Alpine Limnology of the Rocky Mountains of Canada and the USA in the Context of Environmental Change

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Alpine Limnology of the Rocky Mountains of Canada and the USA in the Context of Environmental Change

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**Abstract**

The cumulative impacts of multiple environmental and anthropogenic stressors on freshwater biodiversity have been studied in systems across the globe. The magnitude of multiple interdependent stressors on alpine systems may lead to increased primary productivity and jeopardize these unique communities. In this review, the consequences of individual stressors on alpine lake and pond ecology are synthesized, as well as the cumulative and potentially synergistic or antagonistic effects of multiple stressors. Beside temperature variability, other stressors reviewed include ultra violet (UV) radiation, organic pollutants, nutrient deposition, and biological invasions. Each stressor was evaluated individually and in combination with increasing water temperatures. In alpine environments, climatic warming is anticipated to increase with elevation, therefore amplifying the effects of temperature related responses. The purpose of this review is to highlight the ecological effects of climate change on alpine lakes and ponds in the Rocky Mountains of North America and fill knowledge gaps between disciplines of aquatic studies. This work underscores that in order to better understand and face the overall effects of climate change on alpine biota, investigations must continue to assess the compounded impacts of multiple stressors. Emphasis must be put on the standardization of monitoring methods across alpine regions to aid in consistent trend and prediction analysis within the context of both current and future climate change.

**Key words:** lakes, alpine limnology, biodiversity, climate change, cross-scale interactions, multiple stressors
Introduction

Alpine lakes and ponds are considered to be prime sentinels of climate change as they integrate the effects of air temperature and precipitation across their entire catchments and their effects not local human disturbance (Hauer et al. 1997; Parker et al. 2008; Adrian et al. 2009; Battarbee et al. 2009; Williamson et al. 2009). These nutrient poor ecosystems have relatively low species richness characterized by cold stenothermic organisms, making them highly sensitive to warming (Vinebrooke and Leavitt 2005). Further, the expected impacts of climate change on the timing of biological events (i.e., phenology) are especially high in alpine lakes given that the effects of environmental perturbation is more pronounced at higher elevation (Pepin et al. 2015, Blais et al. 1998). In addition, the retreat of glaciers has altered the state of glacially fed lake systems from highly turbid to clear systems dominated by non-glacial organic matter (Wolfe et al. 2013). The net impacts of climate change on these lakes are complicated by potential cross-scale interactions involving local factors (i.e., exotic sportfish, treeline position) mediating the more regional effects of meteorological events. As a result, forecasting the cumulative impacts of climate change on mountain lakes must include modeling of direct and indirect effects of multiple environmental factors, which are summarized in Figure 1. The planktonic compartment of the lake biota, which consists of short-lived organisms responsive to change, can act as early indicators of greater climatic changes in the catchment (Adrian et al. 2009, Schindler 1987), particularly given the unique differences between deep alpine lake and shallow alpine pond communities. We differentiate between alpine lakes versus ponds as they are expected to respond uniquely to stressors because of their different thermal capacities and biotic communities. Therefore, a potential scenario is considered where certain alpine lakes
become increasingly more pond-like given forecasts of a warmer and drier climate at higher elevations (Parker et al. 2008; Pepin et al. 2015).

Alpine lake systems are characterized by lower productivity and species richness than alpine ponds. Fishless alpine lakes in the Rocky Mountains contain sparse populations of zooplankton (< 4 individuals L⁻¹), which are best represented by only a few species, such as herbivorous filter-feeding *Daphnia middendorffiana* Fischer 1851 and the omnivorous calanoid copeod *Hesperodiaptomus arcticus* Marsh 1920 and *Hesperodiaptomus shoshone* S.A. Forbes 1893 (Paul and Schindler 1994; Paul et al. 1995; Vinebrooke and Leavitt 1999; Fischer et al. 2015). *D. middendorffiana* undertakes peak activity, growth and reproduction at colder temperatures than temperate species with a narrow thermal tolerance range of 13 - 15 °C in laboratory conditions (Yurista 1999). In contrast, zooplankton communities in shallow water alpine ponds often consist of more ubiquitous cladocerans, such as *Daphnia pulex* O.F. Müller 1785, *Alona affinis*, *Ceriodaphnia* spp., and *Chydorus sphaericus* (Anderson 1974; Strecker et al. 2014). Lack of coexistence of alpine *D. middendorffiana* and *D. pulex* may reflect an ecological trade-off among daphnids involving competitiveness and stress tolerance (MacIsaac 1985; Hessen 1996; Fischer et al. 2015). While *H. arcticus* is often the pelagic top predator in fishless alpine lakes, they also rarely inhabit alpine ponds. Instead, alpine ponds can contain a high number of other copepod species, such as *Acanthocyclops vernalis*, *Diaptomus nudus*, *D. tyrelli*, and *H. shoshone* (Strecker et al. 2004; Zettel 2010). Although rotifers represent a small proportion of total zooplankton biomass in both alpine lakes and ponds, fewer rotifer species are also found in alpine lakes than ponds (Paul and Schindler 1994; Strecker et al. 2004). Amphipod species *Gammarus lacustris* G.O. Sars 1864 also play a key role in structuring plankton communities in alpine lakes by predating on daphniids grazers. Thus, *G. lacustris* can release pressure on
phytoplankton and recycle nutrients such as phosphorus (Wilhelm and Schindler 1999). However, deep-water lakes can provide refugia to prey, diminishing the effects of amphipod predation on community structure. Alpine lake plankton are acutely adapted to coldwater, unproductive alpine conditions with low species richness (Lyons and Vinebrooke 2016). As a consequence, zooplankton communities in alpine lakes hypothetically contain less functional insurance than those in alpine ponds against the effects of stressors based on the insurance hypothesis concept (Yachi and Loreau 1999).

The purpose of this review is to highlight the current and future expected effects of climate change on the ecology of alpine lakes and ponds in the Western Cordillera region of the Rocky Mountains of Canada and the United States. There is an urgency to address inhomogeneous monitoring strategies across ecologically distinctive alpine systems in order to understand the intensity of climatic and biological shifts going forward (Table 1). The alpine environment will be defined as the area above treeline where water bodies have low ionic concentrations and relatively cold temperatures. This review will collect, organize and summarize information from previous studies in this region about environmental change in a multiple stressor context of a warmer and drier future climate that is expected to reduce the size of lakes in a shift towards littoral pond-like conditions (Parker et al. 2008).

**Literature Review Methods**

In order to develop the basis for environmental change in alpine water bodies in the Rocky Mountains, key stressors had to be identified. The stressors were chosen based on literature existence, volume and relevance. Each stressor (ultra violet (UV) radiation, organic pollutants, nutrient deposition, and biological invasions) was tested in literature.
searches using Web of Science and Google Scholar using the words “alpine”, “environmental change”, “warming”, “climate change” as well as the individual stressor words. Biological invasions included literature on alien fish introduction, non-native fish stocking and montane species range expansion. To limit the spatial extent of review, “Canada”, “Rocky Mountains” and “Sierra Nevada” were also used. From there, the literature was extensively searched to ensure a holistic review was produced. The relationship of stressors to climate warming was realized, and integrated into each stressor to utilize literature in a multi-stressor context.

Water temperature

Warming

According to the Intergovernmental Panel on Climate Change (IPCC), inland water reservoirs are some of the most sensitive ecosystems to the predicted climate change conditions (IPCC 2007). Rapid warming at high latitudes has been observed, and similarly there is a growing body of evidence that suggests there may be an elevational effect on warming (Pepin et al. 2015). Warming of high elevation regions in the winter and spring has been already amplified due to decreased perennial snow pack and therefore increased snow-albedo feedback (Giorgi et al. 1997; Fyfe and Flato 1999). Model projections of climate change indicate significant increases in temperature along the American Cordillera region, with predictions of greater than 3 degrees Celsius for the high mountains of the North American Rockies (Bradley et al. 2004). As global warming decreases snow and ice cover extent, coldwater species become increasingly threatened as mountain catchments warm more rapidly (Battarbee et al. 2009).
Temperature decreases at a rate of ~10 degrees Celsius per 1000 m rise in elevation (Lyons and Vinebrooke 2016). Therefore, alpine sites are often used as indicators for investigations of climate change because warming can damage their cold-adapted communities. The effects of warming on alpine community composition have been extensively investigated (i.e. Strecker et al. 2004; Holzapfel and Vinebrooke 2005).

Moderate warming stimulates large daphniid species, but suppresses (Weidman et al. 2014; Fischer et al. 2011) or reduces reproduction (Thompson et al. 2008) in larger *Hesperodiaptomus*. Alternatively, in growth chamber experiments warmed to temperature >20 °C, total biomass decreases due to a decline in both large alpine taxa (i.e., *D. middendorffiana* and *H. arcticus*; Holzapfel and Vinebrooke 2005). Natural warming of 3.6 °C also suppresses total zooplankton biomass due to a taxonomic shift away from larger daphniids, such as *D. pulex*, and towards smaller rotifer species (Strecker et al. 2004).

Shifts in zooplankton communities towards smaller species have cascading effects at all trophic levels. For example, warming stimulates smaller species that are metabolically superior at these temperatures but are unable to graze at the rate of large daphniid species, in turn increasing algal biomass (Holzapfel and Vinebrooke 2005). There is not complete consensus on future temperatures forecasts with climate change, but zooplankton community composition will undoubtedly be affected, with shifts being more prominent at higher temperatures.

**Temperature Variability**

With investigations of climate change predicting not just warmer, but also drier conditions, shifts by lake ecosystems towards more thermally unstable ponds are increasingly probable (Parker et al. 2008; Bradley et al. 2004). In addition, an increase in the frequency of
extreme weather events, such as drought, is predicted (Easterling et al. 2000). As water levels decline, numerous buffered lakes could shift towards shallower ponds with important consequences for biodiversity and ecosystem function (Parker et al. 2008). Shallow alpine ponds are considered especially sensitive to environmental change due to their small volume and high solar energy absorption (Vinebrooke et al. 2014). Pond ecosystems are polymictic so they lack the stratification needed to buffer against rapid changes in temperature (Lewis 1983). They experience marked diurnal cycles in water temperature making them one of the most physically variable aquatic environments in the world (Neldner and Pennak 1955), with temperature ranging as much as 24°C (McMaster 2003). Such thermal variability can significantly decrease the somatic growth and fitness of planktonic species that are unable to adjust metabolic rates accordingly (Reichwaldt et al. 2005; Chen and Stillman 2012). In contrast, deeper alpine lakes are less variable and have higher thermal stability (Vallentyne 1957) making non-adapted planktonic organisms from these systems potentially sensitive to larger scale temperature variation predicted by climate models (Weyhenmeyer et al. 2011; Fischer et al. 2015). However, individual lake morphometry vary and in some cases warming may cause the stabilization of lake systems due to changes in the period and intensity of thermal stratification during the ice-off season (Gerten and Adrian 2001). The complex morphology and individuality of lake systems makes it difficult to draw large-scale generalizations, but it further identifies shallow alpine ponds as sensitive to warming given their lack the buffering capacity.

Littoral habitats within smaller basins typically experience greater short-term temperature variation than deeper, larger lake basins (Finlay et al. 2001). Here, higher temperatures can favour a shift towards smaller body size as larger organisms experience greater metabolic costs with increasing temperature (Moore et al. 1996). Pervasive pond
species, *D. pulex* has been found to acclimate and reduce their metabolic rates under more variable thermal conditions, resulting in slower growth rates (Chen and Stillman 2012). Lower available energy for growth compared to temperate daphniids may be a competitive disadvantage for *D. middendorffiana*, given that growth and reproduction peak at lower temperatures (Yurista 1999). As the climate begins to favor more temperate and wide-range species acclimated to warmer and shallower conditions (i.e., *D. pulex*) it is possible that they could replace cold-adapted *D. middendorffiana* (Fischer et al. 2015). In addition to lower growth rates of large taxa and taxonomic shifts with higher thermal variation, the effects of warming that will shift the community to smaller, more metabolically plastic zooplankton taxa may also be compounded.

Evidence suggests that warming temperatures decreases the reproduction and growth of large alpine zooplankton and allows smaller taxa to gain a competitive advantage, therefore decreasing overall grazing pressure. An investigation that integrates the combined effects of warming with further stressors is imperative to understanding the overall effect of combined multiple stressors in lake systems (Christensen et al. 2006). By reviewing the individual and additive or non-additive effects of stressors related to environmental change, we can get a more holistic view of future ecosystem changes.

**UV Radiation**

UV-B radiation increases by ~20% per 1000 m of elevation (Blumthaler et al. 1992), therefore, high elevation, clear alpine ponds are particularly sensitive to its damaging effects. In many alpine plankton species, a “cocktail of defenses” are combined as adaptive measures to protect against ultraviolet radiation (UV), including pigmentation and daytime vertical migration that are exacerbated with greater UV transparency (Hansson
et al. 2010; Fischer et al. 2015). There is an apparent trade-off however, between pigmentation production and growth rates in zooplankton, making pigmented individuals competitively inferior, particularly when there are predatory fish present (Hessen 1996).

Dissolved organic carbon (DOC) can reduce the effects of UV exposure by attenuation mechanisms (Scully et al. 1994). However, high altitude ponds are often located in treeless catchments, nearly free of vegetation, so there are few sources of DOC compounds to reduce UV irradiance (Mcknight et al. 1997). Total DOC concentrations of alpine systems can be < 20 µM, and predicted warming and drought conditions will decrease DOC inputs from the catchment, further reducing the beneficial buffer of UV attenuation (Williamson et al. 1996; Schindler and Curtis 1997). Vinebrooke and Leavitt (2005) suggested that under such changing conditions, UV impacts would be greatest near treeline where small changes can affect the influx of DOC and therefore water clarity.

Changes in water clarity would alter depth refugia and diurnal vertical migration processes of UV-sensitive zooplankton (Weidman et al. 2014; Fischer et al. 2015). However, warming may mitigate the effects of increased UV exposure in some taxa by increasing enzymatic photo-repair processes (Williamson et al. 2002). The adaptive capacity of alpine species to develop pigmentation (i.e., melanin, carotenoid) may also decrease the impact of long-term increased exposure, however these mechanisms come with both metabolic and ecological costs (Hessen 1996) and increased sensitivity to predation by visual predators (Hansson et al. 2000). In the case of decreased DOC inputs, warming and the adaptive capacity of alpine species may be able to compensate for increased UV penetration.

Alternatively, in some lakes, climate change may increase DOC in response to increased glacial ablation and treeline advancement, which could in turn increase productivity and diversity (Vinebrooke and Leavitt 1999; Messner et al. 2013). An increase
in DOC in alpine systems could give smaller, UV-sensitive taxa a competitive advantage over endemic alpine species (Weidman et al. 2014). Under these circumstances, the effects of warming may also add to these shifts, further supporting a community dominated by taxa of smaller size classes. Therefore, the fate of DOC under changing climate conditions relies on the physical water catchment, on whether or not it is fed by glacial sources, as well as on the proximity of lacustrine ecosystems to the imminently advancing treeline. By tracking DOC levels, the changes occurring on a broader ecosystem scales (i.e., tree-line shift, deglaciation), and potential consequences for changes in UV exposure can be better understood.

Organic Pollutants

Alpine lakes are relatively pristine systems, with minimal or absent direct anthropogenic inputs. However, they are not immune to the atmospheric deposition of contaminants (Blais et al. 1998; Kallenborn 2006). Cold condensation is a mechanism involving the transport of relatively volatile compounds from warmer regions to areas of cooler temperature (i.e., higher latitudes or altitude), where they ultimately condense and deposit (Simonich and Hitest 1995). Although many of these contaminants have been restricted in developed countries since the early 1970s, long distance transport of these volatile compounds allows for postponed deposition in colder regions (Donald et al. 1999). Studies on the accumulation of persistent organic pollutants (POPs) in the mountains of Western Canada showed a significant positive correlation between volatile compound concentrations and elevation, exhibiting cold condensation at an altitudinal level (Blais et al. 1998).
These compounds have been found to bioaccumulate in fish from mountainous and arctic environments, raising substantial concern about overall ecosystem function (Kallenborn 2006). With many alpine communities being structured around a large zooplankter as its apex predator, the effects of POP accumulation is less clear. Food chain length may not be sufficient to explain the accumulation of POP at higher trophic levels. For example, in a subalpine lake in Western Canada the highest POP concentrations were not in fish but in pelagic zooplankton (*H. arcticus*), which was instead explained by high lipid contents that accompany low nutrient concentrations and cold waters (Campbell et al. 2000). There is also an important elevational component that targets alpine species to the burden of POP accumulation further. Amphipods (*Gammarus lacustris*) in alpine environments have higher accumulation of POPs than at lower elevations, which is compounded by their slower growth rates (Blais et al. 2003). The slow growth rate, high lipid content and pelagic diet of zooplankton in alpine systems makes them highly susceptible to the effects of POP deposition.

Due to warmer summer temperatures, glaciers are becoming an increasingly important source of POPs (Blais et al. 2001). Melting glaciers supplied between 50 to 97% of organochloride compounds to a subalpine lake, between 2 and 50 times higher than from valley stream inputs (Blais et al. 2001). Given that melting layers contain POP contaminants deposited from the 1950s to the early 1990s, peak deposition in freshwaters may occur later than at mid-altitudes, where the delay between emission and deposition may be shorter due to less pronounced condensation processes (Donald et al. 1999). As climate warming increases glacial melt, discharge of these compounds into many freshwater sources around the world could increase. For species that feed on pelagic particulates, they may also have greater POP levels due to the direct absorption or ingestion.
of contaminated glacial input matter (Campbell et al. 2000). Increased warming could
increase evaporation of lower volatile organochloride compounds, further increasing
deposition of new contaminants at higher altitudes (Blais et al. 2003).

**Nutrient Deposition**

Precipitous increases in anthropogenic emissions have increased the deposition of
reactive nitrogen (N) into environmental reservoirs globally (Galloway and Cowling 2002).
In many regions of the world, the N-deposition rate exceeds 10 kg N ha\(^{-1}\) yr\(^{-1}\), which
could double by 2050 (Galloway et al. 2008). N-deposition in mountainous regions
adjacent to urban areas has increased since the intensification of agricultural and industrial
processes in the 1950s, which is currently reflected by increased abundance of algal groups
indicative of N-enrichment (i.e., Colorado Rockies; Baron et al. 2000; Wolfe et al. 2001,
Elser et al. 2009). Nitrogen plays a role as a limiting or co-limiting nutrient in many
oligotrophic alpine lakes with small watersheds, making these systems sensitive to external
deposition (Elser et al. 2007; Paerl and Scott 2010). Although most water bodies in the
Canadian Rockies are Phosphorus (P) -limited, shallow alpine ponds are more likely to be
N-limited due to the internal loading of phosphorus and undetectable levels of nitrogen
(McMaster and Schindler 2005), and could therefore be used as early indicators of N-
deposition (Murphy et al. 2010).

In particular, alpine systems above treeline lack any terrestrial buffer to compensate
for the addition of atmospherically deposited nitrogen, and even in systems that have
sufficient vegetal buffers, nitrogen is still accumulating in receiving waters (Elser et al.
2009). The sensitivity of mountain lake ecosystems to increased N deposition is much
greater in N-limited systems, and is negatively correlated with lake size (Murphy et al.
However, top-down effects by grazers (i.e., crustacean zooplankton) and competition between algal species may limit algal growth in some systems (Van Geest et al. 2007; Vinebrooke et al. 2014). Grazing pressure as well as algal dynamics could reduce the negative impacts of N inputs but understanding these confounding influences is difficult.

In addition to these confounding factors, the synergistic effects of warming and N-deposition could optimize growing conditions for phytoplankton due to longer growing seasons and increased vertical stratification (Thompson et al. 2008; Paerl and Scott 2010). Taxonomic shifts of zooplankton communities related to the synergistic effects of warming and N-deposition are habitat-dependent, and grazers are likely to be suppressed in shallow pond environments (Thompson et al. 2008). In turn, there are dramatic implications for water clarity and productivity given the top-down mechanisms of grazing, however this is dependent on the strength of grazing pressure (Thompson et al. 2008). With N-deposition suppressing large grazers, the effects of warming on community assemblages will sustain the shift toward smaller planktonic taxa.

The deposition of atmospheric nutrients can alter the nutrient limitation status of lakes as well. In regions prone to high N-deposition such as Colorado, Norway and Sweden, studies show that phytoplankton growth was P-limited, while it was N-limited in low deposition regions. This anticipates a shift from N-limitation to P-limitation in relation to increasing atmospheric N-deposition (Elser et al. 2009). Under P-limited conditions, phytoplankton diversity could decrease, favouring species that can compete for limited phosphorus. Additionally, food quality for higher trophic levels (i.e. herbivorous zooplankton) could decrease given lower phosphorus contents (Müller-Navarra 1995, Elser et al. 2001).
Phosphorus loading in nutrient-poor alpine lakes may also have a profound effect on P-limited lakes (Murphy et al. 2010); however, studies on P-deposition are less common. Deep alpine lakes are highly oligotrophic and commonly phosphorus-limited and unresponsive to N-enrichment (Murphy et al. 2010). P-deposition could have a great impact on these P-limited systems. Forest fire has a profound impact on the dry deposition of phosphorus over boreal and mountain watersheds in North America (McEachern et al. 2000; Emelko et al. 2016). Phosphorus, and to a lesser degree N, can be liberated by such fires, depending on the magnitude of the disturbance and the catchment’s ability to retain nutrients (McEachern et al. 2000). More research must be conducted to draw conclusions about the delicate balance of nutrient limitation in alpine systems.

**Biological Invasion**

Thermophilization, or the increase in competition among cold-adapted species in response to warming and immigration of warm-adapted species, has been assessed in plant communities, and is an imminent threat to alpine systems (Gottfried et al. 2012). Upwards shifts in ranges of alpine species to cooler regions in response to warming may cause range contraction rather than expansion due to the nature of the mountain topography, making them thermally and physically isolated to areas that do not support survival or reproduction (Forero-Medina et al. 2010). Although vegetal communities experience more direct range expansion and competition, this too is a concern in aquatic mountain communities. Montane plankton invaders may persist under colder laboratory conditions, bringing to question dispersal limitation, predation exclusion or competition in natural environments (Holzapfel and Vinebrooke 2005). These limitations may be reduced under changing environmental conditions at higher elevations, making upward shifts of montane plankton
species more likely. Regional dispersal of montane species can also mediate the response of an introduced stressor (i.e., trout stocking) by increasing response diversity as facilitated by increased functional diversity related to predator avoidance (Loewen and Vinebrooke 2016). Given the heightened species richness of montane communities (Lyons and Vinebrooke 2016), their dispersal could act as a rescue effect, however this has not been displayed in the field. Despite the potential adaptive capacity of montane species to alpine environments, topographic barriers may limit transverse dispersal to unoccupied sites (Jenkins and Underwood 1998; Donald et al. 2001).

Many alpine water ecosystems are naturally fishless, creating dynamic pelagic communities that are particularly sensitive to external changes (Kong et al. 2016). In the Canadian Rockies, 20% of naturally fishless lakes were stocked with cutthroat, rainbow and/or brook trout from the early 1900s to 1980s for recreational angling (Donald 1987). Non-native fish stocking has been shown to drastically alter food web dynamics in pelagic alpine communities (Schindler and Parker 2002; Knapp et al. 2005; Eby et al. 2006; Loewen and Vinebrooke 2016). Given the small size and isolation of alpine lakes, it is relatively easy to examine the cascading effects across trophic levels (Eby et al. 2006).

Trout stocking in the Canadian Rockies typically eliminated larger alpine zooplankton such as *D. middendorffiana* and *H. arcticus*, leaving smaller zooplankton to compensate, resulting in larger phytoplankton taxa flourishing and decreasing water clarity (McNaught et al. 1999; Schindler and Parker 2002). The initial low species richness in alpine ecosystems compound the trophic cascade effects because smaller species play a minor role and are unable to functionally compensate for the loss of larger alpine-adapted species (Parker and Schindler 2006). There is also evidence that introduced trout persists better under alpine conditions given the low accessibility of sites to anglers and favourable living
conditions (i.e., low temperature, high dissolved oxygen concentration; Messner et al. 2013). Resilience of rare zooplankton species is much lower in lakes with longer fish residence times because resting egg stores in the sediment become depleted, and the Allee effect may limit mating potential in copepods (McNaught et al. 1999; Sarnelle and Knapp 2004). Mountains can act as topographic barriers to overland dispersal of zooplankton, further limiting the recovery of native species via dispersal (Jenkins and Underwood 1998; Donald et al. 2001).

In Yosemite National Park (California, USA), fish stocked sites had 16% fewer taxa than expected in the absence of stocking, with these effects strengthening with increasing elevation (Knapp et al. 2005). The introduction of alien fish species has cascading effects that indirectly affect the terrestrial food web as well. Non-native trout have in part eradicated populations of *Rana muscosa*, a frog species endemic to the Sierra Nevada and Transverse and Peninsular Ranges of Southern California from more than 95% of localities (Vrendenburg et al. 2007). The removal of these introduced trout has allowed for the rebound of these populations by rapidly increasing tadpole and frog densities and subsequent recolonization to unoccupied habitats (Knapp et al. 2007). The removal of non-native fish may be an important conservation action for the revival of amphibian populations and potentially central to the reestablishment of keystone invertebrate species as well.

Fish may also increase the thermal sensitivity of zooplankton communities, exacerbating the size selection for smaller body size by releasing smaller taxa from predation by larger invertebrate zooplankton and competition for algal food sources (MacLennan et al. 2015). In warmer lakes, this can allow total zooplankton biomass and species richness to increase (Messner et al. 2013). In contrast, some evidence shows that...
the introduction of non-native trout may be able to override any effect of warming on fishless alpine planktonic communities, if the greater regional species pool to rescue them from the negative impact of introduced fish (Loewen and Vinebrooke 2016). Management practice therefore must include the combined effects of both the legacy of fish introductions and the future forecasts for warming.

Conclusion

When forecasting future trends in alpine aquatic ecosystems, it is imperative that environmental changes are examined taking into great consideration interactions existing between different stressors (Figure 1). With multiple environmental stressors acting on alpine lakes to increase the thermal sensitivity of these fragile communities, some stressors may add to the shifts towards smaller body size at the expense of endemic alpine species (i.e., POP deposition, nutrient deposition, alien fish introductions). Conversely, certain stressors (i.e., increased UV) may act to enhance the adaptive capacities of such large alpine species. There is a need to test these stressors in combination with not just warming, but with each other in order to assess the overall effect on community composition, and the long-term consequences for ecosystem function. Non-additive effects of multiple stressors may result in the first stressor selecting tolerant species therefore reducing the community response to the next stressor (Vinebrooke et al. 2004). As a result, redundant stressors may exert an antagonistic net effect that is less than the sum of the individual community responses (Jackson et al. 2016).

In the North American Rockies, there is a lack of meteorological stations at high elevations (Bradley et al. 2004). Given the vast geographical extent and number of lakes in North America, with many being isolated from civilization, there are limitations within the
human capacity to monitor sites frequently enough to develop long-term data.

Environmental monitoring should be integrated and standardized across Canada in order to reconcile differences across collection methods and monitoring units (Table 1). Given that warming is expected to be greater at higher elevations (Pepin et al. 2015), it is vital to have baseline and change data for climatic shifts in temperature and precipitation. In addition to meteorological data, monthly surveys of chemical, physical and biological data should be completed over the course of the ice-off and ice-on season (Hampton et al. 2017) to identify community and ecosystem function shifts that accompany climate change in alpine environments. Further applications in remote sensing techniques might also represent a future solution for monitoring a large number of lakes across North America. Enclosure experiments in alpine environments could be used to manipulate communities with multiple stressors including warming, nutrient deposition, atmospheric deposition of pollutants and non-native fish introduction in order to disentangle the additive and synergistic effects of perturbations on zooplankton community composition and ecosystem function.
417 **Literature Cited**

418 Adrian, R., O’Reilly, C.M., Zagarese, H., Baines, S.B., Hessen, D.O., Keller, W.,
Livingstone, D.M., Sommaruga, R., Straile, D., Van Donk, E., Weyhenmeyer, G.A.,


Paul, A.J., Schindler, D.W., Hardie, A.K., and Leavitt, P.R. 1995. Direct and indirect effects of predation by a calanoid copepod (subgenus: Hesperodiaptomus) and of


Vinebrooke, R.D., and Leavitt, P.R. 2005. Mountain lakes as indicators of the cumulative

Vinebrooke, R.D., MacLennan, M.M., Bartrons, M., and Zettel, J.P. 2014. Missing
effects of anthropogenic nutrient deposition on sentinel alpine ecosystems. Glob.

Vredenburg, V.T., Bingham, R., Knapp, R., Morgan, J.A.T., Moritz, C., and Wake, D.
2007. Concordant molecular and phenotypic data delineate new taxonomy and
conservation priorities for the endangered mountain yellow-legged frog. J. Zool.

Weidman, P.R., Schindler, D.W., Thompson, P.L., and Vinebrooke, R.D. 2014.
Interactive effects of higher temperature and dissolved organic carbon on planktonic

Weyhenmeyer, G.A., Cantin, A., Beisner, B.E., Gunn, J.M., Prairie, Y.T., and Winter,

Wilhelm, F.M., and Schindler, D.W. 1999. Effects of *Gammarus lacustris* (Crustacea:


Yachi, S., and Loreau, M. 1999. Biodiversity and ecosystem productivity in a fluctuating  

Yurista, P.M. 1999. Temperature-dependent energy budget of an Arctic Cladoceran,  

Zettel, J. P. 2010. Planktonic responses to elevated nitrogen and phosphorus deposition- a  
replicated natural alpine pond experiment. M.Sc. Thesis, Department of  
Biological Sciences, University of Alberta, Edmonton, Alberta.
**Figure Legend**

Table 1: Recommended parameters to be measured in mountainous lakes and ponds to assess changes over time that may be important for anthropogenic and environmental change.

Figure 1: Flow diagram identifying the cumulative effects of climate change (*Increased temperature and Drier conditions*) and multiple stressors (light grey) as driving factors of environmental responses (white) and community composition and function of alpine lakes (dark grey). Plus signs (+) represent potential non-additive synergistic interactions of stressors. Minus signs (-) represent potential non-additive antagonistic interactions of stressors.
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<td>Continuous temperature profiles</td>
<td>Increased climatic variation may affect community composition and species adaptability</td>
</tr>
<tr>
<td>Turbidity</td>
<td>Secchi disk depth</td>
<td>Decreased glacial inputs may decrease turbidity (Wolfe et al. 2013)</td>
</tr>
<tr>
<td>Dissolved oxygen</td>
<td>Probe</td>
<td>Important for the survival of introduced fish species</td>
</tr>
<tr>
<td>pH</td>
<td>Probe</td>
<td>Enhanced weathering from warming may cause the acidification of alpine lakes (Sommaruga-Wograth et al. 1997)</td>
</tr>
<tr>
<td>Multiple zooplankton hauls</td>
<td>Zooplankton tow nets</td>
<td>Multiple tows allows for greater precision of zooplankton community composition, as well as temporal changes during both the growing season and ice-on season</td>
</tr>
</tbody>
</table>
| Algal biomass                   | Chlorophyll-
| a inferred algal biomass via filtration | Algal biomass is anticipated to increase given warming conditions and atmospheric nutrient deposition that will compound a trophic cascade that starts with the loss of key grazer species (Figure 1) |
| Key limiting nutrients (total phosphorus, total dissolved phosphorus, total kjeldahl nitrogen, inorganic/organic nitrogen) | Laboratory analysis | Atmospheric deposition of key nutrients driving algal biomass may increase in alpine environments (Wolfe et al. 2001)                                                                                   |
| Dissolved organic carbon and colour | Laboratory analysis and observation | Increasing treeline may affect DOC concentrations (Vinebrooke and Leavitt 2005)                                                                                                                          |
| Total suspended solids (TSS)     | Filtration                                         | Contaminant transport (heavy metals, POPs, nutrients)                                                                                                                                                    |
| Anion and cation concentrations  | Laboratory analysis                                | Increased weathering may increase the anion and cation concentrations of typically dilute alpine systems (Sommaruga-Wograth et al. 1997)                                                                  |
Figure 1: Flow diagram identifying the cumulative effects of climate change (Increased temperature and Drier conditions) and multiple stressors (light grey) as driving factors of environmental responses (white) and community composition and function of alpine lakes (dark grey). Plus signs (+) represent potential non-additive synergistic interactions of stressors. Minus signs (-) represent potential non-additive antagonistic interactions of stressors.