

# Chironomid diversity and emergence following climate warming on Spitsbergen

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# Abstract

Over the last decades human activity has caused our climate to change. In the pristine region of the Arctic rising temperatures have had a greater impact than anywhere else on earth, altering the distribution and survival of many species. Insects, for example chironomids (non-biting midges) are one of the groups that are considered the first to be affected by climate change. On Spitsbergen, adult chironomids serve as an important food source for juvenile snow buntings. With rising temperatures, it has been hypothesized that a trophic mismatch would arise between the hatching of juvenile snow buntings and the timing of emergence of chironomid winged adults, as the chironomids are expected to respond more strongly to temperature than snow buntings. In order to predict diversity and abundance of chironomid adults on Spitsbergen, and thereby the future food availability of snow bunting nestlings, it is important to know which environmental conditions are responsible for chironomid diversity, emergence and abundance. Here, I give an overview of these environmental conditions, after which I will explain impacting factors on adult emergence in order to predict if a trophic mismatch between chironomids and snow buntings can arise. Not only air temperature, but also water temperature, depth, trophic status and nutrients such as nitrogen, phosphorus and carbon availability, salinity and oxygen availability can determine the chironomid diversity. Emerging time of chironomid adults can be advanced when temperatures will increase, possibly creating a trophic mismatch with the snow bunting. Unfortunately, the exact timing of emergence and abundance peak is hard to predict, since local conditions such as water temperature, depth, oxygen and nutrient availability, that can vary greatly within a small region and from year to year. As temperatures continue to rise in the Arctic, it is important to take a closer look at local environmental conditions and the possibility for altered life cycles of chironomids.

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# Introduction

Over the last decades human activity has caused our climate to change (IPCC, 2007). An extraordinary increase in carbon emission into the atmosphere has resulted in higher temperatures, impacting ecosystems globally (CDIAC, 2012; Crowley, 2000). In the pristine region of the Arctic, known for its long, cold and dark winters and its strong seasonal cycle, the highest increase in temperature has been observed compared to the rate of increase globally and the impact on these vulnerable ecosystems is stronger than elsewhere on the earth (Chapin *et al.*, 1991; ACIA, 2005; Holland & Blitz, 2003). Effects of rising temperatures in the Arctic include earlier snowmelt, increased precipitation and loss of permafrost (Hansen *et al.*, 2014; Haerberli & Hohmann, 2008). Consequently, it has a severe impact on the flora and fauna inhabiting the Arctic. For example, higher temperatures generally cause an increase in terrestrial as well as aquatic productivity and therefore an increase in vegetation cover (Rouse *et al.*, 1997). Furthermore, the distribution and survival of many animal species is altered (Parmesan & Yohe, 2003; Coulson, 2015). This concerns not only resident species, but also migrant species and possible newcomers who might be able to thrive better in these changed conditions in the Arctic.

Insects are one of the groups that are considered the first to be affected by climate change. Due to their short life cycle they are capable of responding quickly to temperature and other environmental changes (Coulson, 2015). Diptera are better adapted to the cold and harsh environment than any other order of insects and therefore they comprise an important part of the insect fauna in the Arctic region, both with regard to species number (Coulson & Refseth, 2004) and biomass (Bengston *et al.*, 1974). On Spitsbergen, 122 different Diptera species have been observed, of which Chironomidae (non-biting midges) are by far the biggest group on the archipelago, and comprise 66 species (Coulson, 2007). Chironomids are a cosmopolitan group occurring in all zoogeographical regions in the world (Saether, 2000), with different taxa inhabiting different ecological environments. Chironomids have four different developmental stages: the egg, the larva, the pupa and the winged adult. The larval stage consists of four instars. In lakes, the first instar is generally planktonic, whereas later instars are largely sedentary and inhabit hard and soft substrata such as rocks, submerged wood, aquatic macrophytes and sandy or muddy lake bottoms (Oliver, 1971). The pupal stage is brief and mostly sedentary, persisting for a few days at most (Oliver, 1971). At maturity, the pupa rises to the water surface where emergence of the winged adult can take place (Walker, 1987). The adult stage survives a few days to weeks at the most (Walker, 1987). Along latitudinal gradients, a variation in life history among chironomids is found. In tropical regions, multivoltine species are found, which can complete several generations per year. In the Arctic on the other hand, completing one life cycle can take up to several years (Oliver, 1968; Butler, 1982). However, univoltine species dominate, which lay eggs in summer, after which they will develop into larvae. The larvae go into diapause during winter (Thienemann, 1954), and pupal and adult emergence take place in spring (Danks & Oliver, 1972). Consequently, the emergence of adult chironomids is dependent on the onset of spring and the ending of the diapause. Changes in temperature in the Arctic could potentially affect emergence patterns in Arctic chironomid species.

On Spitsbergen, chironomids serve as an important food source for the chicks of migratory bird species, for example the passerine the snow bunting (Hussel, 1972). The snow bunting overwinters in temperate zones, and breeds in Arctic tundra's, like Spitsbergen (Sandberg & Pettersson, 1996). The major part of the diet of young snow buntings consists of adults insects, of which 80% are chironomids (Hussel, 1972). Therefore, their breeding success may depend

on the availability of an abundant and predictable supply of chironomid food (Hodkinson *et al.*, 1996). Chironomids are expected to respond faster to climate change than migratory birds like the snow bunting, which might experience difficulties estimating the onset of spring. This might result in an asynchronization of the hatching of snow bunting young and the emergence of chironomid winged adults. Moreover, climate change could cause a shift in chironomid species diversity and abundance in the Arctic region (Walker *et al.*, 1991b), as new species, from for example warmer regions, with potentially different life cycles and emerging patterns are able to colonize the newly formed niches. Therefore, it is interesting to be able to predict chironomid distribution patterns and which environmental conditions, besides temperature, are responsible for this.

In this review, I will first give an overview of the mechanisms involved in chironomid diversity in the Arctic. Secondly, I will explain what the impacts on the chironomid emergence and life history can be. Last, I will try to predict what the consequences will be for the nestlings of snow buntings on Spitsbergen.

## Environmental factors relevant for chironomid diversity in lakes

Already since the mid-20<sup>th</sup> century, limnologists have suggested that temperature may play an important role in determining which chironomid larvae species may occur in lakes (Thienemann, 1954). Later, Walker *et al.* (1991b) developed the first chironomid-temperature inference model where they reconstructed past temperatures in southeast Canada during the Late glacial period (Walker *et al.* 199a). This was possible because chironomid larval head capsules preserve well as subfossils in the lake sediments, and chironomid subfossil distribution was strongly correlated with mean July air temperature (Walker *et al.*, 1991b). By determining the species of the larval head capsules, the July air temperature they are associated with, and the age of the sediment wherein they were found, the past climate could be inferred. The results from this approach generally agree well with reconstructions of past temperatures based on other paleoclimatic proxy-indicators, like radiocarbon-dated lake sediments and diatom-inferred lakewater pH (e.g. Briner *et al.*, 2006). However, in some cases they disagree with reconstructions based on other proxies (e.g. Rosén *et al.*, 2003). For example, Rosén *et al.* (2003) used sediment cores from four alpine lakes in northern Sweden to see if diatom, chironomid and pollen assemblages consistently inferred Holocene July air temperatures. From 6000 years BP until now, all three proxies suggested similar temperatures. However, in some periods, especially before 7000 BP, there was a large variability in the temperatures that the proxies indicate. Rosén *et al.* (2003) suggest that chironomid, diatom and pollen assemblages were not only determined by temperature, but also by local conditions of the catchments, like snowfields or soil-forming processes. In other cases, different chironomid-based temperature models from the same geographical area can contradict each other. Rosenberg *et al.* (2004) studied chironomid assemblages from the late Holocene in southern British Columbia and found warm indicator species, whereas previous research had evidence for cooling during this period (e.g. Smith *et al.*, 1998). These examples suggest that other variables than just air temperature are involved in the distribution of chironomid species (Eggermont & Heiri, 2012). Temperature may impact organisms indirectly by affecting limnological variables such as oxygen and nutrient availability (Eggermont & Heiri, 2012). Yet at the same time, temperature may affect chironomids directly by influencing biochemical and physiological processes such as development and growth. In this chapter, I will explain which other variables than air temperature can be determinants of chironomid diversity and abundance, which can be useful when predicting chironomid diversity in the future.

## Water temperature and depth

The occurrence of chironomid species in a particular habitat both depends on the terrestrial as well as the aquatic environment (Pinder, 1995). However, the relatively short duration of the terrestrial adult stage compared to the larval stage, along with a general lack of feeding during the adult period, suggest that environmental controls on the larval stage are more important in determining chironomid distribution than terrestrial variables such as air temperature (Medeiros & Quinlan, 2011). Medeiros & Quinlan (2011) studied chironomid surface sediment samples in lakes in the eastern Canadian Arctic and found, consistent with Walker *et al.* (1991b), in deep lakes of colder regions at higher latitudes more chironomid species of the cold-adapted Diamesinae and Orthoclaadiinae subfamilies. In shallower lakes and ponds in the warmer and lower-latitude regions they found species that are considered to belong to warm-adapted taxa such as *Microtendipes*. However, not all lakes followed the simple latitude-temperature-depth relationship. Even though air temperatures decreased towards higher latitudes, some lakes were shallower but colder than lakes ~100 kilometres up north, and contained higher abundances of cold-adapted chironomid taxa such as *Heterotrissocladius*. Similarly, shallow ponds in the colder and northern areas contained several taxa (e.g., *Dicrotendipes* and *Cladopelma*) that are usually considered more warm-adapted. Thus, this study reveals that latitude and depth do not always have the same influence on water temperature and thereby chironomid diversity, and the within-region variability of these variables. Sometimes latitude is a better predictor, other times it can be water depth, and both must be paid attention to. Besides latitude and depth there can be other factors causing the mismatch between air temperature and chironomid assemblages, which will be discussed below.

## Trophic status & nutrients

Environmental factors determining chironomid diversity in Arctic lakes are highly multivariate (Broderson & Anderson, 2002). Due to their high degree of interrelation between these separate variables, it is a hard task determining which are the predominant determinants and which are of less important to chironomid structures in lakes. For example, higher temperatures and shallower lakes are generally associated with higher nutrient availability, which enhances algal production and increases photosynthetic incorporation in plant tissue of limnetic CO<sub>2</sub> and shifts the relative proportion of Dissolved Inorganic Carbon (DIC) towards HCO<sub>3</sub><sup>-</sup>, thereby increasing the pH into an alkaline environment. When comparing chironomid communities in different lakes, it can therefore be difficult to distinguish if water temperature, DIC content or pH has been the determining factor in the emergence of different chironomid assemblages (Michelutti *et al.*, 2010). However, several studies have successfully aimed to disentangle these variables.

For example, Broderson & Anderson (2002) show in their study from lakes in the Sisimiut–Kangerlussuaq region in Greenland that some chironomid species pairs such as *Paracladopelma* sp./ *C. oliveri* can have almost identical temperature optima, but very different trophic optima and thus reflect different lake group preferences. Moreover, their results show that trophic variables, defined by Total Nitrogen (TN) and Total Phosphorus (TP), had the strongest explanatory power for the chironomid species distribution in these lakes, and TN maintained a significant predictor in explaining the chironomid data even after temperature was partialled out. A significant relationship between TN and certain species taxa, such as *Chironomus anthracinus*, was also found in Canada (Medeiros & Quinlan, 2010). In contrast, some taxa (e.g. *Micropsectra insignolobus*-type) were primarily found in lakes and ponds with low TN concentration. In their study of Canadian Arctic lakes, Medeiros & Quinlan (2010)

revealed the importance of DOC and DIC in determining chironomid communities. In particular, *Tanytarsus lugens/Corynocera oliveri* were found in high abundances in lakes with higher DOC concentrations, and were absent from lakes with low DOC concentrations (<1.0 mg/L). These results are backed up by Gajewski *et al.* (2005), who also found *Tanytarsus lugens/Corynocera oliveri* in lakes with high DOC concentrations in the Arctic, whereas they were absent in areas where watershed DOC inputs were limited. Furthermore, in a sample of 44 lakes in the Midlands in England, Brooks *et al.* (2001) found TP to be the main predictor of chironomid distribution. The high concentration of TP is typical for eutrophic lakes, where a high TP promotes the growth of micro-organisms and macrophytes, providing food and shelter for chironomid larvae. Planktonic algae blooms increase the turbidity of the water, which is measured as a reduction in Secchi depth. Consequently, Secchi depth had a significant influence on chironomid diversity too, although this was only due to the high correlation with TP.

Langdon *et al.* (2008) showed that in northwest and west Iceland besides mean July air temperature, Total Carbon (TC) was a dominant predictor in explaining chironomid community structure. Chironomids had a normal distribution with respect to the temperature gradient in this study, whereas there was a clear association with TC, with higher abundances at TC values <4%. In many other chironomid datasets (e.g. Laroque *et al.*, 2001; Bigler *et al.*, 2006), TC co-varied with temperature, as warmer lakes tend to be more productive and organically enriched, and colder lakes are typically less productive and contain more clastic sediments. However, these relationships are not so straightforward in Iceland, as TC and temperature follow different ordination axes in predicting chironomid distribution. This is most likely explained by Iceland's active volcanic nature. The landscape is locally subjected to periodic deposition of nutrient rich tephra during volcanic activity, and subsequent removal of tephra by winds. Thus, regions with a cold air temperature can periodically be extremely nutrient rich, thereby affecting the chironomid community structure in the lakes (Langdon *et al.*, 2008). Moreover, this was not the only study finding an independent influence of sediment organic matter on chironomid assemblage, since Nyman *et al.* (2005) found that besides pH and total organic carbon, sediment LOI (loss-on-ignition) was a key factor determining chironomid diversity in western Finnish Lapland. Furthermore, Nazarova *et al.* (2017) show that in the lakes from the Pechora river basin in Russia, pH is an important explanatory factor in chironomid communities. The pH of most of these lakes are slightly acidic. Studies have shown that low pH values do not always cause any significant reduction in biomass of chironomid communities, but cause changes in their structure and decreases their species diversity (Woodcock *et al.*, 2005).

All these above-mentioned studies tell us that only looking at air temperature for predicting chironomid distribution is not enough, and variables such as water temperature and depth, that can vary locally over small distances, have their independent effect on chironomids. Moreover, even though trophic factors such as TN, TP, DOC/DIC, TC and pH are often related or correlated with temperature, they all exhibit their own influence on chironomid community structures.

## Eutrophication

As the aforementioned studies have shown, nutrients and trophic status of lakes are an important factor in determining chironomid distributions. However, not everywhere eutrophication has a profound effect on the chironomid assemblages in ponds and lakes in the Arctic, as will be revealed by the following examples.

Stewart *et al.* (2013) have done a successful attempt to disentangle the effects of nutrients and oxygen availability. In general, warm and shallow lakes are nutrient-rich, but oxygen depleted. Since both nutrients and oxygen are variables affecting chironomid diversity, it is challenging to determine which has the most profound effect. The seabird-affected ponds at Cape Vera in the high Canadian Arctic offer a solution to this problem. The study ponds span a gradient of nutrient concentrations that is primarily related to their distance from the nesting colony (i.e. ponds closer to the colony are more nutrient-enriched than ponds further away). Other predictor variables including temperature, depth and oxygen availability remain nearly constant. When nutrients would have an important influence on chironomid distribution, differences in chironomid communities among the ponds would be expected. Contrarily, there were large similarities between the seabird-affected and the seabird-free ponds. They found only a low abundance in chironomid taxa that are considered “eutrophic”. These results indicate that not nutrient availability, but oxygen levels regulate chironomid diversity in these ponds, although the higher nutrient abundance did cause an increase in overall chironomid abundance.

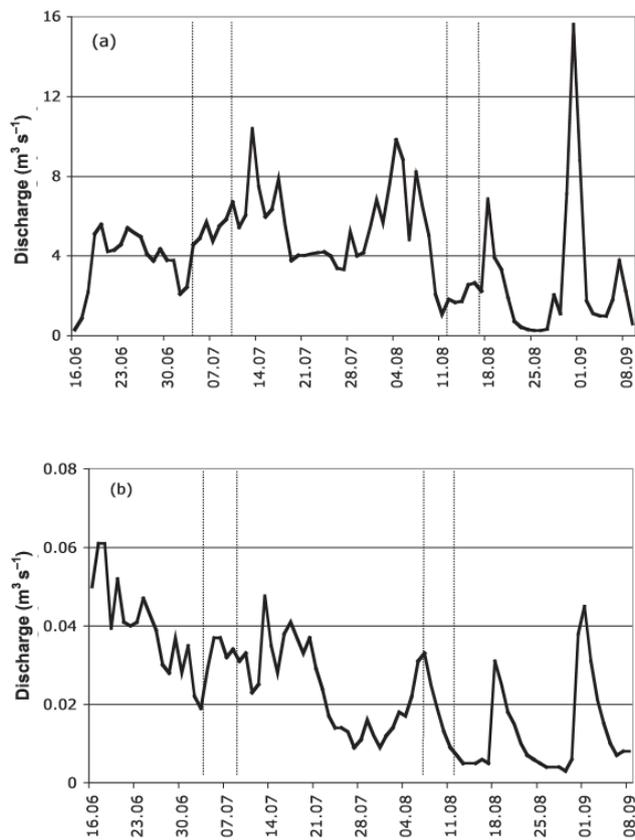
Similarly, Michelutti *et al.* (2010) observed the same ponds to see what variables are responsible for chironomid distribution. Although the ponds harboured similar taxa, they found that on the species level, pH was the only environmental variable that explained statistically significant amounts of variation in the chironomid assemblages. The differences in pH are likely caused by production-related changes driven by limnetic dissolved inorganic carbon (DIC). However, although there were some differences in chironomid assemblages between the ponds, there was a lack of difference in chironomid species between seabird-affected and seabird-free ponds. Therefore, Michelutti *et al.* (2010) suggest that the harsh environment at high latitudes largely override the effect of nutrients. Moreover, seabirds can also act as potent contaminants (Blais *et al.*, 2005). Brimble *et al.* (2009) measured sediment metal concentrations in the ponds at Cape Vera and indeed found that several of the ponds had a metal concentration that were considered toxic and exceeded the Canadian Sediment Quality Guidelines for the Protection of Aquatic Life.

Stewart *et al.* (2014) studied several shallow ponds on Cornwall Island (Nunavut, Canada) that were only recently eutrophicated by human sewage inputs (Schindler *et al.*, 1974). This explain the unusual characteristics of both elevated nutrient and oxygen levels measured in these lakes, whereas typical eutrophic lakes are often oxygen depleted. Besides, they looked at control ponds that were not eutrophicated to see the effect of nutrient enrichment in chironomid community structure. In both the sewage as well as the control ponds they found cold, stenotherm taxa such as *C. arctica*-type and *Hydrobaenus/Oliveridia*. The great similarity of chironomid species between the sewage and the control ponds demonstrate that nutrient concentrations are not directly affecting chironomid assemblages. The lack of typical ‘eutrophic’ chironomid species and the dominance of cold, oligotrophic species suggest that oxygen is a better predictor of chironomid assemblages at these sites, and not nutrients (Stewart *et al.*, 2014). In the eutrophicated sewage ponds a larger abundance of chironomids was found in the sediments, probably due to the higher food availability. Thus, even though nutrients often exhibit influence on chironomid diversity, this effect is not noticeable everywhere in the Arctic and is dependent on local conditions.

### Salinity, treeline & stream origin

Besides trophic status and water temperature, there are more factors influencing chironomid distribution and abundances. For example, Thienpont *et al.* (2015) have studied the effect of storm surges on the chironomid fauna in the MacKenzie Delta in the high Arctic of Canada. The low-lying outer plain of this delta is a lake-rich, freshwater environment, and since it is mostly <2 metres above mean sea level it is susceptible to the impact of storm surges (Rampton, 1988). They have studied 3 lakes in this region, 2 of which had been subjected to saltwater intrusion after a great storm in 1999, and the other served as an unaffected control site. After the storm, there was a decline in abundances of *Sergentia* and *Corynocera oliveri*-type chironomids, which had previously dominated the lakes. Previous studies have shown that these species are poorly represented in saline environments and are generally found in dilute waters (0-100 mg/L) (Walker *et al.*, 1995). Moreover, there was a dramatic increase in abundance of saline tolerant species such as *Paratanytarsus* and *Cricotopus/Orthocladius*, which continued to dominate the lakes to date, suggesting that the chironomid community has not recovered from this storm, and has therefore low resilience against environmental change. In contrast, the chironomid species composition in the control lake had not changed after the storm in 1999. Directly after the storm, the number of chironomids found in the sediments of the inundated lakes was low, but this increased shortly after the saltwater intrusion, creating no overall impact on chironomid abundance (Thienpont *et al.*, 2014). In the future, low-lying coastal ecosystems will be more susceptible to inundation due to sea-level rise and intensified storm activity caused by global climate change (Church *et al.*, 2013). The risk for storms will increase even faster in the Arctic due to the longer duration and extent of sea ice loss (Serreze *et al.*, 2007). This way, temperature is indirectly impacting chironomid communities by increasing storm activity in the Arctic.

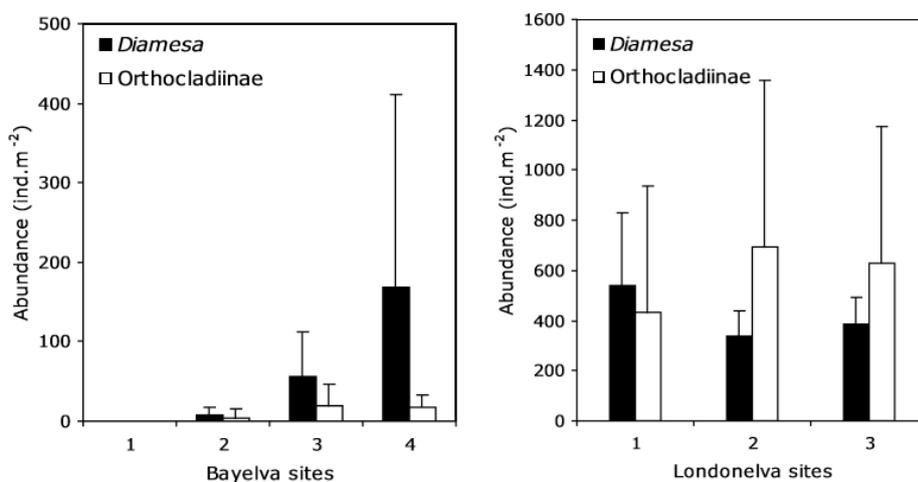
Nyman *et al.* (2005) have studied the chironomid assemblages in 50 shallow lakes located in north-west Finnish Lapland. The lakes are distributed across a gradient of ecosystems, from a coniferous forest to a barren tundra. They found an optimum of taxon richness in lakes within the mountain birch woodland, which represents an ecotonal transition zone between the major biomes of coniferous woodland to barren arctic tundra. This peak in species diversity at an ecotonal zone has been reported for many terrestrial organism groups and can be explained by a high habitat diversity and food availability diversity, as well as the climatic gradient in these regions (Rahbek, 1997). This study reveals the importance of ecological boundary regions for aquatic organisms too. Nyman *et al.*'s study is backed up by Walker & MacDonald (1995) who also found the highest chironomid species diversity in lakes around the treeline in the Northwest Territories in Canada. As climate changes, treelines will shift and thereby affect the chironomid diversity in the Arctic.



**Figure 1** | Average daily discharge in the study year (1997) at the stations **a)** Bayelva and **b)** Londonelva. Vertical dashed lines indicate the sampling periods. Note the different scales for discharge. From Lods-Crozet *et al.* (2007).

Besides lakes and ponds, chironomids can also be found in streams. Lods-Crozet *et al.* (2007) observed the effect of stream origin on chironomid distribution and abundance near Ny-Aalesund, in north-west Spitsbergen. They compared the chironomid community from a glacier-fed stream (Bayelva) with one from a snowmelt-fed stream (Londonelva). The glacier-fed stream Bayelva originates from two glaciers, Austre Brøggerbreen (11.7 km<sup>2</sup> in area) and Vestre Brøggerbreen (5.3 km<sup>2</sup>). The catchment is 30.9 km<sup>2</sup> and largely underlain by sedimentary rock including limestone, sandstone, shale and dolomite (Hodson *et al.*, 1998). Over the last 100 years the glaciers have retreated and the present annual rate of retreat is 0.4 m/year (Tranter *et al.*, 1996). Londonelva is a smaller stream (2200 m, compared to 3400 m for Bayelva). Its catchment area is only 0.7 km<sup>2</sup> and is dominated by exposed calcite marble. They show that stream origin has a major impact in both chironomid diversity and abundances and sediment load, channel stability, water temperature and in particular discharge

regime were important (Fig. 1). Water temperature did not exceed 4 °C at the Bayelva sites and were lower and significantly different from Londonelva. The sediment transport at Bayelva was 7,565 tonnes/year and only 0.91 tonnes at Londonelva (Bogen & Bønsnes 2003). The streams do differ in size, but their analysis showed that stream size was of little importance in explaining species abundance and richness (Lods-Crozet *et al.*, 2007).



**Figure 2** | Total abundance (individuals m<sup>-2</sup>) (arithmetic means with standard deviation) of *Diamesa* and orthocladids at the sampling sites in the two streams. From Lods-Crozet *et al.* (2007).

Between the two rivers, no significant difference in taxon richness was found, whereas there were major differences in abundances between the two streams. Total abundance of chironomids was 10 times larger in the snowmelt-fed Londonelva stream than in the glacial Bayelva stream. The fauna was dominated by the taxa Diamesinae and Orthocladiinae. Figure 2 shows the chironomid abundances found at the different sampling sites in the streams, where site 1 in the Bayelva stream is 300 metres away from the glacier front and site 4 2900 metres. Their analysis revealed that sediment discharge was the primary cause for the difference in total abundance of chironomids at the streams. Even though taxa in the two streams was similar, at species levels there was some variation. *Diamesa aberrata* and *D. bohemani* dominated the glacial stream, whereas *D. arctica* and *D. bertrami* colonised primarily the snowmelt-fed one. This study reveals the importance of water source for chironomid survival in the Arctic, and in particular sediment discharge regime.

These studies demonstrate the indirect effects climate change can have on chironomid diversity and abundance by increasing storm activity, relocating the treeline or increasing discharge by melting glaciers.

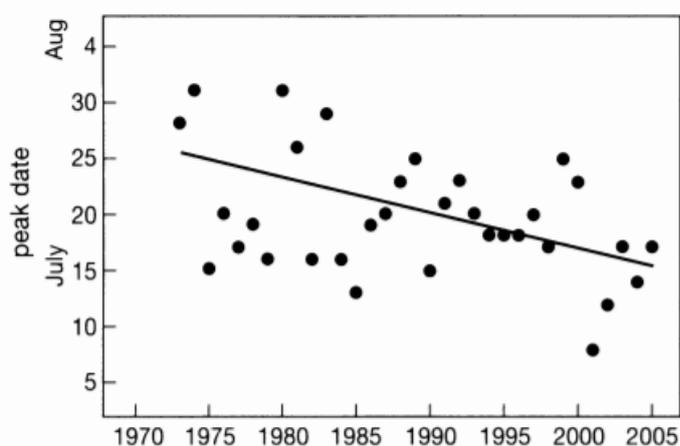
## Effects on adult emergence

Alongside the effects of temperature on chironomid species distribution and abundance, temperature can also influence the development and growth of chironomid individuals. For example, water temperature can impact development rates directly via increased respiration rates (Vannote & Sweeney, 1980), and indirectly by decreasing the oxygen concentration in the water and changing the quantity and quality of available food resources (Tokeshi, 1995). Generally, development and growth rates increase with temperatures (Eggermont & Heiri, 2012). Various temperature-dependent growth-rate models have been developed for aquatic insects, and optimal larval growth rates are associated with a particular temperature, where lower or higher temperatures cause a decrease in growth rate (e.g. Hyrun & Wallace, 1986). As a consequence, chironomid larvae living in regions with temperatures on the higher end of their optima, will commonly grow to be smaller adults than individuals inhabiting cooler regions (e.g. Atkinson, 1994). With rising temperatures, this could possibly occur at Spitsbergen.

Because of the effect temperature has on growth and development of insect larvae it also determines emergence time of adults. As mentioned in the introduction, in warm climates, several generations can be completed per year (Walker, 1987). In the cold Arctic region, however, relatively long life cycles are found, that can even extend up to seven years per generation (Butler, 1982a). However, Arctic chironomid life cycles reported in published articles mention nearly almost univoltine (one generation per year) life cycles. In these life cycles, eggs are laid in summer, larvae develop and go into diapause during the cold winter, where in spring they pupate and after that emerge into a winged adult. As a consequence of the importance of temperature for the development of chironomids, some species can complete only one generation in a colder climate, whereas it can possibly produce several generations in a warmer area (Nebeker, 1971, 1973). Moreover, variation in voltinism can even exist in the same water bodies. For example, Jonasson (1965) studied the *Chironomus anthracinus* population in Lake Esrom, Denmark, and showed that individuals inhabiting the shallower part of the lake emerged after one year, whereas the ones inhabiting the colder, deeper part emerged only after two years.

The effect of temperature on insect emergence peaks have been described in the following studies. Tulp & Schekkeman (2008) investigated weather-related and seasonal patterns in abundance of arthropods during four years in the Siberian tundra. With statistical models and a 33-year weather dataset they predicted timing of the annual arthropod peak from 1973 to 2005 (Fig. 3).

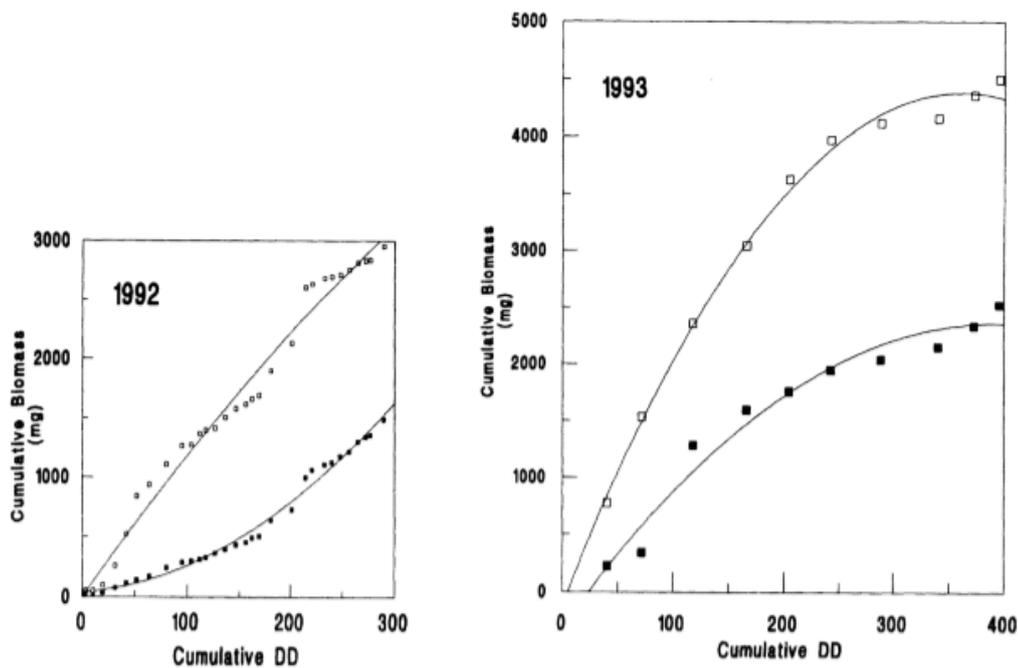
The advanced emergence peak was closely related to increasing temperature, as well as wind and precipitation. Unfortunately, the large



**Figure 3** | Predicted timing of the annual arthropod abundance peak in 1973-2005. From Tulp & Schekkeman (2008).

daily variation in Arctic weather (Myers & Pitelka, 1979) and its strong effect on insects make it hard to predict the exact emergence time of arthropods (Tulp & Schekkeman, 2008). At Spitsbergen, the same effect of temperature on arthropod abundance was observed (Jorna, 2016). Here, chironomid, as well as other Diptera, abundance was monitored over three (2013, 2014 & 2016) years in relation to temperature. In 2013 and 2014 temperature was the main predictor for chironomid abundance, whereas in 2016 abundance was no longer suppressed by low temperatures and seasonal patterns related to their emergence time and maturity cycle played an increased role.

In order to foresee the chironomid abundance and emergence time on Spitsbergen in the near future, it is important to look at the effect temperature can have on the emergence time of chironomid species. Hodkinson *et al.* (1996) investigated the abundance of flying chironomids over two seasons near Ny-Aalesund, West-Spitsbergen, at a polar semi-desert as well as at a tundra heath site. They trapped adult chironomids in eight Malaise traps from the end of June until the end of August, and the traps were emptied and chironomids were counted every two days. They found that in the warmer season (1993), the abundance of chironomids in the traps was very high in the first weeks, whereas it declined later in the season. Contrarily, in the colder season, the abundance of winged adults trapped had stayed stable over the whole season (Fig. 4). They suggest that in the warmer season, all the larvae that have gone into diapause



**Figure 4** | Cumulative biomass of chironomids (mg per trap) plotted against cumulative day degrees above zero for the polar semi-desert (open squares) and tundra heath (black squares) sites during 1992 and 1993. The axis scales are the same for both years to emphasize between-year differences. From Hodkinson *et al.* 1996.

during the winter, can soon pupate and emerge as the warmer spring starts. Later in the season, all the larvae pool have already emerged, and therefore there is a decline in adults later in summer. In the colder season, the threshold for pupating and emergence has not been reached for every individual at the onset of spring, due to variation in individual development rates. Some may have been developed far enough to immediately emerge, but others need more cumulative warm days to reach their temperature threshold and emerge only later in the season. Therefore, a constant abundance of adults is observed in this colder season. This means that an increased temperature can indeed advance the emergence time of chironomids.

Danks & Oliver (1972) have also shown that the emergence of chironomids takes place as early as possible in the season, depending on spring temperatures and the onset of thaw. However, they demonstrate too, that emergence time varies per species and per pond. The same species can have an emergence peak at the beginning of July in one pond, whereas its peak is observed only a few weeks later in another pond, determined by the local conditions of the pond, such as water temperature and depth. This way, in both warmer and colder years, the abundance of chironomid adults stays quite constant over the season in a certain region. This indicates that local environmental conditions have a large impact on the emergence of chironomid adults, and the variability of these conditions determines the abundance of chironomids throughout the season.

## Conclusion

Research on the abundance and diversity of chironomids in the Arctic has revealed that temperature has a large impact on chironomid communities. However, not only air temperature, but also water temperature, depth, trophic status and nutrients such as nitrogen, phosphorus and carbon availability, salinity and oxygen availability can determine the chironomid diversity in an aquatic environment. Even though these variables are sometimes related to air temperatures, they often have an independent impact on the chironomid species that are able to thrive in the lakes. Due to the large local variability of these factors it is hard, if not impossible, to make general predictions of the way chironomid communities will change as a response to climate change at Spitsbergen. Therefore, here I provide a table with lake trophic parameters of several studies discussed in this review. Moreover, the lake parameters of much-studied lakes on Spitsbergen from Van Geest *et al.* (2007) and Rautio *et al.* (2011), that may be of importance to the snow bunting are added as well.

**Table 1** | Water variables of lakes of some of the discussed studies in this review, together with water variables of lakes of two studies at Svalbard.

<i>Study</i>	<i>Location</i>	<i>Nitrogen (ug/l)</i>	<i>Phosphorus (ug/l)</i>	<i>pH</i>	<i>Temperature (°C)</i>	<i>Maximum depth (m)</i>	<i>DOC (mg/l)</i>	<i>Oxygen (mg/l)</i>
Borderson & Anderson (2002)	Greenland	0-1860	0-34		7.3-16.5	1.2-67.0		
Medeiros & Quinlan (2010)	Canada (Nunavut)	89-840	2-42	6.3-8.9	4.9-18.3	0.5-20.6	0.6-42.1	
Langdon <i>et al.</i> (2008)	Iceland	0-2 (in%)		6.1-8.40	6.5-10.8	5.2-12.8	0.3-20.4 (in%)	
Brooks <i>et al.</i> (2001)	England		69-1161	7.1-8.2		0.9-29.5		0-9
Nazarova <i>et al.</i> (2017)	Russia		100-9700	5.1-7.6	11.6-15.5	0.7-25		
Stewart <i>et al.</i> (2013)	Canada (NWT)	180-845	11-128	7.5-10.1	6.0-10.0		1.2-8.6	10-19
Michelluti <i>et al.</i> (2010)	Canada (NWT)	63-1590	0-177	7.2-10.9			0.7-10.8	
Van Geest <i>et al.</i> (2007)	Svalbard	24-296	2-32			0.4-2.5	0.2-1.9 (Part. C)	
Rautio <i>et al.</i> (2011)	Svalbard	166-1354	0-71	7.2-8.2	4.9		0.5-1.9	

This table is meant as a summary of trophic parameters and in which articles to find them, as well as an onset for further research. When trophic parameters of an aquatic environment of interest are known, like from Van Geest *et al.* (2007) and Rautio *et al.* (2011), one could see which article would be interesting to read when one wants to make a first prediction of chironomid structure in the environment of interest.

Furthermore, emerging time of chironomid adults can be advanced when temperatures increase (Tulp & Schekkeman, 2008; Jorna, report; Hodkinson *et al.*, 1996). This could potentially result in a lower food availability during the hatching period of snow buntings. Even though passerine birds start breeding earlier in warmer seasons (Fossoy *et al.*, 2014), their response to higher temperatures might not be as strong as chironomids, resulting in a asynchronization of hatching of juveniles with the chironomid peak. Moreover, as higher development rates can result in smaller adults (Eggermont & Heiri, 2012), the total biomass of chironomid might also decline. Unfortunately, the exact timing of emergence and abundance peak is hard to predict, since local conditions such as water temperature, depth, oxygen and nutrient availability, that can vary greatly within a small region and from year to year (Tulp & Schekkeman, 2008; Danks & Oliver, 1972; Jonasson, 1965). As temperatures continue to rise in the Arctic, it is important to take a closer look at local environmental conditions and the possibility for altered life cycles of chironomids.

# References

- ACIA, 2005. *Arctic climate impact assessment*, Cambridge: Cambridge University Press.
- Atkinson, D. (1994). Temperature and organism size: a biological law for ectotherms. *Advances in Ecological Research*, 25, 1-58.
- Bengston, S.-V., Fjellber, A. & Solhøy, T. (1974). Abundance of tundra arthropods in Spitsbergen. *Insect Systematics and Evolution*, 5, 137-142.
- Bigler, C., Heiri, O., Krskova, R., Lotter, A.F. & Sturm, M. (2006). Distribution of diatoms, chironomids and cladocera in surface sediments of thirty mountain lakes in south eastern Switzerland. *Aquatic Sciences*, 68, 154-171.
- Blais, J.M., Kimpe, L.E., McMahon, D., Keatley, B.E., Mallory, M.L., Douglas, M.S.V. & Smol, J.P. (2005). Arctic seabirds transport marine derived contaminants. *Science*, 309, 445.
- Bogen, J. & Bønsnes, T. E. (2003). Erosion and sediment transport in High Arctic rivers, Svalbard. *Polar Research*, 22, 175-189.
- Brimble, S.K., Foster, K.L., Mallory, M.L., MacDonald, R.W., Smol, J.P. & Blais, L.M. (2009). High Arctic ponds receiving biotransported nutrients from a nearby seabird colony are also subject to potentially toxic loadings of arsenic, cadmium, and zinc. *Environmental Toxicology*, 28, 242 -243.
- Briner, J. P., Michelutti, N., Francis, D. R., Miller, G. H., Axford, Y., Wooller, M.J. & Wolfe, A. P. (2006). A multi-proxy lacustrine record of Holocene climate change on north eastern Baffin Island, Arctic Canada. *Quaternary Research*, 65, 431-442.
- Broderson, K.P. & Anderson, J. (2002). Distribution of chironomids (Diptera) in low arctic West Greenland lakes: trophic conditions, temperature and environmental reconstruction. *Freshwater Biology*, 47, 1137-1157.
- Brooks, S.J., Bennion, H. & Birks, H.J.B. (2001). Tracing lake trophic history with a chironomid±total phosphorus inference model. *Freshwater Biology*, 46, 513-533.
- Butler, M.G. (1982a). A 7-year life cycle for two Chironomus species in arctic Alaskan tundra pools (Diptera: Chironomidae). *Canadian Journal of Zoology*, 60, 58-70.
- Butler, M.G. (1982b). Production dynamics of some arctic Chironomus larvae. *Limnology and Oceanography*, 27, 728-736.
- Carbon Dioxide Information Analysis Center (2012). <http://cdiac.ornl.gov/>
- Chapin, F.S., Jefferies, R.L., Reynolds, J.F., Shaver, G.R., Svoboda, J. & Chu, E.W. (1991). *Arctic Ecosystems in a Changing Climate*. San Diego: Academic Press.
- Church, J.A., Clark, P.U., Cazenave, A., Gregory, J.M., Jevrejeva, S., Levermann A., Merrifield, M.A., Milne, G.A., Nerem, R.S., Nunn, P.D., Payne, A.J., Pfeffer, W.T., Stammer, D. & Unnikrishnan, A.S. (2013). Sea level change. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V. & Midgley, P.M. (eds) *Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the*

- intergovernmental panel on climate change. Cambridge University Press, Cambridge, 1137-1216.
- Coulson, S.J. (2007). Terrestrial and freshwater invertebrate fauna of the High Arctic archipelago of Svalbard. *Zootaxa*, 1448, 41-58.
- Coulson, S.J. (2015). The alien terrestrial invertebrate fauna of the High Arctic archipelago of Svalbard: potential implications for the native flora and fauna. *Polar Research*, 34, 27364.
- Coulson, S.J. & Refseth, D. (2004). The terrestrial and freshwater invertebrate fauna of Svalbard including Jan Mayen. *A Catalogue of the Svalbard Terrestrial and Marine Animals: Invertebrates, Fishes, Birds and Mammals* (eds H.Strøm & H.Goldman). Norwegian Polar Institute, Tromsø.
- Crowley, T. J. (2000). Causes of Climate Change Over the Past 1000 Years. *Science*, 289, 270-277.
- Danks, H.V. & Oliver, D.R. (1972). Seasonal emergence of some high arctic chironomidae (diptera). *Canadian Entomologist*, 104, 661-686.
- Eggermont, H. & Heiri, O. (2012). The chironomid-temperature relationship: expression in nature and palaeoenvironmental implications. *Biological Reviews*, 87, 430-456.
- Fossoy, F., Stokke, B.G., Kåsi, T.K., Dyrset, K., Espmark, Y., Hoset, K.S., Wedege, M.I. & Moksnes, A. (2014). Reproductive success is strongly related to local and regional climate in the Arctic snow bunting (*Plectrophenax nivalis*). *Polar Biology*, 38, 393-400.
- Gajewski, K., Bouchard, G., Wilson, S.E., Kurek, J., & Cwynar, L.C. (2005). Distribution of Chironomidae (Insecta: Diptera) head capsules in recent sediments of Canadian Arctic lakes. *Hydrobiologia*, 549, 131-143.
- Haeberli, W. & Hohmann, R. (2008). *Climate, Glaciers and Permafrost in the Swiss Alps 2050: Scenarios, Consequences and Recommendations*. Fairbanks: Institute of Northern Engineering, University of Alaska, 607-612.
- Hansen, B.B., Isaksen, K., Benestad, R.E., Kohler, J., Pedersen, A.O., Loe, L.E., Coulson, S.J., Larsen, J.O. and Varpe, O. (2014). Warmer and wetter winters: characteristics and implications of an extreme weather event in the High Arctic. *Environmental Research Letters*, 9, 114021.
- Hodkinson, I.D., Coulson, S.J., Webb, N.R., Block, W., Strathdee, A.T., Bale, J.S. & Worland, M.R. (1996). Temperature and the biomass of flying midges (Diptera: Chironomidae) in the high Arctic. *OIKOS*, 75, 241-248.
- Hodson, A., Gurnell, A., Tranter, M., Bogen J., Hagen, J. O. & Clark, M. (1998). Suspended sediment yield and transfer processes in a small High-Arctic glacier basin, Svalbard. *Hydrological Processes*, 12, 73-86.
- Holland, M.M. & Blitz, C.M. (2003). Polar amplification of climate change in coupled models. *Climate Dynamics*, 21, 221-232.
- Hurn, A. D. & Wallace, J. B. (1986). A method in obtaining in situ growth rates in larval Chironomidae (Diptera) and its application to studies of secondary production. *Limnology and Oceanography*, 31, 216-222.

- Hussell, D.J.T. (1972). Factors affecting clutch size in arctic passerines. *Ecological Monographs*, 42, 317-364.
- IPCC (2007). Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. (eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor and H. L. Miller). Cambridge University Press, Cambridge, UK.
- Jonasson, P. M. (1965). Factors determining population size of *Chironomus anthracinus* in Lake Esrom. *Mitteilungen der Internationalen Vereinigung für Theoretische and Angewandte Limnologie*, 13, 139-162.
- Jorna, J. (2016). Summer abundance of arctic arthropods; Relations to environmental and vegetation changes. Master's thesis.
- Langdon, P.G., Holmes, N. & Caseldine, C.J. (2008). Environmental controls on modern chironomid faunas from NW Iceland and implications for reconstructing climate change. *Journal of Paleolimnology*, 40, 273-293.
- Larocque, I., Hall, R.I., & Grahn, E. (2001). Chironomids as indicators of climate change: a 100-lake training set from a subarctic region of northern Sweden (Lapland). *Journal of Paleolimnology*, 26, 307-322.
- Lods-Crozet, B., Lencioni, V., Brittain, J.E., Marziali, L. & Rossaro, B. (2007). Contrasting chironomid assemblages in two high Arctic streams on Svalbard. *Fundamental and Applied Limnology*, 170, 211-222.
- Medeiros, A.S. & Quinlan, R. (2011). The distribution of the Chironomidae (Insecta: Diptera) along multiple environmental gradients in lakes and ponds of the eastern Canadian Arctic. *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 1511-1527.
- Michelutti, N., Mallory, M.L., Blais, J.M., Douglas, M.S.V. & Smol, J.P. (2010). Chironomid assemblages from seabird-affected High Arctic ponds. *Polar Biology*, 34, 799-812.
- Myers, J.P. & Pitelka, F.A. (1979). Variations in summer temperature patterns near Barrow, Alaska - analysis and ecological interpretation. *Arctic and Alpine Research*, 11, 131-144.
- Nazarova, L.B., Self, A.E., Brooks, S.J., Solovieva, N., Strykh, S.L. & Dauvalter, V.A. (2017). Chironomid Fauna of the Lakes from the Pechora River Basin (East of European part of Russian Arctic): Ecology and Reconstruction of Recent Ecological Changes in the Region. *Contemporary Problems of Ecology*, 10, 350-362.
- Nebeker, A. V. (1971). Effects of high winter water temperatures on adult emergence of aquatic insects. *Water Resources*, 5, 777-783.
- Nebeker, A. V. (1973). Temperature requirements and life cycle of the midge *Tanytarsus dissimilis* (Diptera: Chironomidae). *Journal of the Kansas Entomological Society*, 46, 160-165.
- Nyman, M., Korhola, A. & Brooks, S.J. (2005). The distribution and diversity of Chironomidae (Insecta: Diptera) in western Finnish Lapland, with special emphasis on shallow lakes. *Global Ecology and Biogeography*, 14, 137-153.
- Oliver, D.R. (1968). Adaptations of arctic Chironomidae. *Annales Zoologici Fennici*, 5, 111-118.

- Oliver, D.R. (1971). The life history of the Chironomidae. *Annual Review of Entomology*, 16, 211-230.
- Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37-42.
- Pinder, L.C.V. (1995). The habitats of Chironomidae larvae. In *The Chironomidae: biology and ecology of non-biting midges*. Edited by P.D. Armitage, P.S. Cranston, and L.C.V. Pinder. Chapman & Hall, London, UK, 107–133.
- Rahbek, C. (1997). The relationship among area, elevation, and regional species richness in Neotropical birds. *The American Naturalist*, 149, 875-879.
- Rampton, V.N. (1988). Quaternary geology of the Tuktoyaktuk coastlands, Northwest Territories. Geological Survey of Canada, Natural Resources Canada, Ottawa
- Rautio, M., Dufresne, F., Laurion, I., Bonilla, S., Vincent, W.F. & Christoffersen, K.S. (2011). Shallow freshwater ecosystems of the circumpolar arctic. *Ecoscience*, 18, 204-222.
- Rosén, P., Segerström, U., Eriksson, L. & Renberg, I. (2003). Do diatom, chironomid, and pollen records consistently infer Holocene July air temperature? A comparison using sediment cores from four alpine lakes in northern Sweden. *Arctic, Antarctic and Alpine Research*, 35, 279-290.
- Rosenberg, S. M., Walker, I. R., Mathewes, R. W. & Hallet, D. J. (2004). Midge-inferred Holocene climate history of two subalpine lakes in southern British Columbia, Canada. *Holocene*, 14, 258-271.
- Rouse, W., Douglas, M., Hecky, R., Hershey A., Kling, G., Lesack, L., Marsh, P., McDonald, M., Nicholson, B., Roulet, N., and Smol, J.P. (1997). Effects of climate change on the freshwaters of Arctic and subarctic North America. *Hydrological Processes*, 11, 873-902.
- Sæther, O.A. (2000). Zoogeographical patterns in Chironomidae (Diptera). *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie*, 27, 290-302.
- Sandberg, R. & Pettersson, J. (1996). Magnetic orientation of snow buntings (*Plectrophenax nivalis*), a species breeding in the high Arctic: passage migration through temperate zone areas. *Journal of Experimental Biology*, 199, 1899-1905.
- Schindler, D.W., J. Kalff, H.E., Welch, G.J. Brunskill, H.K. & Kritsch, N. (1974). Eutrophication in the High Arctic – Meretta Lake, Cornwallis Island (75N Lat.). *Journal of Fisheries Research Board of Canada*, 31, 647-662.
- Smith, M.J., Pellatt, M.G., Walker, I.R. & Mathewes, R.W. (1998). Postglacial changes in chironomid communities and inferred climate near treeline at Mount Stoyoma, Cascade Mountains, southwest British Columbia. *Journal of Paleolimnology*, 20, 277-293.
- Serreze M.C., Holland, M.M. & Stroeve, J. (2007). Perspectives of the Arctic's shrinking ice cover. *Science*, 315, 1533–1536.
- Stewart, E.M., Michelutti, N., Blais, J.M., Mallory, M.L., Douglas, M.S.V. & Smol, J.P. (2013). Contrasting the effects of climatic, nutrient, and oxygen dynamics on subfossil chironomid assemblages: a paleolimnological experiment from eutrophic High Arctic ponds. *Journal of Paleolimnology*, 49, 205-219.

- Stewart, E.M., McIver, R., Michelutti, N., Douglas, M.S.V. & Smol, J.P. (2014). Assessing the efficacy of chironomid and diatom assemblages in tracking eutrophication in High Arctic sewage ponds. *Hydrobiologia*, 721, 251-268.
- Thienemann, A. (1954). Chironomus. *Leben, Verbreitung und wirtschaftliche Bedeutung der Chironomiden. Binnengewässer*, 20, 1-834.
- Thienpont, J.R., Steele, C., Vermaire, J.S., Pisaric, M.F.J., Kokelj, S.V. & Smol, J.P. (2015). Synchronous changes in chironomid assemblages in two Arctic delta lake ecosystems after a major saltwater intrusion event. *Journal of Paleolimnology*, 53, 177-189.
- Tokeshi, M. (1995). Life cycles and population dynamics. In: *The Chironomidae: The Biology of Non biting Midges*. (eds P. Armitage, P. S. Cranston and L. V. C. Pinder), 225-268. Chapman & Hall, London, UK.
- Tranter, M., Brown, G.H., Hodson, A. & Gurnell, A. (1996). Hydrochemistry as an indicator of subglacial drainage system structure: a comparison of alpine and sub-polar environments. *Hydrological Processes*, 10, 541-556.
- Tulp, I. & Schekkeman, H. (2008). Has prey availability for arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation. *Arctic*, 61, 48-60.
- Van Geest, G.J., Hessen, D.O., Spierenburg, P., Dahl-Hansen, G.A.P., Christensen, G., Faerovig, P.J., Brehm, M., Loonen, M.J.J.E. & Van Donk, E. (2007) Goose-mediated nutrient enrichment and planktonic grazer control in arctic freshwater ponds. *Oecologia*, 153, 653-662.
- Vannote, R. L. & Sweeney, B. W. (1980). Geographical analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *The American Naturalist*, 115, 667-695.
- Walker, I.R. (1987). Chironomidae (Diptera) in Paleoecology. *Quaternary Science Reviews*, 6, 29-40.
- Walker, I.R. & MacDonald, G.M. (1995). Distributions of Chironomidae (Insecta: Diptera) and Other Freshwater Midges with Respect to Treeline, Northwest Territories, Canada. *Arctic and Alpine Research*, 27, 258-263.
- Walker, I. R., Mott, R. J. & Smol, J. P. (1991a). Allerød-Younger Dryas lake temperatures from midge fossils in Atlantic Canada. *Science*, 253, 1010-1012.
- Walker, I.R., Smol, J. P., Engstrom, D. R. & Birks, H. J. B. (1991b). An assessment of Chironomidae as quantitative indicators of past climatic change. *Canadian Journal of Fisheries and Aquatic Sciences*, 48, 975-987.
- Walker, I.R., Wilson, S.E. & Smol, J.P. (1995). Chironomidae (Diptera): quantitative palaeosalinity indicators for lakes of western Canada. *Canadian Journal of Fisheries and Aquatic Science*, 52, 950-960.
- Woodcock, T., Longcore, J., McAuley, D., Mingo, T., Bennatti, C.R., & Stromborg, K. (2005). The role of pH in structuring communities of main wetland macrophytes and chironomid larvae (Diptera). *Wetlands*, 25, 306-316.