metric like "50% cumulative emergence", as these species tend to show more prolonged emergence than the earlier, more synchronous species. We expect a higher-precision approach may detect temperature sensitivity of pre-emergence development for these late-emerging species as well.

4) SUMMARY OF FINDINGS

Key findings from this study include:

- 1) We detected a **significant shift in the seasonal timing of insect emergence** of from tundra ponds at Barrow, Alaska over a 3½-decade time span (1975-77 to 2009-11).
 - a. A shift of toward earlier emergence dates is apparent for the chironomid midge community as a whole, and for most individual species.
 - b. This result is consistent with data indicating earlier dates of spring thaw and warmer pond temperatures at Barrow.
- 2) Our analyses suggest that **emergence timing** for chironomids in Barrow tundra ponds **depends largely on** the following:
 - a. **Species identity** - Each species has a characteristic position in the seasonal sequence, likely determined by taxon-specific **overwintering stages** and **developmental rates**:
 - i. All midges overwinter as larvae; all species must complete pupation prior to emergence as adult flies, but some may require *more* (some *less*) *larval development* prior to pupation.
 - ii. *Temperature-dependent rates of larval and pupal development* that may differ among taxa during these pre-emergence processes.
 - b. Variation in the **onset of pre-emergence development**:
 - i. *Annual variation*: Species' emergence dates shift in response to earlier or later spring thaw at Barrow.
 - ii. *Spatial variation*: Pond type, morphology, and local hydrology create variations in timing of thaw at local scales (between and within ponds).
- 3) We find **rates** for completion of pre-emergence development (remaining larval development plus pupation) to **depend on thermal exposure**. The temperature-dependence of development rate varies among different taxa, but groups of species may respond in similar ways.
- 4) **Non-linear models** better-fit the **response of developmental rate to temperature** than do linear models. The "thermal time" concept (based on a linear relationship between development rate and temperature) seems inappropriate for use in predictive models of emergence phenology for these tundra pond insects.

5) FURTHER RESEARCH NEEDS

We suggest the following priorities toward efforts to predict how a changing thermal environment may alter the seasonal timing of insect emergence in these tundra-pond habitats:

- 1) **Improved characterization of taxon-dependent variables.** Species differences in seasonal phenology exceed differences in the timing of thaw at Barrow. Thus, even for ponds or years with similar timing of snow melt and pond thaw, differences in community composition can produce widely varying patterns of insect emergence. Our data are for dominant species emerging from low-center polygon ponds; within that pond type the community can vary greatly among ponds and years. Other habitat types host some of these same species, but also other insects that are rare or absent from our analyses. With further study, we anticipate that important prey taxa for shorebirds can be grouped according to features most important in determining annual emergence timing:
 - a. **Overwintering stage** - *Early-emerging species* may **overwinter as ‘prepupae’** (needing little if any larval development after pond thaw); alternatively, early taxa may show **rapid development** at the low temperatures after pond thaw in early-mid June. *Later-emerging species* may **need more larval development**, and/or they may **develop more slowly** in some temperature ranges. We need to characterize the midge fauna according to these potential strategies. All pre-emergent larvae of a species may overwinter in a very specific stage, or late-larval development may be less synchronous within a population, or may vary among ponds or between years. We need to analyze larvae collected in their overwintering state from different years and ponds, to determine the importance of this variable as the ‘starting point’ for pre-emergence development.
 - b. **Rates of pre-emergence development** – To predict the time of emergence for a species, we need to know both the starting point and rate(s) of development (which vary with temperature). If **overwintering stage** is viewed as the *starting point* in a ‘race to emerge’, then **rate of development** is analogous to the *speed of the racer*. Because different species run races of differing length (varying in their overwintering starting points), developmental rates we’ve observed at various pond temperatures may not be directly comparable among taxa, as these are composite rates for varying amounts of larval, then pupal development. All midges must pupate between thawing and emergence, so rates of pupation alone should be directly comparable among taxa. [We were able to measure pupation rates for *Trichotanytus alaskensis* (see Fig. 10) because we could isolate individuals on their date of pupation. Most of the abundant chironomids in Barrow ponds have tubicolous (tube-dwelling) larvae and the onset of pupation cannot be monitored.] Thus the measurable developmental response to rearing temperature in our analyses of field data (Figs.9, 10) combines both the time for final larval development plus the time for pupation, when the two processes cannot be separated. We are in fact primarily interested in this composite variable (“pre-emergence development”), as we want to know how long it takes after pond thaw for overwintering midge larvae to reach adult emergence. Rate of late-larval development for a species may vary with temperature in the same way as rate of pupation, or these life stages may respond differently – as our preliminary results for *T. alaskensis* suggest (Fig. 10). By further studying *T. alaskensis*, and possibly other non-tubicolous midge species we can test this potentially simplifying assumption.

We anticipate that chironomid species may fall into distinct groupings with respect to the variables described above – possibly along phylogenetic lines. If so, we may be able to model the expected response of these broader midge groups to varying thermal conditions. We seek a model that can accommodate the taxonomic variation found across the mosaic of aquatic habitats on the tundra, without having to account for each species individually.

- 2) **More precise characterization of environmental drivers.** “Insect emergence” is an emergent ecological property of an insect fauna interacting with its environment. A tundra-pond insect community with a given taxonomic composition will produce adult insects as the life-history adaptations of its constituent species respond to the local environment. We think the most prominent environmental drivers of insect emergence in this system are two thermal variables: **timing of pond thaw** and **subsequent temperature dynamics**. Our work has revealed that:
- a. **Timing of pond thaw is a complex process.** Our use of a single temperature logger to monitor the important variable *date of thaw* has proven inadequate. Insects emerging from a given pond live in a range of microhabitats that can thaw over a period of a week or longer. Also, *among-pond* and *between-year* differences in pond thaw may be large, as thaw timing depends on meteorological and hydrological events in addition to effects of pond variables like morphology, sediment characteristics, and vegetation.
 - b. **Pond temperature dynamics are also variable and complex.** Once insect larvae have thawed, their development toward pupation and adult emergence appears to depend largely on water (and/or sediment) temperatures. The same drivers that influence thaw timing also create diversity in subsequent thermal conditions, both within and among ponds. Temperatures in these shallow tundra ponds oscillate daily, with amplitudes commonly 5-10°C (Miller et al. 1980; McEwen & Butler in prep). Even shallow ponds 20-30cm deep can exhibit temporary thermal stratification, especially within beds of emergent vegetation; deeper, narrower “trough ponds” run cooler, show lower diel thermal oscillation, and can suffer oxygen depletion.

These driving environmental variables must be characterized at spatial and temporal scales appropriate to the level of resolution we hope to achieve in modeling insect emergence.

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7. PRODUCTS.

Publications & manuscripts:

Lougheed, V.L. et al., 2011. Changes in tundra pond Limnology: Re-sampling Alaskan ponds after 40 Years. *Ambio*, 40(6), pp.589–599.

This paper includes a contribution by Butler & McEwen on temperature changes and invertebrate community composition in tundra ponds at Barrow, using data collected under NFWF support in 2009-10. The paper was submitted and published early in the period of ALCC support for our work.

McEwen & Butler (in prep). Four decades of warming in an arctic tundra pond at Barrow, Alaska.

This manuscript on pond temperature changes was reviewed by Arctic in summer 2013, and is currently being revised for resubmission.

Conference papers:

M.G. Butler & D.C. McEwen: *Tundra Pond Chironomids reduce Life Cycle Duration as Arctic Climate Warms.* Oral presentation - Climate Change Session, North American Benthological Society (now Society for Freshwater Science), Providence RI, 24 May 2011.

Braegelman, S.D. & M.G. Butler, & D.C. McEwen: *Will a Changing Climate Cause Arctic Insects to Emerge Before Breeding Birds are Ready?* Oral presentation - Northern Plains Biological Symposium, Fargo, ND 19 April 2012.

Braegelman, S.D. & M.G. Butler: *Emergence Phenologies of Arctic Chironomids: Comparison Across Three Decades.* Oral presentation - Society for Freshwater Science, Louisville, KY 24 May 2012.

Braegelman, S.D. & M.G. Butler: *Thermal controls of insect emergence in some high arctic ponds.* Oral presentation - Ecological Society of America, Minneapolis, MN, 8 August 2013.

Presentations:

Braegelman, S.D.: *Emergence Phenology and Life History Analysis of some High Arctic Arthropods.* Oral presentation - Environmental & Conservation Sciences Greenbag Lunch Series, Fargo, ND. 22 March 2012.

Education and outreach:

Butler and McEwen each gave public outreach presentations at Barrow during summer 2011, through the BASC-sponsored Saturday Schoolyard Program. We were unable to schedule a presentation in 2012.

M.G. Butler: *What's for dinner? Tundra Pond Insects!* 25 June 2011

D.C. McEwen: *Climate Change Impacts on Tundra Ponds – A Historical Perspective* 2 July 2011

Other products resulting from the project:

Nothing to Report