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Controls of climate, catchment erosion and biological production on long-term community and functional changes of chironomids in High Arctic lakes (Svalbard)

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ABSTRACT

Arctic freshwater basins are diversity hotspots and sentinels of climate change, but their long-term variability and the environmental variables controlling them are not well defined. We examined four available lake sediment sequences from High Arctic Svalbard for their subfossil Chironomidae communities, biodiversity and functional traits and assessed the influence of climatic and limnological variability on the long-term ecological dynamics. Our results indicated that collector-filterers had an important role in the oligotrophic sites, whereas collector-gatherers dominated the nutrient-enriched sites with significant bird guano inputs. In the oligotrophic sites, benthic production, taxon richness and taxonomic and functional diversity were highest during the early Holocene, when temperatures showed a rapid increase. An increase in subfossil abundance and diversity metrics was also found in recent samples of the oligotrophic sites, but not in the bird-impacted sites, where the trends were decreasing. When partitioning out the environmental forcing on chironomid communities, the influence of climate was significant in all the sites, whereas in-lake production (organic matter) was significant in two of the sites and catchment erosion (magnetic susceptibility) had only minor influence. The findings suggest that major changes in Arctic chironomid assemblages were driven by climate warming with increasing diversity in oligotrophic sites, but deteriorating ecological functions in environmentally stressed sites. We found that although taxonomic and functional diversity were always coupled, taxonomical and functional turnovers were coupled only in the oligotrophic sites suggesting that the ecological functions operated by chironomids in these low-productivity sites may not be as resilient to future environmental change.

1. Introduction

A significant portion of inland biodiversity in the Arctic is found in freshwater lakes (Rautio et al., 2011). However, ongoing climate warming, which has amplified impacts in the Arctic (Serreze and Barry, 2011; Linderholm et al., 2018) is altering the balance of aquatic communities by rates already exceeding natural variability (Smol and Douglas, 2007). Although it is well-documented that aquatic communities have been increasingly changing in the Arctic (Wrona et al., 2016), less is known about the variability between different types of freshwater systems or limnoecological functioning, especially at long temporal scales. In addition, understanding long-term climate impacts on Arctic lake ecosystems requires separating the effects of climate from within-lake and catchment changes over a long time span (Paull et al., 2017). The paleolimnological approach to studying long-term limnoecological changes provides powerful means of examining ecological shifts and the environmental history of lakes, giving insights into past and present dynamics, but also offering an opportunity to forecast future changes in aquatic environments (Smol, 2010; Pla-Rabes et al., 2011). However, only few quantitative palaeolimnological studies have addressed biodiversity questions, defining the drivers of change in species richness or identifying functional traits that best capture ecosystem processes (Gregory-Eaves and Beisner, 2011; Nevalainen et al., 2018).

Paleoecological research has traditionally focused on using communities as the main unit, since many aquatic organism groups that are well preserved as subfossils, such as diatom algae, Cladocera zooplankton and Chironomidae macrobenthos, respond sensitively to environmental perturbation through community changes (Frey, 1988). Although the potential of using functional traits to characterize long-term aquatic ecosystem changes has been known (Jeppesen et al., 2001) it has gained more interest only recently (Fournier et al., 2015;

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Nevalainen et al., 2015a, 2015b; Nevalainen and Luoto, 2017). Since ecosystem functions rely more on the living habits of organisms than taxonomic categories, the use of functional traits may enable the assessment of ecosystem functioning and stability more comprehensively than traditional taxonomic identification (Cadotte et al., 2011). Benthic invertebrates, including chironomids, have vital functions in lakes operating crucial biogeochemical cycles behind food-web structure by taking part in processes related to detrital decomposition, nutrient release and transfer, prey control and food supply (Palmer et al., 1997; Covich et al., 1999), for example. While being invaluable for lake functions, benthic insect larvae can be the most threatened organisms in lakes (Strayer and Dudgeon, 2010).

For chironomids, the most useful functional traits for ecological studies are related to their feeding habits (Pinder, 1986; Schmera et al., 2017). Although chironomids tend to vary in their modes of feeding depending on their life cycle stage (Grey et al., 2004), their primary feeding preferences can be divided into eight guilds: collector-filterers, collector-gatherers, predators, scrapers, shredders, parasites, omnivores and piercers (Merritt and Cummins, 1996). Collector-gatherers (deposit-feeders) are the most common feeding guild that depends on fine particulate organic matter of sediments. Another common guild, collector-filterers, which often live in tubes, are suspension feeders filtering food particles from the water column, epiphytic algae being the most common food item (Berg, 1995). Among the less dominant guilds, scrapers shear food material from the sediment and submerged rocks, vegetation and wood, whereas shredders feed on coarse particulate organic matter, such as living vascular plants, submerged wood, macro- or colonial algae, or leaf litter (Berg, 1995). Predators on the other hand attack other invertebrates and ingest all part of the prey (engulfers) or pierce the tissues and withdraw the fluids of the prey (piercers) (Cummins, 1973). In paleolimnology, the thus far rarely used chironomid functional feeding characteristics or their paleo-diets estimated through stable isotopic compositions from head capsules (van Hardenbroek et al., 2014; Belle et al., 2017; Schilder et al., 2017) can be used to provide valuable information on past food web structures, biogeochemical cycling or environmental controls.

Previous studies (Brooks and Birks, 2004; Nevalainen et al., 2012) have revealed significant ecological changes in High Arctic lakes in Svalbard, which is located in an intersection of major oceanic currents and is a focal point for the development of the Polar Front (Majewski et al., 2009). Hence, Svalbard represents a climatically and oceanographically sensitive region (Isaksen et al., 2007). Building from previous studies with available chironomid taxonomic biostratigraphies, in this study, we analyze chironomid functional traits (feeding guilds) and compare the findings against independent air temperature reconstructions, sediment organic matter content and magnetic susceptibility measurements. Our analysis has the potential to provide new knowledge on the influence of climate and limnology on High Arctic ecosystem changes at long temporal scales (decades to millennia). More particularly, we test chironomid paleobiodiversity changes in relation to natural variability caused by sudden short-term catchment originated "pulse events" and in relation to long-term climatic "press events" (Massaferro and Corley, 1998). Furthermore, in wetland ecosystems species turnover across environmental gradients is restricted to functionally similar species, i.e. taxonomic and functional turnover are decoupled, which may allow maintaining ecosystem functioning when subject to future environmental change (Robroek et al., 2017). Here, we test this general theory in four High Arctic aquatic ecosystems with different environmental characteristics including typical low-nutrient tundra sites and nutrient-enriched bird-impacted sites with densely vegetated catchments.

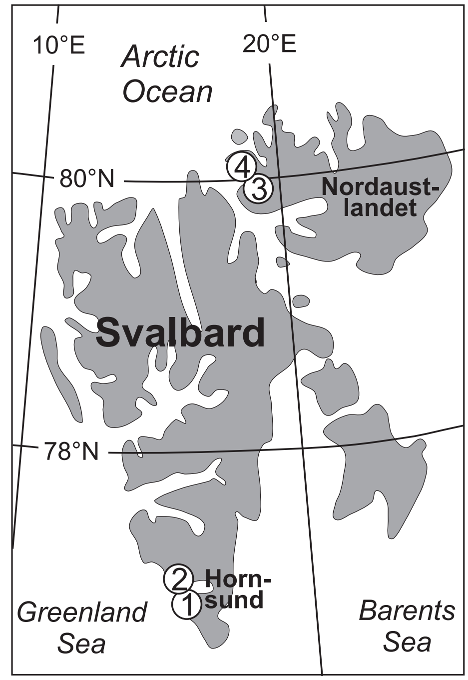

Fig. 1. Study sites. Lakes 1) Svartvatnet, 2) Fugledammen, 3) Einstaken and 4) Kvalroslaguna in Hornsund and Nordaustlandet, High Arctic Svalbard.

2. Material and methods

2.1. Study sites

The four study sites are located in southern (Hornsund fjord area, mean July air temperature 4.2 °C) and northeastern (Nordaustlandet, mean July air temperature 2 °C) Svalbard (Fig. 1). Svartvatnet (76°90′N, 15°68′E; 63 m a.s.l.) is an oligotrophic 80 ha lake located at the southern side of the Hornsund fjord, whereas Fugledammen (77°00′N, 15°52′E; 15 m a.s.l.), located at the northern side of the fjord, is a shallow (2 m) nutrient-rich pond (2 ha). Einstaken (79°58′N; 18°42′E, 54 m a.s.l.) is situated in the Murchisonfjorden area at the southern side of the Isvika bay in Nordaustlandet. The 5 ha lake is currently oligotrophic and has a depth of 8 m. The fourth study site, Kvalroslaguna (79°58′N, 18°34′E; 12 m a.s.l.), is a shallow (1 m) nutrient-rich pond (0.5 ha), located at the northern side of the Isvika bay. Einstaken and Svartvatnet are pristine periglacial basins, whereas Fugledammen and Kvalroslaguna have significant grazing and nesting bird-influence in their catchments. At both sites, birds are present in high numbers and produce a large amount of guano, which is high in nutrients, resulting in thick moss growth in the catchment and giving a murky eutrophic appearance to the ponds. Detailed description of catchment and limnological characteristics can be found from previous publications (Luoto et al., 2011, 2014, 2015, 2016, 2018).

2.2. Sediments and subfossil analyses

Samples consist of two long sediment cores (sampled with a Livingstone piston corer) from Einstaken (134 cm, past ~13,000 years) and Svartvatnet (164 cm, past ~5500 years) and two short cores (sampled with a Russian peat corer) from Fugledammen (100 cm, past ~150 years) and Kvalroslaguna (28 cm, past ~400 years). The cores from Einstaken and Kvalroslaguna were collected during the 2009 field campaign in Nordaustlandet (Kinnvika project) and the Svartvatnet and Fugledammen cores during the 2013 field campaign in Hornsund (QUAL project). The chronologies of the sediment profiles have been previously published (AMS ^{14}C, paleomagnetic, ^{137}Cs and ^{210}Pb dating), alongside analyses of organic matter content (measured as loss