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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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1 **Abstract**

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

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

22 **Introduction**

23 Alpine lakes and ponds are considered to be prime sentinels of climate change as
24 they integrate the effects of air temperature and precipitation across their entire catchments
25 and their effects not local human disturbance (Hauer et al. 1997; Parker et al. 2008; Adrian
26 et al. 2009; Battarbee et al. 2009; Williamson et al. 2009). These nutrient poor ecosystems
27 have relatively low species richness characterized by cold stenothermic organisms, making
28 them highly sensitive to warming (Vinebrooke and Leavitt 2005). Further, the expected
29 impacts of climate change on the timing of biological events (i.e., phenology) are especially
30 high in alpine lakes given that the effects of environmental perturbation is more
31 pronounced at higher elevation (Pepin et al. 2015, Blais et al. 1998). In addition, the retreat
32 of glaciers has altered the state of glacially fed lake systems from highly turbid to clear
33 systems dominated by non-glacial organic matter (Wolfe et al. 2013). The net impacts of
34 climate change on these lakes are complicated by potential cross-scale interactions
35 involving local factors (i.e., exotic sportfish, treeline position) mediating the more regional
36 effects of meteorological events. As a result, forecasting the cumulative impacts of climate
37 change on mountain lakes must include modeling of direct and indirect effects of multiple
38 environmental factors, which are summarized in Figure 1. The planktonic compartment of
39 the lake biota, which consists of short-lived organisms responsive to change, can act as
40 early indicators of greater climatic changes in the catchment (Adrian et al. 2009, Schindler
41 1987), particularly given the unique differences between deep alpine lake and shallow
42 alpine pond communities. We differentiate between alpine lakes versus ponds as they are
43 expected to respond uniquely to stressors because of their different thermal capacities and
44 biotic communities. Therefore, a potential scenario is considered where certain alpine lakes

45 become increasingly more pond-like given forecasts of a warmer and drier climate at higher
46 elevations (Parker et al. 2008; Pepin et al. 2015).

47 Alpine lake systems are characterized by lower productivity and species richness
48 than alpine ponds. Fishless alpine lakes in the Rocky Mountains contain sparse populations
49 of zooplankton (< 4 individuals L^{-1}), which are best represented by only a few species, such
50 as herbivorous filter-feeding *Daphnia middendorffiana* Fischer 1851 and the omnivorous
51 calanoid copepod *Hesperodiaptomus arcticus* Marsh 1920 and *Hesperodiaptomus shoshone*
52 S.A. Forbes 1893 (Paul and Schindler 1994; Paul et al. 1995; Vinebrooke and Leavitt 1999;
53 Fischer et al. 2015). *D. middendorffiana* undertakes peak activity, growth and reproduction
54 at colder temperatures than temperate species with a narrow thermal tolerance range of 13 -
55 15 °C in laboratory conditions (Yurista 1999). In contrast, zooplankton communities in
56 shallow water alpine ponds often consist of more ubiquitous cladocerans, such as *Daphnia*
57 *pulex* O.F. Müller 1785, *Alona affinis*, *Ceriodaphnia* spp., and *Chydorus sphaericus*
58 (Anderson 1974; Strecker et al. 2014). Lack of coexistence of alpine *D. middendorffiana*
59 and *D. pulex* may reflect an ecological trade-off among daphnids involving competitiveness
60 and stress tolerance (MacIsaac 1985; Hessen 1996; Fischer et al. 2015). While *H. arcticus*
61 is often the pelagic top predator in fishless alpine lakes, they also rarely inhabit alpine
62 ponds. Instead, alpine ponds can contain a high number of other copepod species, such as
63 *Acanthocyclops vernalis*, *Diaptomus nudus*, *D. tyrelli*, and *H. shoshone* (Strecker et al.
64 2004; Zettel 2010). Although rotifers represent a small proportion of total zooplankton
65 biomass in both alpine lakes and ponds, fewer rotifer species are also found in alpine lakes
66 than ponds (Paul and Schindler 1994; Strecker et al. 2004). Amphipod species *Gammarus*
67 *lacustris* G.O. Sars 1864 also play a key role in structuring plankton communities in alpine
68 lakes by predating on daphniids grazers. Thus, *G. lacustris* can release pressure on

69 phytoplankton and recycle nutrients such as phosphorus (Wilhelm and Schindler 1999).
70 However, deep-water lakes can provide refugia to prey, diminishing the effects of
71 amphipod predation on community structure. Alpine lake plankton are acutely adapted to
72 coldwater, unproductive alpine conditions with low species richness (Lyons and
73 Vinebrooke 2016). As a consequence, zooplankton communities in alpine lakes
74 hypothetically contain less functional insurance than those in alpine ponds against the
75 effects of stressors based on the insurance hypothesis concept (Yachi and Loreau 1999).

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

87

88 **Literature Review Methods**

89 In order to develop the basis for environmental change in alpine water bodies in the
90 Rocky Mountains, key stressors had to be identified. The stressors were chosen based on
91 literature existence, volume and relevance. Each stressor (ultra violet (UV) radiation,
92 organic pollutants, nutrient deposition, and biological invasions) was tested in literature

93 searches using Web of Science and Google Scholar using the words “alpine”,
94 “environmental change”, “warming”, “climate change” as well as the individual stressor
95 words. Biological invasions included literature on alien fish introduction, non-native fish
96 stocking and montane species range expansion. To limit the spatial extent of review,
97 “Canada”, “Rocky Mountains” and “Sierra Nevada” were also used. From there, the
98 literature was extensively searched to ensure a holistic review was produced. The
99 relationship of stressors to climate warming was realized, and integrated into each stressor
100 to utilize literature in a multi-stressor context.

101

102 **Water temperature**

103 *Warming*

104 According to the Intergovernmental Panel on Climate Change (IPCC), inland water
105 reservoirs are some of the most sensitive ecosystems to the predicted climate change
106 conditions (IPCC 2007). Rapid warming at high latitudes has been observed, and similarly
107 there is a growing body of evidence that suggests there may be an elevational effect on
108 warming (Pepin et al. 2015). Warming of high elevation regions in the winter and spring
109 has been already amplified due to decreased perennial snow pack and therefore increased
110 snow-albedo feedback (Giorgi et al. 1997; Fyfe and Flato 1999). Model projections of
111 climate change indicate significant increases in temperature along the American Cordillera
112 region, with predictions of greater than 3 degrees Celsius for the high mountains of the
113 North American Rockies (Bradley et al. 2004). As global warming decreases snow and ice
114 cover extent, coldwater species become increasingly threatened as mountain catchments
115 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 favour 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 $< 20 \mu\text{M}$, 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 Hites 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).

235 These compounds have been found to bioaccumulate in fish from mountainous and
236 arctic environments, raising substantial concern about overall ecosystem function
237 (Kallenborn 2006). With many alpine communities being structured around a large
238 zooplankton as its apex predator, the effects of POP accumulation is less clear. Food chain
239 length may not be sufficient to explain the accumulation of POP at higher trophic levels.
240 For example, in a subalpine lake in Western Canada the highest POP concentrations were
241 not in fish but in pelagic zooplankton (*H. arcticus*), which was instead explained by high
242 lipid contents that accompany low nutrient concentrations and cold waters (Campbell et al.
243 2000). There is also an important elevational component that targets alpine species to the
244 burden of POP accumulation further. Amphipods (*Gammarus lacustris*) in alpine
245 environments have higher accumulation of POPs than at lower elevations, which is
246 compounded by their slower growth rates (Blais et al. 2003). The slow growth rate, high
247 lipid content and pelagic diet of zooplankton in alpine systems makes them highly
248 susceptible to the effects of POP deposition.

249 Due to warmer summer temperatures, glaciers are becoming an increasingly
250 important source of POPs (Blais et al. 2001). Melting glaciers supplied between 50 to 97%
251 of organochloride compounds to a subalpine lake, between 2 and 50 times higher than from
252 valley stream inputs (Blais et al. 2001). Given that melting layers contain POP
253 contaminants deposited from the 1950s to the early 1990s, peak deposition in freshwaters
254 may occur later than at mid-altitudes, where the delay between emission and deposition
255 may be shorter due to less pronounced condensation processes (Donald et al. 1999). As
256 climate warming increases glacial melt, discharge of these compounds into many
257 freshwater sources around the world could increase. For species that feed on pelagic
258 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 $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, 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.

2010). 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

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

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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.

Parameter	Method	Importance
Temperature variation	Continuous temperature profiles	Increased climatic variation may affect community composition and species adaptability
Turbidity	Secchi disk depth	Decreased glacial inputs may decrease turbidity (Wolfe et al. 2013)
Dissolved oxygen	Probe	Important for the survival of introduced fish species
pH	Probe	Enhanced weathering from warming may cause the acidification of alpine lakes (Sommaruga-Wogarth et al. 1997)
Multiple zooplankton hauls	Zooplankton tow nets	Multiple tows allows for greater precision of zooplankton community composition, as well as temporal changes during both the growing season and ice-on season
Algal biomass	Chlorophyll- <i>a</i> 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-Wogarth 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.

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