When glaciers and ice sheets melt: consequences for planktonic organisms

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Abstract

The current melting of glaciers and ice sheets is a consequence of climatic change and their turbid meltwaters are filling and enlarging many new proglacial and ice-contact lakes around the world, as well as affecting coastal areas. Paradoxically, very little is known on the ecology of turbid glacier-fed aquatic ecosystems even though they are at the origin of the most common type of lakes on Earth. Here, I discuss the consequences of those meltwaters for planktonic organisms. A remarkable characteristic of aquatic ecosystems receiving the discharge of meltwaters is their high content of mineral suspensoids, so-called glacial flour that poses a real challenge for filter-feeding planktonic taxa such as *Daphnia* and phagotrophic groups such as heterotrophic nanoflagellates. The planktonic food-web structure in highly turbid meltwater lakes seems to be truncated and microbially dominated. Low underwater light levels leads to unfavorable conditions for primary producers, but at the same time, cause less stress by UV radiation. Meltwaters are also a source of inorganic and organic nutrients that could stimulate secondary prokaryotic production and in some cases (e.g. in distal proglacial lakes) also phytoplankton primary production. How changes in turbidity and in other related environmental factors influence diversity, community composition and adaptation have only recently begun to be studied. Knowledge of the consequences of glacier retreat for glacier-fed lakes and coasts will be crucial to predict ecosystem trajectories regarding changes in biodiversity, biogeochemical cycles and function.

Keywords

INTRODUCTION

The current rapid retreat of glaciers and ice sheets contitutes one of the most prominent signs of climate change (IPCC, 2007, 2013). Most glaciers are expected to significantly shrink within the next decades and, eventually, many low elevation glaciers will disappear in this century (Zemp *et al.*, 2009). The retreat of glaciers and ice sheets is a global phenomenon and several areas of the world including the Alps, Greenland and the Central

and Southern Andes are identified as particularly vulnerable (IPCC, 2007, 2013). In the Alps, for example, glaciers located below 3000 m above sea level are those showing the most significant reduction in area (Zemp *et al.*, 2009). Changes in the area covered by glaciers are not exclusive of the 20–21th century and several periods of glacier retreat and expansion are known during Earth history (Solomina *et al.*, 2015). An important difference, however, is that compared with the early mid-Holocene, current glacier retreat has a clear anthropogenic component (Marzeion *et al.*, 2014) and rates seem to be higher than in the past (Solomina *et al.*, 2015). Interestingly, the abrupt glacier retreat in the Alps after the mid-19th century maximum (i.e. at end of the Little Ice Age), is attributed to the increase in black carbon emissions, as a consequence of industrialization in Western Europe (Painter *et al.*, 2013).

One obvious consequence of the melting of glaciers and ice sheets is the long-term loss of natural freshwater storage in frozen form (70% of the Earth's freshwater is stored under glaciers and ice sheets) that will have, beside the alteration of the hydrological cycle, also a strong societal impact in many parts of the world (Hinkel *et al.*, 2014; Kohler *et al.*, 2014). The current rapid melting of glaciers and ice sheets has also resulted in the mobilization and transport of different inorganic and organic molecules stored for long periods (Fountain *et al.*, 2012), as well as of pollutants. For example, the melting of rock glaciers in some mountain areas of the Alps has dramatically increased levels of nickel and other metals in lakes that now exceed thresholds for drinking water standards and have unknown hitherto biological effects (Thies *et al.*, 2007). Similarly, the retreat of tropical mountain glaciers has strongly impaired water quality in areas like the Cordillera Blanca, Peru, due to high concentrations of lead and nickel (Fortner *et al.*, 2011). Further, the retreat of glaciers makes available, soils, plant detritus and nutrient resources previously buried under the ice, which are important for both the succession of the biota in terrestrial and aquatic ecosystems. For instance, in glacier forelands, soil heterotrophic microbial communities rely on ancient and recalcitrant carbon sources accumulated in past periods of glacier fluctuations, before primary succession of vegetation takes place (Bardgett *et al.*, 2007). Finally, the shrinking of glaciers is also affecting the biodiversity of rivers and streams (Jacobsen *et al.*, 2012), where more studies are available compared with lakes.

Yet, the melting of glaciers and ice sheets has another important consequence, that is, the creation of many new proglacial and ice-contact lakes (Fig. 1) around the world, where terrain topology allows (Carrivick and Tweed, 2013). Some of those newly created lakes are not stable and can be emptied through dangerous outburst floods. Nevertheless, the number of new lakes, as well as the increase in glacial lake area are relevant. For example, estimates based on a scenario where all glacier ice disappears in the Swiss Alps, predict ~500 new lakes (>1 ha) (Linsbauer *et al.*, 2012), which represents ~30% more lentic systems for Switzerland. In other regions, such as in northern Patagonia, total glacial lake area has increased by ~65% from 1945 to 2011 (Loriaux and Casassa, 2013).

Lakes of glacial origin are probably the most numerous on Earth (Wetzel, 2001), but surprisingly, little is known about their plankton and general ecology at creation and during their early ontogeny, particularly when turbidity levels were high. Thus, the newly created lakes offer an opportunity to understand for example, the structure and functioning of the

food-web, who are the first colonizers and what environmental factors shape these communities. The current retreat of glaciers also offers almost natural laboratory conditions in the form of deglaciation chronosequences that help us to elucidate what changes take place when turbid glacial lakes shift to a clear condition after they lose connectivity with the glacier. The study of deglaciation chronosequences, for instance, has been for many decades a crucial research strategy to understand primary succession in terrestrial ecosystems (e.g. William *et al.*, 1971; Kaufmann, 2002; Raffl *et al.*, 2006).

In this Horizons article, I will discuss how the melting of glaciers and ice sheets can influence planktonic organisms and processes and then, identify open questions that may guide future research in this area. Though most of the information is based on lakes, examples of coastal areas affected by glacier meltwaters discharge are also included.

Why are aquatic ecosystems affected by meltwaters unique?

A singularity of proglacial and ice-contact lakes, as well as of coastal areas receiving discharge of glacier meltwaters is the presence of a high concentration of mineral suspensoids. These particles, so-called glacial flour or glacial milk, resulting from subglacial erosion of the bedrock (actually it should be named "rock flour") are delivered to recipient aquatic ecosystems by proglacial streams/rivers or by runoff (Smith, 1978; Hodder *et al.*, 2007). The mineralogical characteristics of glacial flour depends largely on the lithology of the underlying bedrock (Ashley, 2002), but its size range falls typically within that of clays and fine silt (Smith, 1978; Gallegos *et al.*, 2008; Chanudet and Filella, 2009; Sommaruga and Kandolf, 2014). Thus, the fine-sized mineral suspensoids give waters a typical "milky" look (Fig. 1), as well as a high reflectance (Gallegos *et al.*, 2008). Glacial flour in young proglacial/ice-contact lakes gives a characteristic gray hue to the water, which is probably the water color at the origin of glacial lakes (Fig. 1). Later, as lakes become less turbid and more productive, their color shifts to a bright turquoise (Fig. 1).

Several factors influence turbidity levels in aquatic ecosystems receiving glacier meltwaters, such as for example, glacier proximity (proximal or distal proglacial lakes), the glacier to lake area ratio, water residence time, maximum depth of the water body, wind fetch (resuspension), ice-cover duration, thermal/salinity stratification and the relative contribution of glacier runoff and proglacial streams to the total water inflow from the catchment. Under exceptional runoff conditions, turbidity can reach extreme values, as observed for example, in reservoirs of the Swiss Alps where up to 644 nephelometric turbidity units (NTU) have been recorded [Bonalumi *et al.*, 2011, in the original paper formazin turbidity units (FTU) are used]. However, even at turbidity values that are one order of magnitude lower, the abundance of mineral suspensoids is very high. For example, at 14 NTU [corresponding to a 1% depth for photosynthetically active radiation (PAR) of ~0.5 m], the abundance of glacial particles in the size range 0.7–4 μm is ~2.8×10^6 mL^{-1} (Sommaruga and Kandolf, 2014). This is one order of magnitude higher than the bacterial abundance and three orders of magnitude higher than the phytoplankton abundance, typically found in oligotrophic aquatic ecosystems (Wetzel, 2001). Similarly important from a food-web perspective, is the overlap in size of glacial and food particles (pico- and nanoplankton) available to filter-feeding planktonic species. Further, in contrast to inorganic

particles found in productive aquatic ecosystems (typically estuaries or shallow eutrophic lakes), particles in glacial flour tend to have very low organic coating and no or very few attached bacteria (Sommaruga and Kandolf, 2014). Analyses by scanning electron microscopy of glacial flour from a proglacial mountain lake also indicate that particles have sharp edges and, thus, have a potential for causing physical damage when ingested (Sommaruga and Kandolf, 2014). Altogether, these characteristics make aquatic ecosystems affected by glacier meltwaters to be very special.

Consequences of glacier meltwaters for planktonic organisms

Sediment records for Lake Baikal show a widespread negative effect of glacier meltwaters on the food-web during the last glacial maximum. For example, diatoms, chrysophyte cysts and zooplankton are absent during this period despite being found before it (Karabanov *et al.*, 2004). Similarly, the discharge of glacier meltwaters at the start of the Younger Dryas has been argued to largely affect the survival of lake organisms (Birks *et al.*, 2000). A high concentration of glacial flour certainly represents a challenge for filter- and interception-feeding planktonic organisms, particularly, if they cannot discriminate against them. This is because either they will largely fill their gut with inorganic particles or they will need to invest more energy in finding a suitable food particle among the "cloud" of mineral suspensoids. This in turn, will results in a decrease in feeding efficiency, as well as in the allocation of energy to somatic growth and reproduction. If one adds the effect of glacial flour to the oligotrophic condition of proglacial and ice-contact lakes, the resulting scenario concerning food resources is extreme. One pioneering study on the effect of glacial flour on lake biota is that of Koenings *et al.* (Koenings *et al.* 1990), who in laboratory experiments demonstrated that growth and survival of *Daphnia* is significantly reduced in the presence of mineral suspensoids. Similarly, Sommaruga and Kandolf (Sommaruga and Kandolf 2014) found in experiments with a natural heterotrophic nanoflagellate (HNF) community from a clear alpine lake and with single phagotrophic HNF species that the addition of glacial flour negatively affects growth and survival depending on the concentration of particles. They also established that the negative effect is due to the interference of glacial flour with the efficient uptake of bacteria (i.e. it causes a decrease in clearance rates) rather than to physical damage. High turbidity levels caused by the discharge of glacier meltwaters into clear lakes have been found to also alter trophic interactions between planktivorous fish species and *Daphnia* with an overall positive effect for the prey (Jönsson *et al.*, 2011).

The discharge of meltwaters from glaciers or ice sheets into a lake or coastal area can affect planktonic organisms by several other mechanisms that do not involve a direct effect of glacial flour. For example, the massive discharge of glacier meltwaters into coastal fjords has been implicated in extensive zooplankton mortality (Weslawski and Legezyriska, 1998). However, whether this is consequence of the load of glacial particles or of changes in salinity and osmotic stress remained unanswered (Weslawski and Legezyriska, 1998). Another physical factor affected by the discharge of glacier meltwaters into recipient waterbodies is temperature (Svendsen *et al.*, 2002;Slemmons *et al.*, 2013). The average water temperature in the water column of glacier-fed lakes is typically lower than in clear ones (Gallegos *et al.*, 2008), though in distal proglacial alpine lakes, maximum temperatures at the surface can reach similar values. It is noteworthy that, during strong glacier runoff and

precipitation events, holomixis in glacier-fed alpine lakes can occur several times during summer (Peter and Sommaruga, unpublished). This "polymictic" kind of thermal regime contrasts with the typical dimictic one, known for clear alpine lakes located in the temperate zone. Further, the discharge of cold waters with a high content of glacial flour can cause density underflows in the recipient lakes (Gilbert and Crookshanks, 2009; Bonalumi *et al.*, 2011).

The discharge of turbid glacier meltwaters also significantly reduces the extent of the euphotic zone (Modenutti *et al.*, 2000; Svendsen *et al.*, 2002; Hylander *et al.*, 2011; Rose *et al.*, 2014) and this in turn, is expected to reduce photosynthetic rates and integrated primary production rates as found, for example, in fjords receiving glacier runoff (Piwosz *et al.*, 2009). Paleolimnological studies also provide evidence that primary production is reduced during prolonged periods of glacier meltwater discharge caused by climatic warming (Vinebrooke *et al.*, 2010). However, measurements of primary production conducted in distal glacier-fed alpine lakes of the central Rocky Mountains, USA, showed the opposite effect (Slemmons and Saros, 2012). In a comparison with lakes receiving runoff from both snow and glacier meltwaters with those that are fed only by snow meltwater, higher primary production rates were found in the former type of lakes (Slemmons and Saros, 2012). This was attributed mainly to the stimulatory effect of the higher supply of reactive nitrogen provided by glacier meltwaters in that area (Saros *et al.*, 2010; Slemmons and Saros, 2012). Further, the glaciers in this case are distant enough from the lakes, so that lake primary production is not impaired by inorganic turbidity (Slemmons and Saros, 2012).

The reduction in PAR by glacial flour may also have consequences for the stoichiometry of phytoplankton and grazers (Laspoumaderes *et al.*, 2013). Following the predictions of the light:nutrient ratio hypothesis (Sterner *et al.*, 1997), these authors found that the food quality of primary producers and the competition outcome between herbivorous zooplankton with different phosphorus requirements, such as *Daphnia* and the copepod *Boeckella*, are affected by the strong horizontal gradient in water transparency formed by the discharge of glacier meltwaters into a clear lake. Along this transparency gradient, the light:phosphorus supply ratio positively covaries with the seston C:P ratio (i.e. a higher C:P means a lower nutritional quality) and results in a decrease of the relative abundance of P-rich *Daphnia* to low-P *Boeckella* when light penetration increases. In other words, the turbid conditions improve the nutritional quality of phytoplankton during this time-window (Laspoumaderes *et al.*, 2013).

The horizontal gradient in water transparency observed in lakes receiving the discharge of turbid glacier meltwaters affects also the vertical distribution of phytoplankton and zooplankton in the water column (Hylander *et al.*, 2011). In this context, it is important to consider that not only is PAR rapidly attenuated in a turbid system, but also UV radiation (UVR, Svendsen *et al.*, 2002; Rose *et al.*, 2014; Tartarotti *et al.*, 2014), which in high-mountain and polar areas, is a relevant environmental stress factor (Sommaruga, 2001; Vincent *et al.*, 2007). Thus, the discharge of glacier meltwaters protects primary producers from UV stress (Martyniuk *et al.*, 2014). Since UVR is also important in regulating daytime depth distribution of zooplankton (Williamson *et al.*, 2011), species living in turbid glacier-fed lakes probably do not follow the typical daytime escape reaction from surface waters

observed in clear alpine lakes (Fisher *et al.*, 2014, B. Tartarotti *et al.* in prep.). Further, the rapid UV attenuation in the water column will minimize negative effects on sensitive processes, such as on heterotrophic bacterial production (Sommaruga *et al.*, 1997). Though the high scattering of short UV wavelengths caused by glacial flour (Rose *et al.*, 2014) can result in higher UV to PAR ratios and eventually impair sensitive organisms (Leavitt *et al.*, 2003), this effect is expected to be only significant very close to the water surface, where UV irradiance (particularly of the short wavelengths UV-B) is high. In fact, direct measurements of backscattering in turbid glacier-fed lakes ("turquoise" lakes) show low values in comparison to those expected based on reflectance (Gallegos *et al.*, 2008).

As mentioned before, glaciers, at least in some regions, supply inorganic nutrients such as nitrogen accumulated from local and distant sources over time, to recipient water bodies. It is becoming clear, however, that glacier meltwaters also supply significant amounts of organic carbon in dissolved (Hood *et al.*, 2009, 2015; Singer *et al.*, 2012) and in particulate form (e.g. as estimated for Greenland, Hood *et al.*, 2015). These recent estimates indicate that global glacier/ice sheet runoff contributes 1.04 ± 0.18 TgC year^{-1} to proglacial freshwater systems and coastal areas of the world (Hood *et al.*, 2015). Interestingly, glacier-derived dissolved organic carbon (DOC) appears to be highly biologically available (Hood *et al.*, 2009, 2015). Another essential nutrient supplied by glacier meltwaters is phosphorus (Hodson, 2006). Most of the phosphorus is probably not biologically available (being adsorbed in the mineral clay phases), but if a small fraction is made available as reactive phosphorus, the large supply of glacial flour in glacial meltwaters could compensate for its adsorption and low availability (Hodson *et al.*, 2008) and stimulate production. Experimental evidence indicates that the addition of dry glacial flour to a natural bacterial glacier meltwater community significantly stimulates bacterial production when incubated at water temperatures found in proglacial lakes (Mindl *et al.*, 2007). Actually, many of the prokaryotes occurring in proglacial lakes may derive from the glacier itself (Anesio and Laybourn-Parry, 2012) and find better growing conditions (e.g. higher water temperatures) in the recipient water body (Mindl *et al.*, 2007). Anesio *et al.* (2009), however, observed that bacteria living in cryoconite holes in glaciers can attain high activity, even at low water temperatures. Thus, nutrients supplied by glacier meltwater can compensate for low water temperatures.

The planktonic food-web structure of turbid glacier-fed lakes

In newly created proglacial/ice-contact lakes with high glacial flour content, the structure of the planktonic food-web is probably simple and dominated by microbes (Fig. 1) and characterized by very low predatory or grazing losses (Koenings *et al.*, 1990; Sommaruga and Kandolf, 2014). The low phytoplankton abundance mainly allows for the establishment of cold-adapted rotifers (Fig. 1). Nondiscriminating zooplankton filter-feeding species such as *Daphnia*, *Bosmina* and *Holepedium* (Koenings *et al.*, 1990), but also HNF, that are the main predators on bacteria, are excluded or present at low abundance in those very turbid young glacier-fed lakes (Sommaruga and Kandolf, 2014). The exclusion of key-stone species such as *Daphnia* suggests that the planktonic food-web is truncated at this stage (Fig. 1). Perhaps the only functional group that can act as an important trophic link to bacteria is that of mixotrophic phytoplankton because the combination of photosynthesis and

phagotrophy, makes them less sensitive to the negative effect of glacial flour, like for example found for *Dinobryon* (Sommaruga and Kandolf, 2014).

Another source of mortality for the aquatic microbial community is viruses. However, it is unknown whether viruses could act instead as a shaping force of the composition and diversity of microbial communities in highly turbid glacier-fed lakes. Indeed, the occurrence of high number of glacial particles can potentially impair the establishment of viruses in these ecosystems, because the high ratio of these particles to bacteria will presumably result in a low encounter rate with the potential host. Further, if nonspecific adsorption to glacial flour particles occurs, encounter rates will be further reduced because this process is one of the major causes of viral inactivation and decay (Murray and Jackson, 1992). Thus, lakes receiving high loads of glacial flour may represent a unique type of aquatic ecosystem where microbial mortality by viruses and grazers is significantly reduced. If this is confirmed, theory predicts a reduced microbial diversity (Thingstad, 2000). However, it may be possible that prokaryotes colonizing turbid proglacial lakes carry viral DNA/RNA (i.e. lysogenic life cycle) and a lytic cycle is triggered when they meet suitable conditions for growth. So, there may exist "hot moments" in those lakes, when turbidity decreases (e.g. at times of low runoff) and viral encounter rates with the host increase, so that lytic infection is possible. Further, because organic coating of glacial flour particles is very low, perhaps viral loss or inactivation by adsorption is not as relevant as it is with organic-coated particles (Murray and Jackson, 1992).

Changes during the first steps in lake's ontogeny and when glacier connectivity is lost

Most of the information on what changes occurred in the biota during lake's ontogeny after glaciers receded is limited to studies on remnants found in the sediment. Unfortunately, in many cases, it is difficult to extrapolate results from benthic (sometimes littoral) indicator species to the planktonic realm because light, temperature, nutrient conditions, and trophic interactions are different. Nevertheless, results from paleolimnological studies suggest that when lake turbidity decreases and light conditions improve, relatively rapid changes in species composition take place (e.g. Lotter *et al.*, 2006). Paleolimnological studies also identify the importance of considering the effects of succession in terrestrial vegetation for proglacial lakes. For example, the initial phase after deglaciation in many areas is characterized by lake oligotrophication resulting from nutrient sequestration by the slow establishment of terrestrial vegetation (Anderson *et al.*, 2008). Further, from studies of deglaciation chronosequences, we know that the succession in the terrestrial environment significantly affects the chemistry of lakes and their biota (Engstrom *et al.*, 2000). For example, in lakes located along a chronosequence (but without measureable levels of glacial flour turbidity) in Glacier Bay, Alaska, zooplankton species richness increased only when lakes reach a certain degree of UV protection given by the input of terrestrially-derived DOC, thus, allowing colonization by additional UV-sensitive species (Williamson *et al.*, 2001).

For how long taxa such as *Daphnia* remain excluded from highly turbid glacial lakes will largely depend on how rapidly the ratio of glacial flour to food particles decreases (Koenings *et al.*, 1990; Sommaruga and Kandolf, 2014). Thus, any potential lake nutrient

fertilization, for example, by bird droppings as typically observed in the Arctic, could promote phytoplankton growth and accelerate this process. When conditions improve, then colonization is possible providing that a seed population can immigrate to the system and species sorting can take place. Paleolimnological evidence from Kråkenes Lake, Norway, indicates that once glacial flour settled, colonization by planktonic algae and *Daphnia* was relatively rapid (Birks *et al.*, 2000). Certainly, the increase in primary productivity when turbidity levels decrease (Vinebrooke *et al.*, 2010) allows for the establishment of larger populations of zooplankton selective feeders (Fig. 1) such as copepods and rotifers (Kirk, 1991; Koenings *et al.*, 1990).

The shift in water transparency that took place in the past after the last deglaciation is occurring currently at rapid pace as a consequence of glacier retreat. Though the time needed for such a shift will depend on the specific geographical area, the particular topology (e.g. mountain vs. lowland coastal terrains), but also on glacier size, runoff and other factors, it may occur in some cases very rapidly (25–30 years), as for example, in Lake Grünau, Austrian Alps (R. Psenner, personal communication). Now, independent of the duration of this process, it is reasonable to argue that such a shift in water transparency will impact the biota that colonized and established under the originally turbid condition. So, we may expect ecological (among species) and evolutionary responses (within species) of the biota to take place (Urban *et al.*, 2012). As mentioned before, changes in UV water transparency determine the chances of UV-sensitive species establishing a population in newly created lakes (Williamson *et al.*, 2001). By analogy, it is arguable that depending on the depth refuge available in a lake, some species are lost during the shift from turbid (i.e. UV-protected) to a clear and high UVenvironment, and that changes in community composition take place, though plausibly, this is not the only environmental factor that will be responsible for such a change (Sommaruga and Casamayor, 2009). Recent comparative studies in clear and turbid glacier-fed lakes using deep-sequencing analysis of 18S rDNA from microbial planktonic communities provide evidence for such a shift in community composition. For example, significant differences in protistan plankton community composition have been found between clear and turbid lakes in two different biogeographical areas (Kammerlander *et al.*, 2015). Similarly, bacterial community structure from three interconnected glacier-turbid lakes and from one adjacent lake that lost its connection with the same glacier largely differs (H. Peter *et al.*, submitted).

A recent comparative study of populations of the copepod *Cyclops abyssorum tatricus*, living in clear alpine and turbid glacier-fed lakes, illustrates what are the adaptive mechanisms allowing survival in a high UVenvironment. In this species, investment in UV photoprotection and efficiency in repairing DNA damage are part of those mechanisms (Tartarotti *et al.*, 2014). Similarly, when conditions make colonization of lakes by *Daphnia* possible, these are typically melanized, a phenotypic trait, that probably appeared after Pleistocene glaciations and made possible colonization of vacant shallow high UV habitats (Colbourne *et al.*, 1997).

Conclusions and perspectives

The information discussed here supports the view that turbid glacier-fed lakes provide contrasting growth conditions (e.g. reduced predation/grazing and PAR/UVR availability, increased supply of inorganic and organic nutrients) for planktonic organisms compared with those found in lakes that became clear at a later stage. Because predation and resource availability/productivity are recognized as strong structuring forces at the community level (Hairston *et al.*, 1960; Pace and Funke, 1991; Currie *et al.*, 1999), it remains an open question how these contrasting conditions shape the structure of the planktonic community under turbid conditions and what level of diversity can be attained. For example, is microbial (both prokaryotic and eukaryotic) diversity in glacier-fed systems low due to reduced predation/grazing/viral lysis or can they attain similar or even higher diversity because of the input of microbes by glacier runoff as observed for bacteria in glacier-fed streams (Wilhelm *et al.*, 2013). Further, what percentage of that diversity is metabolically active in glacier-fed systems or are just few dominant active taxa present? Testing what mechanisms explain differences in diversity and community composition between turbid and clear lakes or along a turbidity gradient remains challenging, because beside the change in water transparency, several other factors including the occur-rence of keystone taxa such as *Daphnia*, known to shape the microbial food-web, also change (Fig. 1). So, here experimental work is needed to disentangle the effects along the environmental gradient during early lake's ontogeny. Regarding the effects of glacier meltwaters on production, though clearly more data are needed to draw any firm conclusion, the supply of limiting resources and nutrients such as DOC and phosphorus/nitrogen has the potential to stimulate prokaryotic secondary production in recipient fresh and marine waters. In the case of primary producers, more data on how glacier meltwaters affect primary production is needed, as well as on how the contrasting effect of PAR/UVR reduction and of potential higher nutrient supply balance under turbid conditions. Further, how important mixotrophy is among phytoplankton and other groups such as ciliates needs to be assessed together with the role of viruses. Comparative studies between turbid and clear lakes on the stoichiometry of (mixotrophic) plankton and how this relates to zooplankton growth will provide data on more integrative aspects of the effect of glacier meltwaters. A major effort is needed to understand which and how organisms adapt during early lake's ontogeny (Fig. 1) and on how colonization and genetic/phenotypic variation in plankton are related along lake deglaciation chronosequences. Studies based on chronosequences will be also crucial to disentangle the relevance of the time component in succession and diversity patterns.

It is evident that the magnitude and impact of hydrological variability caused by the melting of glaciers on the food-web also needs to be evaluated. The melting of glaciers and ice sheets subjects recipient waters to large interseasonal and interannual hydrological variability (Casassa *et al.*, 2009; Carrivick and Tweed, 2013). However, it is unknown how this variability influences the dynamics and distribution of planktonic organisms in those ecosystems. In addition, physical processes (e.g. changes in water density and holomixis) will have consequences for the spatial distribution of planktonic organisms, particularly, of those with low motility, but this has not yet been considered.

Since alpine and polar lakes are excellent sentinels of global changes (Adrian *et al.*, 2009), further studies on how glacier meltwaters impact those ecosystems will allow us to better define their past and future ecological trajectories, as well as to learn how those unique environments function. Finally, even long after the disappearance of glaciers, stochastic events such as resuspension of glacial particles, for example, by large storms could reset succession and cause regime shifts similar to those known to occur in other aquatic ecosystems (Scheffer *et al.*, 2001).

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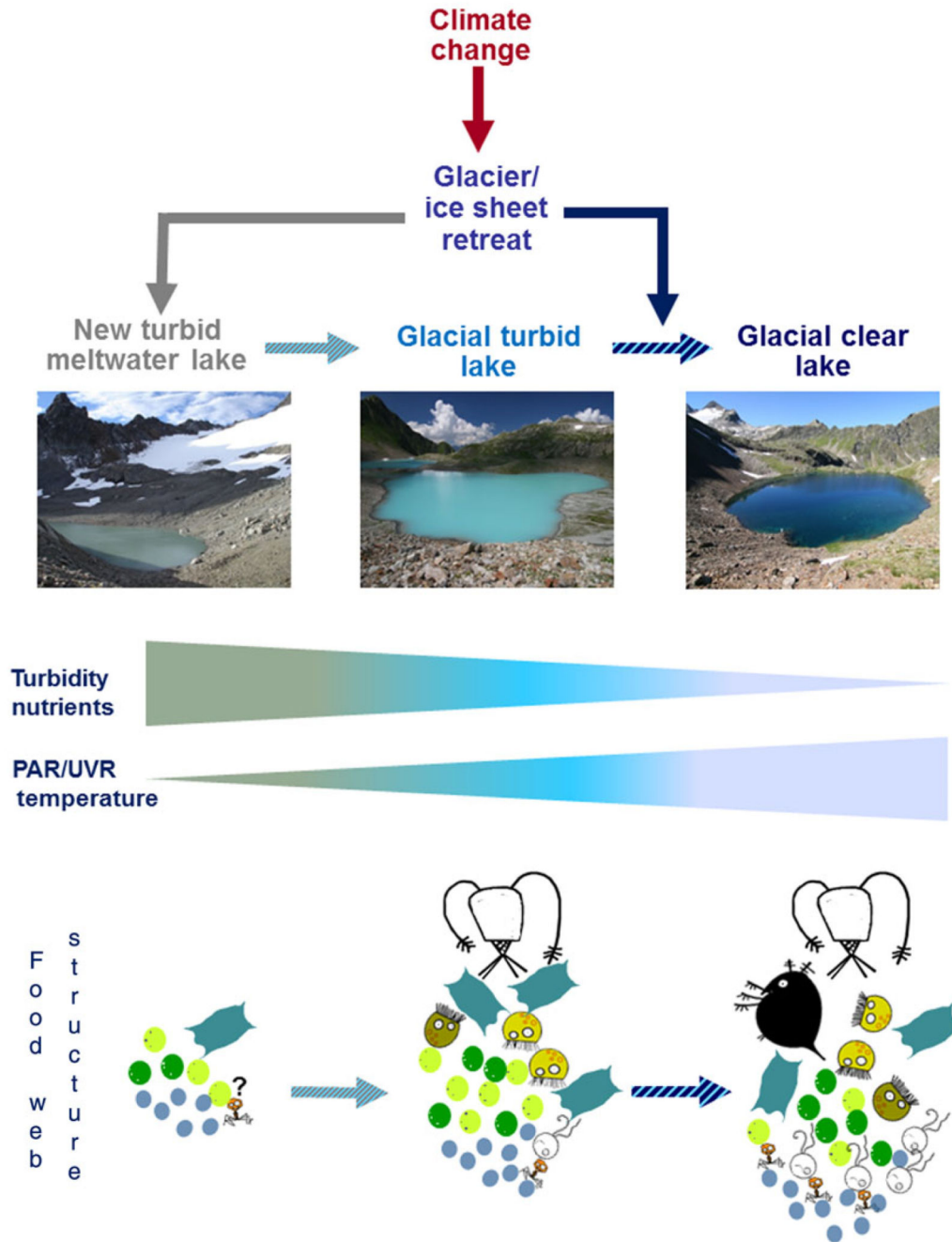
Fig. 1.

The retreat of glaciers and ice sheets caused by climate change creates new highly turbid meltwater proglacial/ice-contact lakes that during its ontogeny became less turbid (bright turquoise color) until they lose hydrological connectivity with the glacier and shift to a clear condition with high water transparency. The rapid glacier retreat also accelerates the shift from a turbid to a clear state (blue solid arrow). Along this lake's ontogeny, strong gradients in turbidity, potentially also in nutrient concentrations, as well as in PAR/UVR and water temperature are found. The planktonic food-web in the highly turbid proglacial lakes is

largely dominated by microbes with few metazoans present such as rotifers. As soon as turbidity and other in-lake conditions change (see text for more explanation), higher abundance of a more diverse planktonic food-web including copepods are feasible, but usually cladocerans such as *Daphnia* are found only when turbidity substantially decrease or the ratio of food to glacial particles improves. The food-web structure should be considered as a transition representation rather than a fixed one. Further steps in lake's ontogeny, for example, when dissolved organic carbon (DOC) inputs from the catchment make lakes less UV transparent are not shown. Color-coded cartoons in the food-web structure: Blue, prokaryotes; light green, mixotrophic phytoplankton; dark green, phototrophic phytoplankton; yellow, mixotrophic ciliates; brown, heterotrophic ciliates; white, heterotrophic nanoflagellates. Depiction of rotifers, copepods, *Daphnia* and viruses are self-evident.