Running head: Arctic pond macroinvertebrate abundance

In hot water? Patterns of macroinvertebrate abundance in Arctic thaw ponds and relationships with environmental variables

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Abstract

1. Ongoing environmental change across the Arctic is affecting many freshwater ecosystems, including small thaw ponds that support macroinvertebrates, thus potentially affecting important forage for fish and bird species. To accurately predict how fish and wildlife that depend on these macroinvertebrates will be affected by ecosystem change at high latitudes, understanding proximate factors that influence macroinvertebrate abundance is critical.
2. To better understand factors that affect spatial and seasonal (i.e phenology) patterns in abundance, we collected macroinvertebrates throughout the growing season of a single year from 33 thaw ponds on the Arctic Coastal Plain in northern Alaska. We used hierarchical *N*-mixture models to provide detection-corrected estimates of abundance (of the population exposed to sampling) in relation to pond type and seasonal patterns in potential environmental variables (i.e., cumulative water temperature, nutrient levels) for five taxonomic groups representing key food items for birds and fish – Anostraca (Arthropoda: Branchiopoda), Chironomidae (Insecta: Diptera), Cladocera (Arthropoda: Branchiopoda), Limnephilidae (Insecta: Trichoptera), and Physidae (Mollusca: Gastropoda)
3. For three of five taxa (Anostraca, Cladocera, Limnephilidae), abundance varied across pond types and was lower in pond types where water temperatures increased more rapidly. Further, seasonal temperature profiles in ponds affected phenology, suggesting that seasonal patterns in abundance were influenced by changes in water temperature.
4. These findings suggest that increases in water temperature in northern areas could alter macroinvertebrate phenology, possibly with consequences for upper level predators if availability of macroinvertebrate prey is reduced or shifted seasonally. Our results will

facilitate improved predictions of how changing abiotic conditions could affect inland waters in northern areas, a critical need for conservation of Arctic wildlife and ecosystems.

1 INTRODUCTION

Across the circumpolar Arctic, annual averages for air temperature and precipitation are increasing (Walsh *et al.*, 2011; Bintanja & Andry, 2017). Concurrent with these climatic changes, hydrological shifts, including localized redistribution of water and increasing water temperatures, are also occurring (Lougheed *et al.*, 2011; Jorgenson *et al.*, 2015; Liljedahl *et al.*, 2016). In addition, permafrost thaw is mobilizing solute-rich water, leading to elevated nutrient concentrations in many Arctic freshwater systems (Toohey *et al.*, 2016; Koch *et al.*, 2018b; Tank *et al.*, 2018). Increasingly, there is evidence that such changes are influencing aquatic biota (Kendrick, Hershey & Huryn, 2019; Heino *et al.*, 2020; Pennock *et al.*, 2021), and that ectothermic organisms, particularly freshwater macroinvertebrates, are likely to be disproportionately affected, because many of the biological functions (i.e. metabolism, reproduction) for these taxa are highly responsive to environmental conditions (Ellwood *et al.*, 2012; Lento *et al.*, 2022a).

In Arctic areas of North America (hereafter, the Arctic), diverse communities of freshwater macroinvertebrates, including aquatic insects and zooplankton (Van Geest *et al.*, 2007; Christoffersen *et al.*, 2008), inhabit small thaw ponds ($< 10^4$ m^2), which can account for as much as 95% of the number of water bodies on tundra landscapes (Muster *et al.*, 2013) and store large amounts of carbon and nutrients (Rautio *et al.*, 2011; Koch *et al.*, 2018a). Such ponds – including (i) deep troughs that form above thawing ice wedges, (ii) shallow, low-centered polygons that form between troughs, and (iii) larger coalescent ponds that form with further thawing of troughs and polygons – thus make important contributions to biodiversity and provide key food resources for fish and bird species (Cunningham, Kesler & Lanctot, 2016; McFarland, Wipfli & Whitman, 2018). How environmental change at high latitudes will affect these resources, however, is unclear.

Variation in abundance of macroinvertebrates across the Arctic landscape is not well quantified, and although within-season patterns in the abundance (i.e. phenology) of many aquatic invertebrates has been well-documented, few studies have directly assessed factors that control seasonal patterns, especially in northern systems (Laske *et al.*, 2021; Shaftel *et al.*, 2021). As such, the specific environmental drivers of spatial and seasonal patterns of abundance of macroinvertebrates in thaw ponds, as elsewhere, remain poorly understood (Sánchez-Bayo & Wyckhuys, 2019; Woods, Kaz & Giam, 2021), limiting our ability to anticipate the potential impacts of changing conditions across years (related to climate) and within years (related to changes in the timing of seasonal events). For example, the influences of increasing water temperatures and nutrient concentrations on invertebrate fauna in lacustrine and riverine systems can be highly variable (Alric *et al.*, 2013; Nelson, Bennett & Cardinale, 2013), depending on existing trophic interactions within each system and variation in the physiology and life history strategies of different taxa (Wojtal-Frankiewicz, 2012; Batzer, 2013; Abrego *et al.*, 2021). Additionally, in small thaw ponds, biotic responses to warming air temperatures and thaw-derived nutrient enrichment are likely to depend on pond morphology, with larger coalescent ponds being less likely to derive nutrients and provide habitat during periods of change (Koch, Gurney & Wipfli, 2014).

To begin to assess the potential impacts of environmental change in the Arctic on freshwater macroinvertebrate phenology and to identify potential wildlife outcomes associated with these changes, evaluating mechanistic components that regulate abundance of key taxa will be critical (Van Hemert *et al.*, 2015; Cardoso *et al.*, 2020). As filter-feeding crustaceans that are often abundant in shallow freshwater habitats, both Anostraca (Arthropoda: Branchiopoda, fairy shrimp) and Cladocera (Arthropoda: Branchiopoda, water fleas) can affect nutrient cycling through impacts on abundance of bacteria and algae (Hobbie, 1980; Vinebrooke *et al.*, 2014), with Cladocera being particularly important prey for both birds and fish (Dodson & Egger, 1980; Laske *et al.*, 2017). Larval Chironomidae (Insecta: Diptera, midges) and Limnephilidae (Insecta: Trichoptera, caddisflies) are similarly important prey resources (Holmes, 1966; Gerik, 2018), as are Physidae (Mollusca: Gastropoda, bladder snails), which can also comprise a substantial proportion of overall biomass in northern wetlands (Bartonek & Murdy, 1970; Gurney *et al.*, 2017).

To address questions related to impacts of warming temperatures and elevated nutrient availability on seasonal patterns of abundance of Arctic freshwater macroinvertebrates and provide improved predictions, we modeled the impact of physical, chemical, and biological variables in troughs, polygons, and coalescent ponds on the Arctic Coastal Plain ecoregion of northern Alaska in relation to macroinvertebrate abundance measures. We selected macroinvertebrate taxa documented as important to the structure (biomass) and function (nutrient cycling, food resources) of Arctic thaw ponds. Specifically, our objectives were to evaluate (i) variation in macroinvertebrate abundance among pond types and (ii) the effects of water temperature and nutrient concentrations on macroinvertebrate abundance throughout the growing season.

Due to the unique morphology of troughs, which results in increased drainage of water and nutrients from the surrounding terrain relative to other pond types (Koch, Gurney & Wipfli, 2014; Koch *et al.*, 2018b), we predicted that macroinvertebrate abundances would be highest in these less ephemeral habitats. Although macroinvertebrates should be adapted to seasonal changes in temperature, variable thresholds of thermal tolerance among ectothermic species make it difficult to make generalized predictions about how phenology of diverse taxa will vary across ponds with different seasonal temperature profiles (Musolin, 2007; Sunday, Bates & Dulvy, 2011). We did expect, however, that late season declines in macroinvertebrate abundance would become more pronounced in ponds with greater changes in temperature (Dallas & Rivers-Moore, 2012). Conversely, we predicted positive associations between patterns of macroinvertebrate abundance and nutrient concentrations, as freshwater biota in northern systems should be well-adapted to take advantage of seasonal increases in nutrients and resources (Lewis *et al.*, 2014; Moquin *et al.*, 2014). We assert that although our findings will not be directly relevant to predicting future changes associated with global climate change, they will provide important insights regarding how freshwater biota will respond to environmental conditions that vary across inter and intra-annual time scales.

2 METHODS

2.1 Study area and experimental design

During 2013, we studied variation in macroinvertebrate abundance in small thaw ponds at the Chipp River North Study Area (70.68°N, 155.30°W), located approximately 80 km southwest of Utqiaġvik (formerly Barrow), Alaska, within the Arctic Coastal Plain ecoregion (Figure 1A). The dry, polar climate of the region is characterized by short, cool summers and long, cold winters, with average July temperatures ranging from 8 to 19°C and average annual temperatures ranging from -13 to -10°C (Alaska Department of Fish and Game, 2006; Woodward & Beever, 2011). The landscape is characterized by polygonal-patterned terrain that forms as massive subterranean ice wedges displace soil upward (Jorgenson, Shur & Walker, 1998). Vegetation varies across the landscape and is strongly influenced by microtopography. Pendantgrass (*Arctophila fulva*), water sedge (*Carex aquatilis*), cottongrass (*Eriophorum spp.*), tundragrass (*Dupontia spp.*), forbs, and mosses dominate in low-lying areas, whereas sedges (*C. aquatilis*, *C. bigelowii*), tussock cottongrass (*Eriophorum vaginatum*), and shrubs such as entireleaf mountain-avens (*Dryas integrifolia*) and willow (*Salix lanata, Salix planifolia*) are more abundant in areas of higher terrain between basins (Billings & Peterson, 1980; Martin *et al.*, 2009).

Our stratified random sampling design was based on three main types of small thaw ponds (troughs, polygons, and coalescent ponds), with the latter divided into small (<50 m diameter) and large (50 – 150 m diameter) categories to account for differences in geomorphology, water chemistry, and pond age (Koch, Gurney & Wipfli, 2014)(Figure 1B). To select the ponds that populated the strata, we used ArcMap to limit the sampling area, exclude lakes with diameter > 150 m (surface area > 0.018 km^2), and randomly select study ponds within our classification scheme.

2.2 Field methods

To keep a continuous record of water temperatures, we suspended a portable temperature logger (Hobo® Tidbit V2, Onset Computer Corporation, Bourne, MA, USA) in the water column of each pond (approximately 5 – 10 cm below the surface), following spring thaw of surface water (9-June to 15-June), and logging continued for approximately 8 weeks. Pond area, volume, electrical conductivity (EC), pH, dissolved oxygen (DO), nutrient concentrations, and pelagic and benthic zone ash-free dry mass (AFDM) and chlorophyll-*a* were measured in the pond biweekly (Koch et al., 2014; Koch et al., 2019). Measurements of AFDM and chlorophyll-*a* (to approximate abundance of autotrophs) were repeated until the end of the growing season, during each of five or six resampling events (i.e., visits), between 19-June and 4-August, 2013.

Additionally, we collected macroinvertebrates during each visit (n = 5 – 6 per pond). We based our sampling protocol on other studies of shallow water wetland invertebrates (Gleason & Rooney, 2018; Swartz *et al.*, 2019), selecting a sampler type and mesh size that effectively captures larger-sized invertebrates in the absence of substantial vegetation (Meyer, Davis & Bidwell, 2013). To collect each of four or five replicate samples per visit, we pulled a D-frame net (500-μm mesh, surface area = 0.0604 m^2) upward through the extent of the water column (to include nektonic and benthic species) at randomly selected locations within the pond. Those macroinvertebrates large enough to be trapped by our net were identified to family level, or the lowest taxonomic resolution possible, and enumerated in the field when possible (Thorp & Covich, 2001; Merritt, Cummins & Berg, 2008); pupae were excluded from all counts. When logistical constraints prevented processing of samples in the field, specimens were preserved in 70% ethanol and counted later.

2.3 Data analyses

For each macroinvertebrate sample, we calculated the sampled water volume as the surface area of the net times sample depth and corrected all counts for volume sampled. We subsequently used an N-mixture modelling approach for our analyses (Royle, 2004), whereby the variation in replicate samples was used to estimate the average number of individuals of a given taxon exposed to sampling during each replicate sampling event (hereafter, abundance). Note that we do not compare measures of abundance among taxa given that estimates do not represent absolute abundance (see Barker *et al.*, 2018; Link *et al.*, 2018). Also note that because we used a 500-µm mesh, our inference was limited to individuals large enough to be captured by this mesh size. Because we were not estimating absolute abundance or directly comparing measures of abundance among taxonomic groups, undersampling of smaller individuals within taxa did not influence our findings.

To evaluate variation in abundance across visits in relation to covariates representing our hypotheses of interest, we structured our model to be open to changes in abundance between visits to a given pond but closed within replicates within a visit. The basic model for the observed counts can be written as:

$$n_{ijk} \sim Bin(N_{ij}, p_{ijk})$$

where the observed count, n_{ijk}, at pond *i* during visit *j* and replicate *k* is a binomial function of abundance at each pond during each visit, N_{ij}, and detection probability, p_{ijk}, at the observation level. For our study, p_{ijk} can be interpreted as a combination of incomplete detection and spatial variation in invertebrate density within a pond on a given visit. Abundance is assumed to arise from a Poisson distribution

$$N_{ij} \sim Pois\ (\lambda_{ij})$$

and can be modeled as function of covariates:

$$log\ (\lambda_{ij})\ =\ \alpha_i + \beta_l x_{ijl} + e_{ij}$$

where α_i are intercepts, x_{ijl} are values for covariate *l*, β_l are the associated coefficients, and e_{ij} are random effects. We used this basic model structure to assess the effects of measured covariates on the spatial and seasonal patterns of abundance for each of five coarse taxonomic groups that represent important prey items for consumers and that contribute substantially to overall biomass, as well as to energy and nutrient cycling in Arctic ponds.

After assessing collinearity among predictor variables (Zuur, Ieno & Elphick, 2010), we specified a single model for each taxonomic group. Based on a number of studies highlighting the importance of pH and dissolved oxygen on abundance and productivity of aquatic invertebrates (Table 1; Merritt et al. 2008), predictor variables for each group-specific model included these variables, as well as factors related to our hypotheses of interest: cumulative growing degree days (CGDD, calculated as the cumulative water temperature above a minimum threshold of 0°C; Cayton et al. 2015), ammonium (NH_4), and two indices of autotroph abundance: AFDM and chlorophyll-*a*, which were measured both in the pelagic (pAFDM, pCHLA) and benthic (bAFDM, bCHLA) zones. These indices were correlated for pelagic measurements (i.e. pAFDM and pCHLA), so only pCHLA was included in the models tested.

Ammonium was chosen as the best indicator of nutrient availability and biogeochemical cycling because other potentially limiting nutrients (e.g., nitrate and phosphate) were often below detection limits (Koch et al., 2014). In contrast to other nutrients, NH_4 is present in measurable quantities due to shallow thawing permafrost and has proven useful as an indicator of active biogeochemical cycling in other ponds and lakes in this region (Koch et al., 2014; 2018a; 2018b). To test for non-linear patterns in abundance related to water temperature, we also evaluated a quadratic term for CGDD (Bolker, 2008). Given that we were specifically interested in identifying the potential environmental mechanisms associated with temporal patterns in abundance, rather than simply describing the observed seasonal patterns, we did not include time itself (i.e. sampling day) as a covariate.

To test for variation in abundance of macroinvertebrates in relation to pond type, we included pond type as a fixed categorical term. A random effect term accounted for remaining variation in the data and overdispersion (i.e., extra-Poisson variation) in the counts that could lead to lack of fit. We also treated p_{ijk} as a random effect to address variation in detection probability. For each taxon, we fit the corresponding model to the data using JAGS 4.3.0 (Plummer, 2003) and R 3.1.0 (R Team, 2014), following the basic approach of Kéry and Schaub (2012). We used uninformative priors for all parameters, however, we did limit p to values ≥ -3 on the logit scale to avoid boundary issues. We ran each model for 80,000 iterations with 20,000 discarded as burn-in, retaining the remaining 60,000 for inference. We assessed model fit using the Bayesian p-value described by Kéry and Schaub (2012), and based inference of fixed effects on the precision (95% Bayesian credible intervals) of regression coefficients. If credible intervals of estimated parameters included zero, effects associated with these parameters were considered to be uninformative.

3 RESULTS

3.1 Physical and chemical characteristics of study ponds

For all study ponds (n=33), pH measurements indicated circumneutral conditions, but other physical and chemical characteristics (water temperature, dissolved oxygen, electrical conductivity, nutrients, AFDM, and chlorophyll-*a* concentrations) were more variable (Table 2). Across pond types, troughs were distinct both physically (smaller, deeper, colder) and chemically (lower pH and dissolved oxygen, higher electrical conductivity), and tended to warm more slowly (Figure 2). Based on chlorophyll-*a* levels, troughs also tended to have higher autotroph abundance in the benthic zone, compared to other pond types, but this pattern was not observed for pelagic chlorophyll-*a*, which was typically higher in coalescent ponds (Table 2).

3.2 Macroinvertebrate abundance

Our data summaries indicated that the three taxa we most commonly sampled in our study ponds (n=702 samples) were non-insect arthropods: Cladocera, Copepoda (Crustacea:Maxillopoda), and Collembola (Arthropoda:Hexapoda), followed by larval Chironomidae and Physidae. Conversely, for several taxa – larval Ephemeroptera (Insecta) and some Coleoptera (Insecta), as well as Oligochaeta (Clitellata), counts were exceptionally low. More taxonomically detailed summaries of the macroinvertebrate data (total estimated counts) are available as Supporting Information (see Table S1), and raw physical, chemical, and macroinvertebrate data are available at: https://doi.org/10.5066/P9K5EV4N (Koch *et al.*, 2019).

Results were generally consistent with our expectation of higher abundance in troughs, relative to all other pond types, but statistical differences varied among taxa. Anostraca was an exception to the general pattern – being essentially absent from trough ponds and only rarely collected from large coalescent ponds, with the highest numbers in polygons and small coalescent ponds. Cladocera were detected in all pond types, with the greatest abundance in troughs and small coalescent ponds. Whereas limnephilid larvae were primarily absent from polygon ponds, chironomid larvae and Physidae tended to be equally abundant across all pond types (Figure 3).

As with the effect of pond type, the relative influences of water temperature and NH_4 on abundance were variable across taxa. For four of the five taxa that we examined (Anostraca, Chironomidae, Cladocera, Limnephilidae), there was a relationship between cumulative temperature and abundance – and the effect of water temperature was consistent across pond types. We identified a negative relationship between water temperature and abundance for Anostraca, Limnephilidae, Chironomidae, and Cladocera, with evidence of a quadratic (non-linear) relationship for the latter taxon (Figure 4). Contrary to our expectation of positive relationships between abundance and nutrients, we did not detect an effect of NH_4 levels, and only the limnnephilid larvae became more abundant with increasing autotroph abundance (as indexed by bCHLA). Physid abundance was related neither to temperature nor NH_4 – but was most strongly related to pH levels, with lower numbers in more alkaline water (Table 3).

We found large variation among replicate samples, with low estimates of detection probability ($p < 0.2$) for all five taxa considered, reflecting the substantial variation in counts among replicates (2 – 200 fold) that we observed in our samples. Despite large amounts of observed variation, our posterior predictive checks (as represented by Bayesian *p*-values) indicated that model fit was adequate for all taxa (Table 3).

4 DISCUSSION

Our findings suggested that macroinvertebrate abundance in small thaw ponds of the Arctic Coastal Plain was variable across pond types, with troughs tending to support more abundant populations for most of the taxa we studied. In these high latitude ecosystems – as in other freshwater habitats where macroinvertebrate communities have been assessed –seasonal patterns of abundance were generally related to accumulated water temperatures (Everall *et al.*, 2015). Conversely, levels of a key nutrient – ammonium – had no detectable effect on seasonal patterns of abundance for any of the taxa that we assessed, and only in one case (limnephilid larvae), did we find evidence of a relationship between indices of primary productivity (chlorophyll-*a*, AFDM) and seasonal patterns of abundance. As environmental conditions and freshwater resources in the Arctic continue to change, including drying of polygons and increased numbers of troughs (Jorgenson *et al.*, 2015), these findings will facilitate an improved understanding of how populations of pond macroinvertebrates may respond, thereby contributing to more-informed decisions about conservation.

4.1 Variables associated with seasonal patterns of abundance for key wetland macroinvertebrates

As expected, trough ponds tended to have larger populations of the macroinvertebrates we studied, although specific differences related to pond type varied across taxa and were not statistically significant for larval Chironomidae or Physidae. Anostraca were an exception to the general pattern, and were not observed in troughs, possibly due to their inability to actively disperse into these habitats (Wiggins, Mackay & Smith, 1980). Consequently, this group may be vulnerable to landscape changes forecast for the Arctic Coastal Plain (i.e., increasing prevalence of trough habitats; Liljedahl *et al.*, 2016), whereas a shift toward more troughs on the Arctic Coastal Plain may be beneficial to other macroinvertebrates that appear to thrive in these habitats (e.g., limnephilids and Cladocera). However, we caution that predicting the specific responses of macroinvertebrate productivity to increasing trough habitat will require careful study across broader spatial and temporal scales.

Wetland macroinvertebrate communities are highly dynamic, varying substantially at both local and regional spatial scales (Batzer & Ruhí, 2013; Gurney *et al.*, 2017). Studies attempting to link this variability to causative factors, however, are limited and often provide conflicting results (Culler, Smith & Lamp, 2014; Kneitel *et al.*, 2017). In particular, whereas the ecological significance of water temperature in riverine ecosystems has been well established (Olden & Naiman, 2010; Lento *et al.*, 2022b), the consequences of thermal changes for the functioning of freshwater wetlands are less clear (Lee *et al.*, 2015; Helbig *et al.*, 2017). By directly assessing the relationship between cumulative water temperature and macroinvertebrate count data across the growing season, our study identifies relationships with water temperature for a number of taxa. For sampled Cladocerans in our study ponds, seasonal changes in abundance are related to water temperature in a curvilinear fashion, and across all pond types, abundance decreases above a cumulative water temperature of 450 degree days. This suggests that phenology of Cladocera is influenced by early-season warming, although the presence of different species in ponds with different seasonal temperature profiles may also contribute to the observed effect (Stross, Miller & Daley, 1980). Further studies, at a finer taxonomic resolution, are needed to understand species-specific thermal tolerance ranges and responses to warming (Wojtal-Frankiewicz, 2012). With respect to phenology, our results suggest that increasing water temperatures could advance the seasonal timing of peak abundance of Cladocera, but to directly evaluate this potential outcome, longer-term studies are necessary.

For Anostraca and larval Limnephilidae, the relationships we observed between abundance and water temperature seemed to indicate that seasonal warming did not influence phenology – at no point, did higher water temperatures correspond to increased abundance of these taxa. We speculate that the lower numbers of larval limnephilids we observed as pond temperatures warmed over the season are, in part, explained by increasing rates of emergence under such conditions. Development times and timing of adult emergence for insects can be highly sensitive to increases in water temperatures, with earlier emergence closely linked to heating treatments in several studies (Hogg & Williams, 1996; Braegelman, 2016). The seasonal decrease in abundance of limnephilid larvae that we observed (Koch *et al.*, 2019) is consistent with this idea.

Seasonal patterns of abundance of larval Chironomidae, which show initial declines as pond temperatures warm, before slightly increasing, might also be related to more rapid emergence in ponds that warm more quickly, although the temporal patterns that we observed in these species are less clear. Instead, the observed effect of temperature on chironomid larvae might reflect different species assemblages in warmer habitats, or potentially the addition of a new cohort of larvae later in the season (Butler & Braegelman, 2018; McFarlin *et al.*, 2018). Studies on timing of emergence of aquatic insects in relation to water temperatures and finer-scale taxonomic assessments will add valuable insight (Laske *et al.*, 2021), especially because faster development in warmer water may negatively affect body mass or size at maturity for adult insects, particularly for females (Sweeney, Vannote & Dodds, 1986; Rempel & Carter, 1987). Because larger size tends to confer greater fecundity to female insects, temperature-induced changes in development rates – in combination with shifting sex ratios in warmer water – might reduce reproductive output for insect fauna in small thaw ponds and lead to population-level declines (Peckarsky *et al.*, 2001; Sardiña *et al.*, 2017). Yet, it remains unclear whether such effects are being realized in northern ecosystems.

Lewis et al. (2016) suggest that warming water temperatures may be impacting populations of freshwater invertebrates in subarctic lakes, but Lougheed et al. (2011) report no change in pond invertebrate communities on the Arctic Coastal Plain in response to decadal changes in water temperature.

Based on our data, relative to other pond types, trough ponds are likely to reach the optimum growing degree days for certain taxa more slowly, with peak abundance of macroinvertebrates potentially occurring later in these habitats. Directed long-term studies are needed to fully understand the effects of sustained increases in water temperature on invertebrates in small thaw ponds. A clearer understanding of how changes in water temperature on the Arctic Coastal Plain will affect phenology of invertebrates is a particularly important research need in the context of phenological mismatch. The Match-Mismatch Hypothesis, which suggests that survival and recruitment of consumer populations decline when consumers and their prey become temporally decoupled during key life cycle events (Durant *et al.*, 2007), has been proposed as a mechanism linking climate change to declining populations across diverse animal taxa (Donnelly, Caffarra & O'Neill, 2011; McKinnon *et al.*, 2012).

For the taxa that we studied, we detected no direct influence of ammonium levels on abundance, which is generally consistent with other studies that highlight variable responses of aquatic invertebrates to nutrient concentrations. Collectively, such studies suggest that invertebrate responses to nutrients are likely indirect and dependent on how nutrient concentrations affects available food resources (i.e. autotrophs, detritus)(Cross *et al.*, 2006; Batzer, 2013). The magnitude of ammonium entering small trough ponds, and thus the potential for assimilation, can vary greatly depending on trough pond age (Koch *et al.*, 2018b), which may limit our ability to detect an impact through our indices of food resources for invertebrates (chlorophyll-*a* concentration and ash-free dry mass in the benthic and pelagic habitats). These indices were only weakly correlated to ammonium concentration, and resource availability (benthic chlorophyll-*a*) was related to abundance for only one of our study taxa (Limnephilidae).

Larval limnephilids are generally detritivores that primarily feed on decaying plant material or benthic algae (Merritt, Cummins & Berg, 2008; Klemmer *et al.*, 2012), and our results suggest that increasing nutrient inputs to small thaw ponds may positively influence their abundance, if such inputs lead to increases in benthic productivity. Whether detritivores, in general, are more likely to be impacted by increasing nutrients in the small thaw ponds of the Arctic Coastal Plain warrants further investigation. For example, abundance of Physidae was influenced by neither temperature nor nutrient levels, but was instead negatively correlated with pH, in contrast to previous studies in snails (Lodge *et al.*, 1987). Given the relatively narrow range of pH in the ponds we studied (6.6 – 8.9) and the low abundance of Physidae across all pond types, the effect we observed may have been related to covariance of pH with another more biologically relevant parameter, potentially macrophyte biomass or diversity (Lombardo & Cooke, 2002; Watson & Ormerod, 2004).

4.2 Conclusion

By identifying variables that influence the phenology of specific macroinvertebrate taxa occurring in small Arctic thaw ponds, our study highlights how seasonal patterns of abundance for these species might be affected by environmental change. Specifically, variation in seasonal patterns of warming in freshwater habitats is likely to exert a considerable influence on invertebrate fauna. Conversely, we found limited support for a direct influence of a key nutrient on seasonal changes in invertebrate numbers. Identifying the variables that influence invertebrate populations will facilitate improved predictions of how ongoing changes on the land will affect wildlife and ecosystems, a critical need for conservation, particularly in northern areas.

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AUTHOR CONTRIBUTION STATEMENT

Conceptualisation: KBG, JK, JAS, MW. Developing methods: KBG, JK, JAS, JHS, MW. Conducting the research: KBG, JK. Data analysis: KBG, JK, JHS. Data interpretation: KBG, JK, JHS. Preparation of figures and tables: KBG, JK, JHS. Writing: KBG, JK, JAS, JHS, MW.

DATA AVAILABILITY STATEMENT

Raw physical, chemical, and invertebrate data generated in this study for the Chipp North ponds are reported in Koch et al., 2019 (https://doi.org/10.5066/P9K5EV4N).

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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TABLE 1. To evaluate the influence of environmental factors on abundance, for each invertebrate taxon, we constructed a single model that included known factors of influence (from previous assessments), as well as factors related to our hypotheses of interest. NH_4 = ammonium, bAFDM = ash-free dry mass (benthic), CGDD = cumulative growing degree days (> 0°C), bCHLA = chlorophyll-*a* concentration (benthic), pCHLA = chlorophyll-*a* concentration (pelagic), DO = dissolved oxygen.

Taxon	**Model specification**
Anostraca	NH_4 + bAFDM + CGDD + $CGDD^2$+ pH^{a}
Chironomidae (larvae)	NH_4 + bCHLA + CGDD + $CGDD^2$ + pCHLA
Cladocera	NH_4 + bAFDM + CGDD + $CGDD^2$ + pH^{b}
Limnephilidae (larvae)	NH_4 + bCHLA + CGDD + $CGDD^2$ + DO^{c}
Physidae	NH_4 + bAFDM + CGDD + $CGDD^2$ + pH^{d}

[a] (Prophet, 1963; Havas & Hutchinson, 1982) [b] (Price & Swift, 1985) [c] (Nebeker *et al.*, 1996)

[d] (Holcombe, Phipps & Marier, 1984; Økland, 1992)

TABLE 2. Physical and chemical parameters (range shown, with mean (standard deviation) below) varied across pond types (n = number of ponds sampled).

	Trough (n = 15)	**Polygon (n = 5)**	**Coalescent, small (n = 6)**	**Coalescent, large (n = 7)**
Pond area (m^2)	5.0 – 49.0 22.3 (9.8)	38.3 – 292.8 133.5 (63.8)	228.1 – 1349.0 624.2 (308.7)	473.7 – 3594.0 11642.0 (827.5)
Average pond depth (m)	0.08 – 0.43 0.24 (0.07)	0.05 – 0.23 0.12 (0.04)	0.07 – 0.37 0.16 (0.08)	0.04 – 0.26 0.14 (0.06)
Water volume (m^3)	0.7 – 18.9 5.6 (3.5)	1.9 – 50.8 16.8 (12.9)	1.2 – 463.7 117.3 (122.4)	22.5 – 802.8 230.0 (192.2)
pH	6.59 – 7.92 7.26 (0.31)	6.99 – 8.49 8.00 (0.32)	7.14 – 8.56 8.07 (0.38)	7.34 – 8.88 8.19 (0.41)
DO (%)	4.0 – 134.1 52.8 (31.5)	80.4 – 137.5 108.8 (13.9)	66.2 – 152.0 113.4 (13.3)	79.9 – 146.4 117.1 (13.9)
EC (mS/cm)	0.084 – 0.709 0.36 (0.13)	0.079 – 0.421 0.212 (0.083)	0.036 – 0.327 0.161 (0.073)	0.151 – 0.465 0.263 (0.076)
Temperature (C)	4.2 – 16.6 8.8 (2.8)	5.0 – 20.9 12.8 (4.4)	5.4 – 19.9 12.4 (3.7)	4.5 – 21.5 14.1 (4.4)
NH_4 (mg/L)	<0.010 – 0.070 0.019 (0.012)	0.011 – 0.086 0.021 (0.013)	<0.010 – 0.039 0.020 (0.008)	<0.010 – 0.033 0.020 (0.005)
Chlorophyll-*a*, benthic (mg/L)	0.000 – 15.621 3.496 (3.008)	0.179 – 2.848 0.929 (0.680)	0.299 – 6.264 1.777 (1.288)	0.000 – 4.234 1.813 (1.323)
Chlorophyll-*a*, pelagic (mg/L)	0.047 – 11.833 0.913 (1.365)	0.311 – 4.473 1.243 (1.082)	0.139 – 10.816 1.168 (1.773)	0.232 – 9.891 2.287 (2.677)
Ash-free dry mass, benthic (mg/m^2)	30.0 – 260.0 100.6 (37.2)	30.0 – 160.0 83.1 (27.6)	60.0 – 150.0 88.5 (17.9)	40.0 – 258.2 80.8 (36.6)

TABLE 3. Mean parameter estimates (standard deviation) for the taxon-specific models highlighted key effects of temperature (for four key taxa). General goodness-of-fit for each model is represented by the Bayesian *p*-value (values between 0.01 and 0.99 indicate adequate fit). Covariates with an interpretable effect are indicated in bold. Cells with a '–' indicate that the covariate was not included in the specified model.

	Bayesian *p*-value	**pH**	**Dissolved Oxygen**	**CGDD**	**$CGDD^2$**	**NH_4**	**pChla**	**bChla**	**bAFDM**
Anostraca	0.95 (0.01)	0.66 (0.37)	–	**-0.92 (0.29)**	-0.30 (0.27)	-0.43 (0.31)	–	–	-0.65 (0.36)
Chironomidae (larvae)	0.76 (0.02)	–	–	**-0.22 (0.10)**	0.19 (0.10)	-0.01 (0.10)	-0.11 (0.09)	0.18 (0.10)	–
Cladocera	0.76 (0.02)	-0.17 (0.24)	–	**1.36 (0.22)**	**-1.16 (0.20)**	-0.26 (0.23)	–	–	0.19 (0.17)
Limnephilidae (larvae)	0.93 (0.01)	–	0.01 (0.30)	**-1.35 (0.28)**	0.18 (0.24)	0.13 (0.14)	–	**0.37 (0.16)**	–
Physidae	0.81 (0.02)	**-0.47 (0.18)**	–	-0.04 (0.11)	0.16 (0.10)	0.14 (0.12)	–	–	-0.15 (0.13)

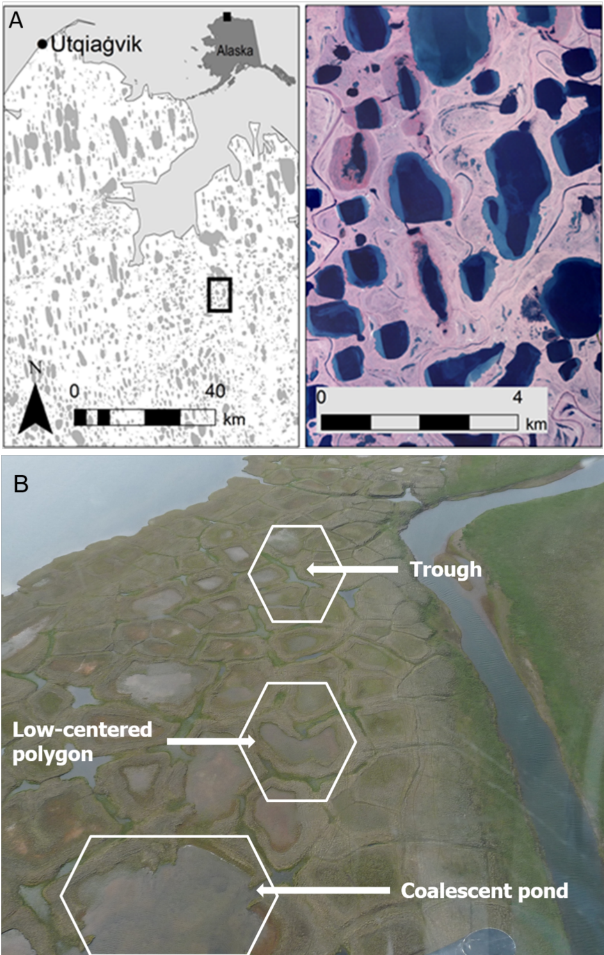
FIGURE LEGENDS

FIGURE 1 Invertebrates were collected from small thaw ponds on the Arctic Coastal Plain of Alaska: (A) Chipp River North Study Area (black rectangle, left panel, satellite view, right panel), and sampled ponds included (B) deep troughs, shallow, low-centred polygons, and larger coalescent ponds.

FIGURE 2 Relationship between water temperature (as measured by cumulative growing degree days) and Julian date for each of 4 pond types. All plots show raw data, as well as regression lines and estimated slope values (± 95% confidence intervals).

FIGURE 3 Predicted values for abundance for selected freshwater invertebrate taxa (restricted to individuals exposed to sampling using a net with a 500-µm mesh) at the Chipp River North Study Area in 2013 (note variable scales for each taxon). All plots show model-based estimates (mean ± 95% credible interval) of abundance for each pond type, as indicated on the x-axis. Means that do not share a letter are significantly different based on Bayesian *p*-values.

FIGURE 4 Predicted values (lines) for abundance of selected freshwater invertebrate taxa (restricted to individuals exposed to sampling using a net with a 500-µm mesh) at the Chipp River North Study Area in 2013 (note variable scales for each taxon). All plots show model-based estimates (mean ± 95% credible intervals) of abundance for each pond type. Raw observation data (points) are also plotted on the same scale for visual comparison.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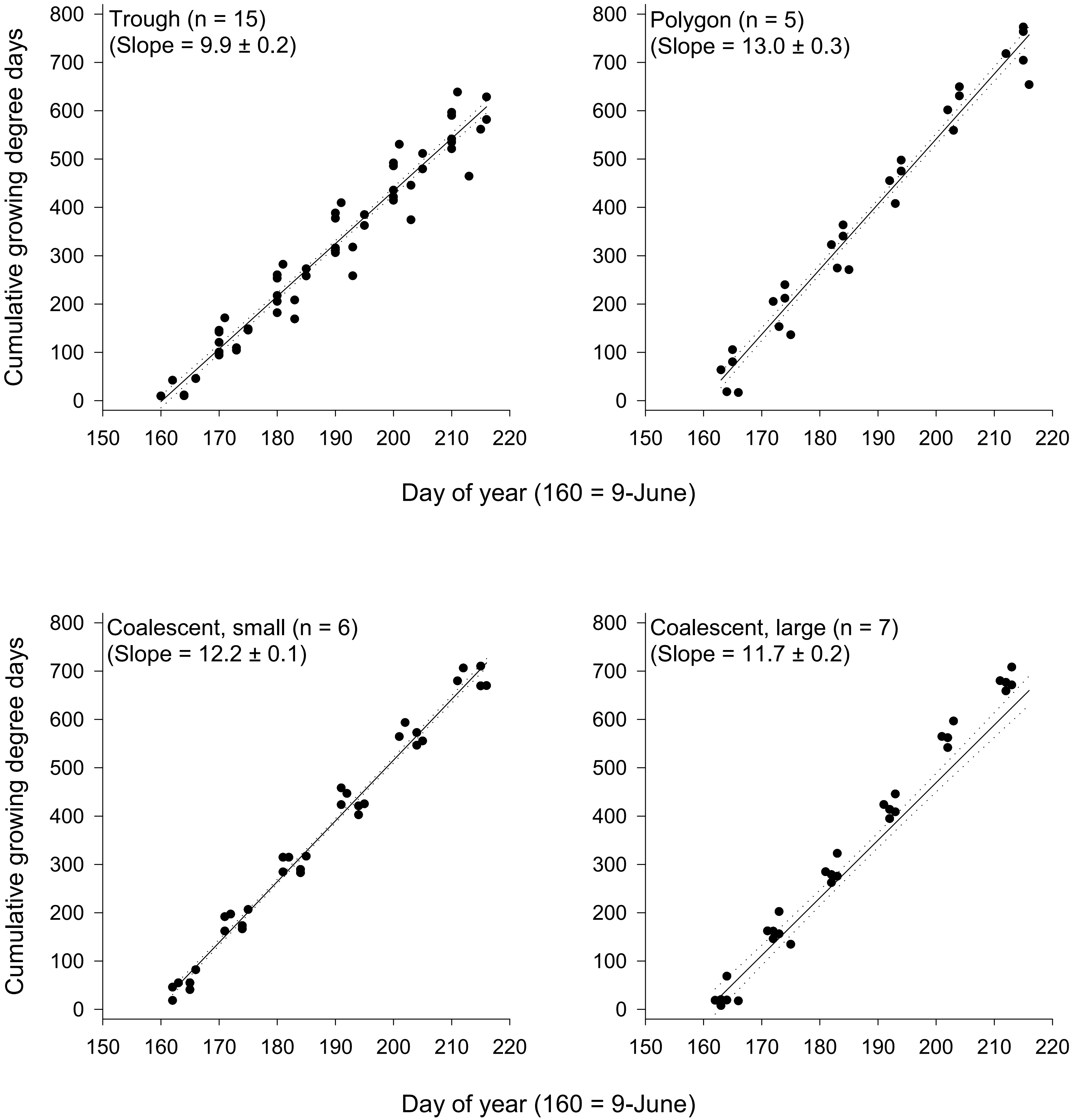
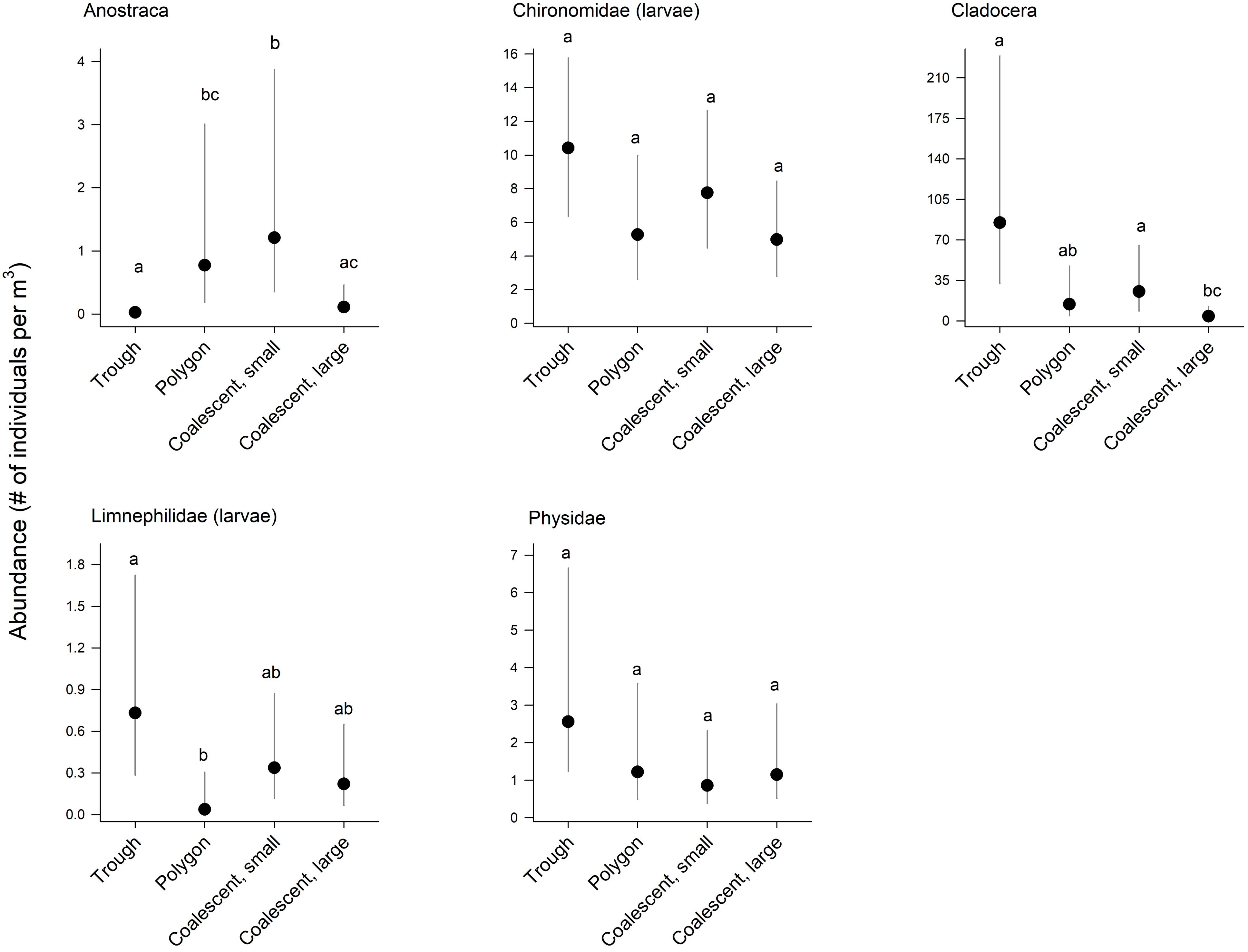
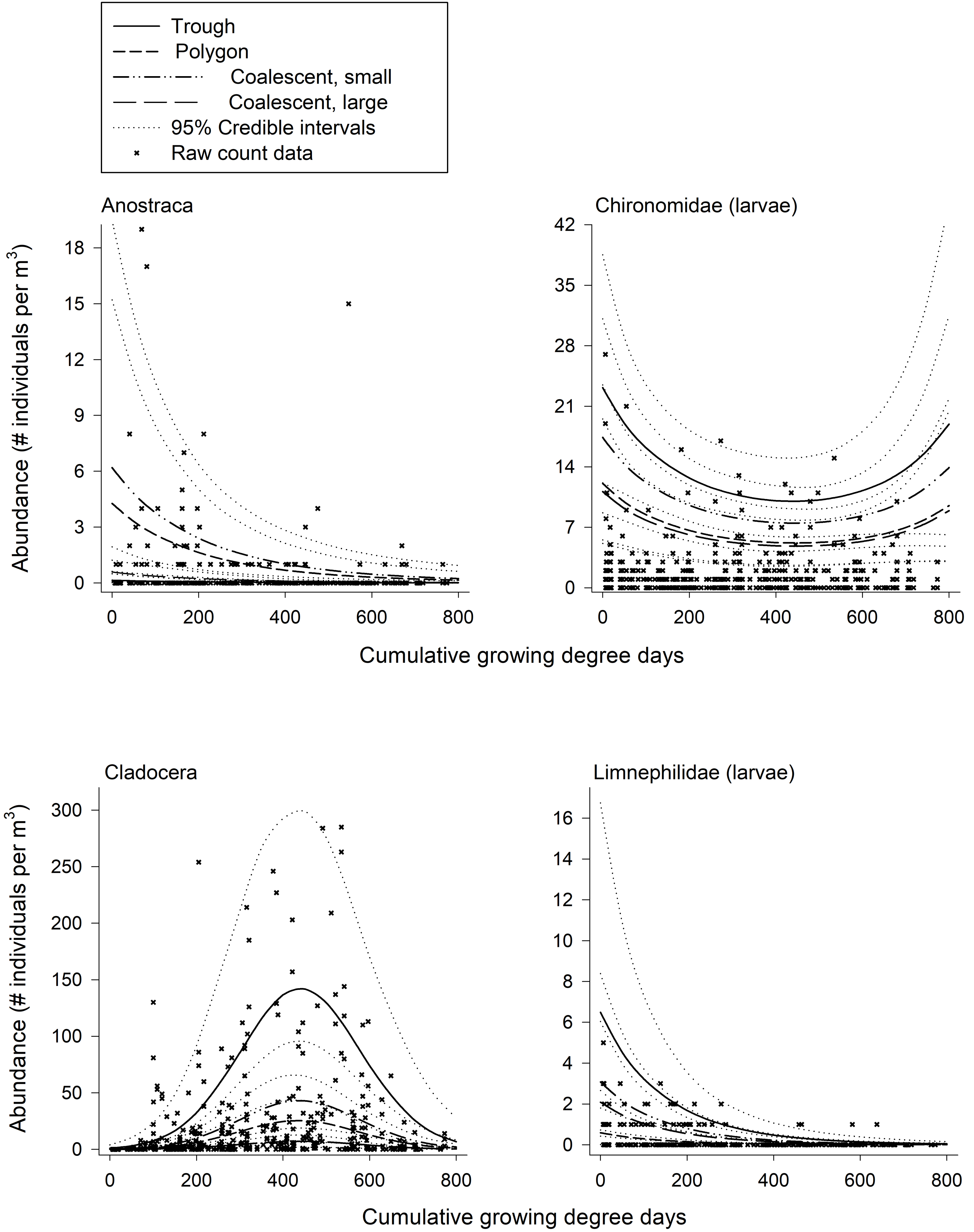

Trough (n = 15)
(Slope = 9.9 ± 0.2)
Polygon (n = 5)
(Slope = 13.0 ± 0.3)
Coalescent, small (n = 6)
(Slope = 12.2 ± 0.1)
Coalescent, large (n = 7)
(Slope = 11.7 ± 0.2)
Cumulative growing degree days
Cumulative growing degree days
Day of year (160 = 9-June)
Day of year (160 = 9-June)
0
100
200
300
400
500
600
700
800
150
160
170
180
190
200
210
220


Abundance (# of individuals per m^3)
Anostraca
0
1
2
3
4
a
bc
b
ac
Trough
Polygon
Coalescent, small
Coalescent, large
Chironomidae (larvae)
0
2
4
6
8
10
12
14
16
a
a
a
a
Trough
Polygon
Coalescent, small
Coalescent, large
Cladocera
0
35
70
105
140
175
210
a
ab
a
bc
Trough
Polygon
Coalescent, small
Coalescent, large
Limnephilidae (larvae)
0.0
0.3
0.6
0.9
1.2
1.5
1.8
a
b
ab
ab
Trough
Polygon
Coalescent, small
Coalescent, large
Physidae
0
1
2
3
4
5
6
7
a
a
a
a
Trough
Polygon
Coalescent, small
Coalescent, large


Trough
Polygon
Coalescent, small
Coalescent, large
95% Credible intervals
Raw count data
Anostraca
Chironomidae (larvae)
Cladocera
Limnephilidae (larvae)
Abundance (# individuals per m^3)
Cumulative growing degree days
0
3
6
9
12
15
18
0
7
14
21
28
35
42
0
50
100
150
200
250
300
0
2
4
6
8
10
12
14
16
0
200
400
600
800