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RESEARCH ARTICLE

The life aquatic in high relief: shifts in the physical and biological characteristics of alpine lakes along an elevation gradient in the Rocky Mountains, USA

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Abstract

Rapidly occurring environmental changes in alpine lakes highlight the importance of better understanding the ecological structure and function associated with these systems. Previous research has identified how the physical characteristics of lakes change as a function of landscape position, but comparatively little is known about shifts in the biotic community across mountain regions. In 2016, we sampled 19 lakes across an elevation gradient (2480–3550 m a.s.l.) within the Rocky Mountains, USA, to evaluate how both the abiotic characteristics of lakes and their planktonic biological communities covaried with elevation. Based on generalized linear mixed models (GLMMs), increases in elevation were associated with decreases in most nutrient concentrations (with the exception of nitrate), dissolved organic carbon, water temperature and lake stratification. Conversely, elevation increases were positively related to nitrate concentrations and water clarity. Extending this analysis to the biological community, we found that higher-elevation lakes exhibited lower phytoplankton and zooplankton densities, whereas elevation associated positively with average zooplankton size. Our data are consistent with the hypothesis that the alpine environment acts as a strong niche filter, limiting the quantity and diversity of taxa to groups capable of tolerating the short growing season, high flushing rate, strong variation in interannual precipitation, intense ultraviolet radiation exposure, and lower resource availability associated with such habitats.

Keywords Landscape limnology · Mountain lake · Elevation gradient · Freshwater ecology · Zooplankton · Phytoplankton

Introduction

Worldwide, an estimated 20% of lakes are located higher than 1000 m a.s.l. (Verpoorter et al. 2014). Growing evidence suggests that these mountainous, often remote aquatic systems are critical to downstream ecosystems and may differ considerably from low-elevation lakes in both their physical and biological properties (Moser et al. 2019). For instance, mountain lakes often function as a hot spot for nutrient cycling (Alexander et al. 2007; Brown et al. 2008) and are a key source of freshwater for humans (Beniston 2003; Viviroli et al. 2007). Relative to lakes at lower elevations, which have a much longer history of study (Jacobsen and Dangles 2017), alpine lakes (those above treeline) are characterized by sparse surrounding vegetation, extended ice-cover (Caine 2002; Hampton et al. 2017), intense spring flushing rates (McGuire et al. 2005; Clow 2010), and high exposure to solar radiation (Blumthaler et al. 1997). The steep topography, abrupt transition in vegetation patterns, unique basin shapes, dynamic weather patterns, and

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interannual variation in winter snowpack of alpine environments make it probable that lakes will also vary broadly in responses to forecasted environmental changes, underscoring the importance of research on the ecology of mountain lake ecosystems (Kamenik et al. 2001; Kraemer et al. 2015).

Previous limnological research has emphasized the importance of landscape position, or the concept of a lake's hydrologic position within the local to regional flow system, in shaping the physical characteristics of both lakes and streams in regard to patterns of loading, transport, storage, and utilization of inorganic and organic materials (Vannote et al. 1980; Kratz et al. 1997; Martin and Soranno 2006). Notably, the Landscape Position Model (LPM) postulates that in temperate lake systems, downward shifts in landscape position are associated with larger lake size, increased hydrologic connectivity, longer water residence times, and increased fish species richness (Kratz et al. 1997; Martin and Soranno 2006; Soranno et al. 2010). Application of these and related frameworks have helped capture variation among mountain lakes or across stream networks with respect to nutrient concentrations, primary production, and patterns of biodiversity (Sadro et al. 2012; Epstein et al. 2013; Read et al. 2015). For mountain lakes in particular, the landscape position of a lake relative to forest treeline has enormous potential to affect in-lake ecological processes. For instance, both the extent and chemical quality of dissolved organic matter (DOM) derived from the surrounding landscape sharply influence the attenuation of UV radiation (McKnight et al. 1997). Allochthonous DOM derived from terrestrial vegetation and soils is typically enriched in yellow-colored, humic materials, which strongly absorb visible and UV radiation. However, clear water lakes above treeline (i.e., alpine) tend to support sparse terrestrial vegetation and thus have lower DOM concentrations often dominated by autochthonous (derived from within-lake processes) rather than allochthonous inputs (McKnight et al. 1994; Hood et al. 2003b). As a result, UVR often penetrates deeper in the water column, and the carbon subsidy offered by terrestrially derived DOM is typically lacking or much reduced (e.g., Miller et al. 2009; Sadro et al. 2011).

Concomitantly, these extreme and dynamic physical characteristics of high-elevation ecosystems likely exert strong influences on the biological communities of mountain lakes. Compared with low-elevation lakes, alpine lake ecosystems generally support lower species richness (Füreder et al. 2006; Fjellheim et al. 2009) and have simplified food webs, often with fewer than three trophic levels (Ward et al. 1904; McNaught et al. 1999). These patterns could reflect abiotic characteristics such as cold temperatures (Dodds 1917; Havens et al. 2015), high flushing rates during snowmelt (Obertegger et al. 2007), variable patterns of precipitation (Sadro and Melack 2012) short ice-free seasons, intense ultraviolet radiation (UVR) and potentially limiting nutrient concentrations (Hansson et al. 2007; Miller and McKnight 2015). For instance, in a survey of lakes in the Pyrenees, macroinvertebrate richness decreased by 57% for lakes above 2800 m a.s.l. (De Mendoza and Catalan 2010). Similarly, Lyons and Vinebrooke (2016) found that zooplankton species richness in Canadian Rockies decreased from an average of 10.7 species per lake for lakes at or below 1000 m a.s.l. to 1.9 species per lake for lakes at or above 2600 m a.s.l. However, decoupling the extent that elevation influences lake basin characteristics and biogeochemical processes and how these ambient conditions interactively affect the biological properties and community structures, is relatively understudied, especially in regards to zooplankton (Vadeboncoeur et al. 2002; Cole et al. 2011).

To better understand how the physical and biological characteristics that covary with elevation shape alpine lake zooplankton communities, we conducted repeat sampling of mountain lakes along an elevation gradient (2480–3550 m a.s.l.) within Colorado's Rocky Mountains, USA. Our specific goal was to evaluate the strength and consistency of correlations between lake elevation and variation in features such as nutrient concentrations, thermal stratification and planktonic communities (across multiple trophic levels). Lakes were selected to encompass a range in altitude alongside a representatively broad gradient in lake size, depth, and catchment area. We used a mixed-modeling framework to assess how measured characteristics shifted with elevation while accounting for lake-level characteristics (e.g., deepest depth, surface area, and fish presence) and sources of autocorrelation (e.g., catchment identity, lake identity and sampling period). As our survey area encompassed 10 different catchments and had a meridional extent of 36 km, we also compared the relative influence of geographic distance and elevation on the taxonomic composition of zooplankton and phytoplankton among lakes. Building on previous research related to landscape position (1) we expected elevation and the associated, patterns of surrounding vegetation, UVR, and ice-free period, to act as a niche filter, leading to communities characterized by lower taxonomic richness and lower population densities. Additionally, (2) we hypothesized that the difference in elevation between sites would more strongly relate to community similarity compared with straight-line distance or watershed identity alone, owing to the large number of physical variables that covary with elevation. The current study offers a novel contribution by characterizing how a broad range of variables, including physical attributes, nutrient profiles, and biological communities, vary both within lakes (e.g., between depths and through the open-water season) and along an elevation gradient. While numerous previous investigations have investigated the relationship between elevation and specific lake-level dimensions, comparatively few have used hierarchical statistical approaches to comprehensively assess shifts in lake ecosystems over altitudinal ranges.

Methods

Field sampling

Throughout the ice-free season of 2016, we sampled 19 lakes from 10 catchments in the Front Range of Colorado's Rocky Mountains (Fig. 1, Table 1). Each lake was surveyed approximately three times (every other week) immediately following ice-off to reconcile any variation attributed to seasonal extremes. Within this region, treeline typically occurs between 3300 and 3450 m a.s.l. (Greenland 1989; Humphries et al. 2008), and we designated lakes as 'alpine' if they were above treeline with no surrounding trees in the catchment and terrestrial vegetation, if present, was comprised of short grasses or shrubs (n = 6 lakes, elevation range of 3425–3550 m a.s.l.). The remaining lakes (n = 12), all of which had tree groves visible from the shoreline, were classified as 'subalpine' (elevation range of 2980–3345 m a.s.l.). Additionally one lake was far enough below treeline to be considered montane (2480 m a.s.l.) (Rose et al. 2015). On each visit, we used an inflatable raft to census the deepest point in the lake (located with a Venterior VT-FF001 Portable Fish Finder and georeferenced for ease of subsequent sampling) and measured temperature, conductivity and pH at 1-m depth intervals using a YSI 556 multi-probe meter, and photosynthetically active radiation (PAR) using a Li-Cor meter with a quantum sensor probe. We recorded water clarity to 0.25 m resolution using a Secchi disk (30 cm width). We collected water samples using a Van Dorn vertical sampler from both the lake surface (0.5 m) and from the hypolimnion (2 m above the deepest depth, for lakes deeper than 4 m) and analyzed them for nutrients [total dissolved nitrogen (TDN), nitrate (NO_3), total dissolved phosphorus (TDP), phosphate (PO_4)], ions, dissolved organic carbon (DOC), phytoplankton communities and chlorophyll a (chl-a) concentrations. Lastly, we collected zooplankton with an 80 µm Wisconsin net (20 cm opening) from the deepest point in the lake. The contents of two vertical tows were combined and preserved in 80% ethanol. We established fish presence or absence using a combination of techniques, explicitly a portable Fish Finder, that were later corroborated with

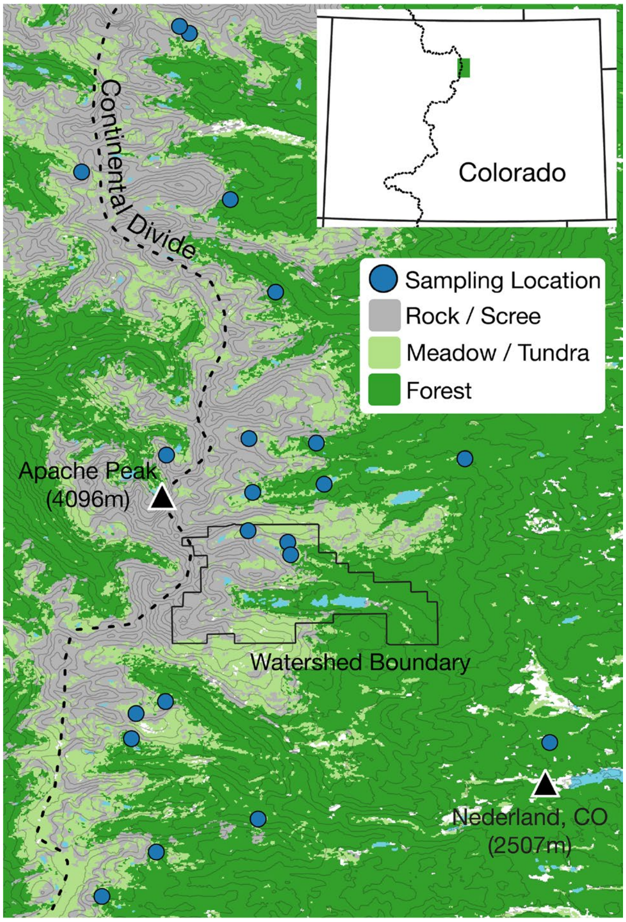

Fig. 1 Locations of surveyed lakes compiled from USGS National Gap Analysis Program. 2005. Southwest Regional GAP Analysis Project—Land Cover Descriptions. RS/GIS Laboratory, College of Natural Resources, Utah State University

Table 1 Morphometric lake qualities including; elevation in m a.s.l., lake surface area (SA) in m^2, maximum depth (MD) in m, and the normalized difference vegetation index (NDVI) for the 19 surveyed lakes

Site	Elevation (m a.s.l)	SA (m^2)	MD (m)	NDVI
Mud	2480	14,803	2.50	0.5489
Lost	2983	24,983	4.00	0.6452
Red Deer	3163	61,923	20.00	0.5723
Red Rock	3200	25,286	1.75	0.6569
Pear Reservoir	3226	61,783	16.00	0.5548
Long	3253	161,340	7.00	0.6653
Yankee Doodle	3267	16,072	7.50	0.5135
Mitchell	3272	53,606	1.75	0.5113
Jasper	3296	24,983	10.00	0.5053
Forest	3308	30,656	3.00	0.5121
Isabelle	3313	125,121	8.00	0.4788
Diamond	3335	67,692	7.00	0.5480
Lake Albion	3345	129,744	15.00	0.4255
GL1	3425	35,444	8.00	0.4133
Lion Lake 2	3432	17,815	9.00	0.3425
Upper Diamond	3460	6410	3.00	0.3975
Blue	3461	91,581	42.00	0.2981
Snowbank	3512	35,060	7.50	0.2829
GL4	3550	45,192	13.00	0.2963

stocking records from the Colorado Department of Parks and Wildlife. Additional information on sampling procedure, water chemistry and chl-a, phytoplankton, zooplankton analysis, observations for precipitation and fish occurrence, as well as our estimates of lake and basin characteristics are included in the supplementary information (SI).

Water chemistry and chlorophyll analysis

From each water sample, we filtered subsamples for nutrient analysis (100 mL), DOC (125 mL) and chl-a (500 mL) through pre-rinsed Millipore 47 mm GF/F filters (0.7 µm pore size) into high density polyethylene (HDPE) (nutrients) or acid-washed, pre-combusted amber glass bottles (DOC) (see SI). We calculated the fluorescence index (FI) to determine the molecular character of a sample's DOM to estimate its source as either derived from terrestrial sources (degraded plant and soil organic matter; lower FI values) or microbial sources (extracellular release and leachate from bacteria and algae; higher FI values) (SI; McKnight et al. 2001; Hansen et al. 2016). This value ranges from 1.2 to 1.8 in natural waters (Helms et al. 2008; Fleck et al. 2014). The Arikaree Environmental Laboratory performed chemistry analyses in accordance with standard methods for nutrients and DOC concentrations and certain ions (SI).

Zooplankton and phytoplankton identification and quantification

We examined zooplankton samples from each lake-visit using an Olympus SZX10 stereo dissection microscope. We identified all zooplankton to the species-level for large-bodied cladocerans and to the genus level for copepods, ostracods, rotifers, mites, and aquatic insects, using taxonomic keys (Weglenska 1976; McCauley 1984; Dodson 1989; Haney 2013). Zooplankton taxonomic richness for each visit was estimated as the total number of morphometrically distinct taxa per sample. For *Daphnia* spp., we classified adults based on development of the brood chamber, which is undeveloped in neonates (Ebert 2005), while copepods adults were differentiated from nauplii based on developmental stage (Haney 2013). We estimated zooplankton density (L^{-1}) by counting the number of individuals within a sample (summed across all life stages for cladocerans and copepods) and dividing by the lake water volume (L) sampled across the two vertical tows (see SI). Smaller taxa that were not quantified reliably, such as rotifers, or relatively rare groups, such as mites and aquatic insects, were excluded from density estimates. We estimated average zooplankton size (mm) by measuring the length of the carapace or chitinous body structure of the first 50 adult cladocerans and adult copepods of any species of a given sample and weighted these values by their densities (see SI). While collecting size measurements on this subset of adult zooplankton, we simultaneously quantified prevalence of gravid zooplankton among cladocerans and copepods based on the frequency of eggs and/or ephippia among adults in a given sample (also weighted by their relative sample densities).

To assess phytoplankton taxonomic diversity and overall abundance, we used a Benchtop B3 Series FlowCAM® (Fluid Imaging Technologies)—an automated system for imaging particles within a fluid—and the associated software (VisualSpreadsheet) to image algal cells for community diversity and obtain estimates of cell density. The FlowCAM was outfitted with a 10× objective and 100 µm × 2 mm Flow Cells with silicon tubing (FlowCAM; Poulton and Martin 2010; Álvarez et al. 2014; Camoying and Yñiguez 2016). We analyzed two replicates of concentrated 5 mL sample for a given lake-date-depth by manually sorting FlowCAM's output images into morphometrically unique groups with the help of taxonomic guides (Smith 1933; Prescott 1964; Baker 2012). We algal cells for each run (Spaulding et al. 2012) and calculated cell density (L^{-1}), then averaged the densities between the duplicate runs of each sample (SI). Although these approaches were applied consistently across all collected samples, the capacity of the FlowCAM to taxonomically identify all groups of encountered phytoplankton is constrained by the range in morphological characteristics within a species for some algal groups. As such, we treat these as taxonomic units rather than as a finely resolved estimate of species richness.

Estimates of lake and basin characteristics

We estimated lake stratification by examining the change in water density (as a function of temperature) between the surface and hypolimnion ($\Delta\,\rho$ kg m^{-3}) using the Thiessen–Scheel–Diesselhorst Equation (SI; McCutcheon et al. 1993). For estimates of water clarity, we calculated the diffuse attenuation of PAR (K_{PAR} reported in m^{-1}) (SI; Buiteveld 1995; Markager and Vincent 2000). We measured lake circumference and surface area using the 'path' function in Google Earth Pro (09/07/2016 map). Lastly, to quantify the potential inputs of the surrounding terrestrial vegetation into each lake and reinforce our estimates of treeline, we calculated the normalized difference vegetation index (NDVI) using the Landsat 8, Tier-1, surface-reflectance product, provided by the United States Geological Survey (SI).

Statistical analyses

We used generalized linear mixed-effects models (GLMMs) to evaluate how the physical and biological characteristics of lakes changed along the elevation gradient. These models, which are fit iteratively using maximum-likelihood based estimation, have distinct advantages in terms of being able to accommodate a range of response variable distributions often encountered in ecological data, handle unbalanced designs, and include a combination of fixed effects and random effects, thereby incorporating sources of non-independence (e.g., samples from different depths within a lake, repeated visits to the same site over time, or lakes positioned within the same catchment) (Bolker et al. 2009). More specifically, we used GLMMs to model the influence of elevation on response variables in two broad categories. (1) Physicochemical characteristics: DOC (mg C L^{-1}), FI, total dissolved nitrogen (TDN) (μmol L^{-1}), nitrate (NO_3) (μmol L^{-1}), total dissolved phosphorus (TDP) (μmol L^{-1}), phosphate (PO_4) (μmol L^{-1}), sulfate (SO_4) (μ eq L^{-1}), specific conductance (μS cm^{-1}), Secchi depth (m), K_{PAR} (m^{-1}), water temperature (°C), and $\Delta \rho$. (2) Biological responses: chl-a (μg L^{-1}), phytoplankton density (L^{-1}), zooplankton density (L^{-1}), phytoplankton taxa richness, zooplankton taxa richness, zooplankton average size (mm), and zooplankton fecundity. For continuous response variables, we used linear mixed effects models (Gaussian distribution with an identity link) on either the raw or $\log_{10}$-transformed data (with the addition of + 1 for any transformed variables that included zeros). For discrete counts such as taxonomic richness, we used a Poisson distribution with a log-link function. Finally, for zooplankton fecundity we used a binomial distribution with a logit-link function to model the number of fecund versus non-fecund adults (combined using the 'cbind' function in R). Models were built using the lme4 package (Bates et al. 2014) and implemented in R version 3.0.1 (R Development Core Team 2018).

In each model, we included fixed effects for elevation and lake size [both surface area (SA) and maximum depth (MD)] as well as random intercept terms for lake identity and visit number (early, middle, late season). To avoid collinearity, we evaluated pairwise correlations between predictor variables and ensured all relationships were low ($\rho \leq |0.60$) before including predictor variables into models. Depending on the response, we also included fixed factors for sample location (epilimnion = 1, hypolimnion = 0, for all analyses based off of collected water samples) and fish presence (yes = 1, no = 0). In our initial models, we tested whether there were significant, two-way interactions between elevation and each of the following: maximum depth, sample location, and fish presence. We did not include all possible interactions both because of a lack of a priori hypotheses and a desire to avoid overfitting; non-significant interaction terms were removed and models re-run to improve coefficient estimates.

For all models, we checked for variance inflation using VIF (implemented in the car package) and estimated the significance of individual terms using likelihood ratio tests (implemented in the lmerTest package) (Fox and Weisberg 2011; Kuznetsova et al. 2017). Approximate R^2 values for the final, reduced models were obtained using the function rsquaredglmm (Barton and Barton 2015).

Community composition

To evaluate how geographic and elevational distance influenced variation in lake community composition for planktonic communities for a given lake, we used Mantel tests to calculate the correlation between each lake-pairs' community dissimilarity and either the Euclidean distance between those lakes (UTM straight-line distance) or their elevational distance (i.e., that raw difference in elevation between the lakes) (Legendre et al. 2015). We calculated dissimilarity metrics for a subset of 15 lakes with complete richness counts in the vegdist{vegan} package (Oksanen et al. 2013) based on the occurrence of 113 different morphometrically distinct groups for both phytoplankton and zooplankton. Finally, we calculated gamma diversity (total number of distinct groups for all lakes found during the entire sampling period) and beta diversity (ratio between gamma (regional) and alpha (local, the amount of distinct groups for a single lake found during the entire sampling period) diversities for lakes above and below treeline (Baselga and Orme 2012; Baselga 2013).

Results

Lake characteristics

Sampled lakes ranged in elevation from 2480 to 3550 m a.s.l. (1 SD = 32.84 m a.s.l.), in surface area from 4366 to 161,340 m^2 (mean ± 1 SD: 56,017 ± 5811 m^2) and deepest depth from 1.5 m to 42 m (mean ± 1 SD: 10.81 ± 8.97 m) (see Table 1 for a summary lake morphometric characteristics). Our estimates of NDVI around the lakes (range: 0.28 to 0.67) correlated strongly with elevation ($\rho = -0.899$, $P < 0.001$), with lakes below treeline (3345 m) typically having NDVI scores of 0.42 or greater. As expected, lakes with NDVI scores below 0.42 (all above treeline) were associated with low DOC concentrations that averaged < 1.2 mg C L^{-1} (Table 2, see SI). Overall, 14 of the 19 lakes supported fish, including *Oncorhynchus clarkii stomias* (greenback cutthroat trout), *Oncorhynchus mykiss* (rainbow trout), *Salmo trutta* (brown trout) and tiger trout (sterile hybrid of brook and brown, *Salmo trutta* × *Salvelinus fontinalis*). During the 12 week-long survey period we observed little precipitation prior to each sampling visit and all lakes slightly increased in thermal stratification from the first to thirds visits (β_{visit}: 0.014 ± 0.007, $P = 0.05$, $R^{2c} = 0.44$).

Table 2 Response averages and ranges for measured variables across all measured depths reported as average (range)

Site	Physiochemical parameters										Biological parameters		
	DOC	FI	TDN	TDP	NO_3	PO_4	SO_4	Water temp.	pH	Cond.	Chl-a	Phytoplankton	Zooplankton
	(mg C L^{-1})		(µmol L^{-1})	(µmol L^{-1})	(µmol L^{-1})	(µmol L^{-1})	(µeq L^{-1})	(°C)		(S cm^{-1})	(µg L^{-1})	Density (L^{-})	density (L^{-})
Mud	7.71	1.39	27.81	0.004	0.07	0.223	58.62	16.62	7.19	77.6	5.73	2451.2	56.99
	(6.80–8.56)	(1.38–1.41)	(22.04–30.43)	(0.001–0.014)	(0.02–0.23)	(0.148–0.327)	(56.78–61.32)	(11.44–19.24)	(6.98–7.99)	(71.0–108.0) (0.95–14.20)	(0.95–14.20)	(718.62–9661.06)	(47.79–75.07)
Lost	2.33	1.37	13.41	0.017	0.28	0.185	130.33	12.65	7.53	38.9	4.92	1601.61	32.38
	(1.95–2.75)	(1.34–1.39)	(11.23–18.12)	(0.007–0.036)	(0.11–0.58)	(0.106–0.266)	(117.76–143.92)	(8.58–16.49)	(6.65–8.23)	(35.0–42.0)	(2.16–8.48)	(383.93–3556.10)	(21.33–49.37)
Red Deer	1.23	1.40	11.50	0.101	1.62	0.146	36.03	7.12	7.25	9.4	3.17	409.63	10.91
	(1.03–1.37)	(1.35–1.48)	(8.65–20.30)	(0.010–0.177)	(0.16–2.86)	(0.100–0.187)	(33.77–38.56)	(4.15–13.69)	(6.25–8.03)	(9.0–11.0)	(1.15–6.04)	(163.81–611.60)	(6.38–13.52)
Red Rock	6.05	1.40	25.83	–	–	0.278	5.10	10.54	7.31	26.3	4.16	–	48.19
	(6.02–6.08)	(1.39–1.40)	(24.66–26.99)			(0.235–0.321)	(5.03–5.16)	(10.49–10.57)	(7.30–7.32)	(26.0–27.0)	(3.39–4.93)		(48.19)
Pear Reservoir	2.35	1.37	15.85	0.067	1.08	0.182	20.80	8.43	6.80	10.3	10.40	320.20	7.71
	(2.03–2.78)	(1.33–1.40)	(10.31–27.55)	(0.014–0.130)	(0.23–2.10)	(0.120–0.252)	(18.28–22.44)	(5.50–13.61)	(6.02–7.76)	(8.0–23.0)	(2.86–23.27)	(107.98–753.85)	(3.37–15.95)
Long	1.34	1.33	11.99	0.293	4.73	0.167	59.44	9.09	6.99	11.0	3.80	1403.88	14.95
	(0.87–2.07)	(1.30–1.36)	(4.60–18.42)	(0.103–0.577)	(1.66–9.31)	(0.134–0.249)	(58.25–62.50)	(4.83–12.23)	(6.55–7.26)	(9.0–13.0)	(2.12–6.97)	(702.38–2736.35)	(7.40–24.89)
Yankee Doodle	0.71	1.40	9.36	–	–	0.184	28.93	11.09	7.05	11.3	6.68	2233.77	33.73
	(0.58–0.82)	(1.35–1.48)	(4.38–22.85)	(0.094–0.268)	(27.09–30.40)	(6.96–14.92)	(6.28–7.31)	(9.0–16.0)	(2.08–10.63)	(664.05–5931.58)	(18.87–48.58)		
Mitchell	1.34	1.32	20.55	0.659	10.63	0.161	50.19	7.78	7.20	18.17	3.15	—	0.265
	(1.28 1.40)	(1.32)	(18.45–22.65)	(0.649–0.669)	(10.47–10.79)	(0.140–0.182)	(49.89–50.49)	(4.69–10.57)	(7.02–7.32)	(10.0–27.0)	(0.91–4.93)		(0.265)
Jasper	1.43	1.38	16.85	0.486	7.83	0.158	28.90	–	7.27	14.5	7.68	1220.78	12.65
	(1.20–1.74)	(1.33–1.49)	(11.96–19.31)	(0.348–0.685)	(5.61–11.05)	(0.097–0.187)	(21.59–44.10)		(6.53–7.72)	(11.0–29.0)	(2.21–20.78)	(338.50–3589.91)	(5.55–19.76)
Forest	0.62	1.36	9.40	0.228	3.68	0.161	18.71	10.71	7.76	14.5	8.24	7365.33	15.52
	(0.59–0.66)	(1.30–1.46)	(8.21–10.14)	(0.145–0.324)	(2.34–5.23)	(0.134–0.187)	(17.47–20.01)	(8.13–13.88)	(7.33–8.29)	(12.0–19.0)	(4.66–12.60)	(110.06–29,069.69)	(2.87–28.17)
Isabelle	0.97	1.36	19.12	0.564	9.09	0.153	65.90	7.21	7.12	9.9	6.92	1791.92	17.37
	(0.78–1.47)	(1.33–1.40)	(9.01–29.68)	(0.220–0.986)	(3.55–15.90)	(0.120–0.182)	(55.57–82.88)	(3.55–12.01)	(5.41–7.93)	(8.0–12.0)	(2.62–15.06)	(635.41–5323.97)	(4.13–42.04)
Diamond	0.82	1.39	8.86	0.202	3.26	0.156	40.08	11.14	7.64	20.2	2.16	219.43	9.31

Table 2 (continued)

Site	Physiochemical parameters										Biological parameters		
	DOC	FI	TDN	TDP	NO_3	PO_4	SO_4	Water temp.	pH	Cond.	Chl-a	Phytoplankton	Zooplankton
	(mg C L^{-1})		(μmol L^{-1})	(μmol L^{-1})	(μmol L^{-1})	(μmol L^{-1})	(μeq L^{-1})	(°C)		(S cm^{-1})	(μg L^{-1})	Density (L^{-})	density (L^{-})
	(0.70–0.10)	(1.31–1.44)	(5.83–12.36)	(0.027–0.420)	(0.44–6.77)	(0.103–0.193)	(32.75–45.10)	(6.66–13.79)	(7.30–8.06)	(14.0–41.0)	(1.15–3.95)	(73.20–408.06)	(8.91–9.67)
Lake Albion	1.40	–	8.81	0.061	5.45	0.188	81.47	11.20	6.93	14.0	10.57	1372.97	47.51
	(1.29–1.62)		(5.81–13.35)	(0.025–0.123)	(3.52–8.33)	(0.077–0.299)	(77.03–92.62)	(7.00–14.40)	(6.24–8.05)	(13.0–16.0)	(2.17–22.38)	(668.69–4039.38)	(12.26–73.93)
GL1	1.19	–	10.54	0.048	5.26	0.162	124.53	11.76	7.51	31.2	4.43	536.47	17.22
	(1.05–1.35)		(6.17–15.53)	(0.008–0.120)	(3.96–7.73)	(0.046–0.241)	(103.98–131.20)	(8.09–13.58)	(6.24–8.54)	(29.0–39.0)	(1.15–13.77)	(85.43–1170.07)	(3.54–38.56)
Lion Lake 2	0.81	1.37	13.22	0.163	2.63	0.174	17.80	10.08	7.06	6.6	7.29	744.56	5.26
	(0.72–0.92)	(1.32–1.41)	(6.35–23.95)	(0.011–0.228)	(0.18–3.68)	(0.154–0.190)	(16.47–19.15)	(7.06–12.06)	(6.41–7.50)	(5.0–9.0)	(2.43–12.67)	(159.00–1719.86)	(3.38–7.49)
Upper Diamond	0.71	1.37	9.68	0.376	6.06	0.128	59.35	7.71	7.37	21.9	2.97	190.23	3.30
	(0.49–1.23)	(1.33–1.41)	(7.33–12.75)	(0.249–0.486)	(4.07–7.84)	(0.063–0.151)	(49.09–72.16)	(4.06–9.70)	(7.14–7.61)	(16.0–26.0)	(0.42–8.26)	(122.28–299.43)	(0.05–6.75)
Blue	0.67	1.39	15.42	0.680	10.96	0.181	30.24	5.55	6.84	5.7	2.51	386.57	1.78
	(0.52–1.10)	(1.34–1.47)	(9.58–21.79)	(0.420–0.803)	(6.77–12.95)	(0.103–0.285)	(28.19–31.52)	(2.64–9.90)	(6.24–7.57)	(4.0–6.0)	(0.52–3.81)	(174.70–573.44)	(1.38–2.12)
Snowbank	0.77	1.36	14.79	0.310	4.99	0.148	20.13	10.04	7.21	7.4	4.69	260.30	7.38
	(0.64–0.94)	(1.35–1.39)	(13.00–19.81)	(0.294–0.316)	(4.74–5.10)	(0.112–0.187)	(18.24–22.03)	(7.82–11.44)	(7.03–7.38)	(5.0–14.0)	(2.07–6.96)	(147.11–445.98)	(2.98–12.08)
GL4	0.57	–	5.27	0.082	5.36	0.176	55.11	9.69	7.41	8.2	5.62	914.79	1.50
	(0.52–0.70)		(1.35–10.96)	(0.006–0.200)	(1.65–20.41)	(0.106–0.275)	(49.22–64.69)	(6.21–11.76)	(6.73–8.80)	(6.0–10.0)	(0.37–15.91)	(377.72–4032.52)	(0.94–2.51)

Data for DOC, FI, TDN, TDP, NO_3, PO_4, SO_4 Chl-a, and phytoplankton density are from surface and hypolimnion samples. Water temperature (temp.), pH and Conductivity (Cond.) are from every meter transects from surface to hypolimnion. Zooplankton data are from vertical tows. Full data available on EDI via Niwot Ridge LTER's webpage. Dashed lines in place of numbers indicate data not processed or collected

Table 3 Model-averaged scaled elevation coefficients, unconditional standard errors, significance, the conditional coefficient of determination for Generalized mixed-effect models, and number of observations included in each model for both physiochemical characteristics: TDN, TDP, NO_3, PO_4 in μmol L^{-1}; SO_4 in μeq L^{-1}, DOC in mg C L^{-1}, FI, water temperature in °C, specific conductance (Sp.C.) in μS cm^{-1}, pH, Secchi depth in m, K_{PAR} in PAR m^{-1}, Δ ρ in kg m^{-3}, as well as biological responses: zooplankton (zoo.) and phytoplankton (phyto.) density L^{-1}, zoo. and phyto. richness, zoo. average size in mm, zoo. fecundity and chlorophyll-a (chl-a) in μg L^{-1}

Response	$\beta_{elevation}$	SD error	Significance	R^{2c}	n
Physiochemical characteristics					
$\log_{10}(NO_3 + 1)$	0.204	0.052	0.0020	0.811	115
PO_4	− 0.014	0.004	0.0023	0.142	125
Δ ρ	− 0.018	0.004	0.0003	0.647	55
$\log_{10}(K_{PAR})$	− 0.059	0.014	0.0001	0.362	52
$\log_{10}$(Sp.C)	− 0.145	0.030	0.0003	0.866	111
$\log_{10}$(DOC +1)	− 0.160	0.033	0.0003	0.968	125
Water temperature	− 1.091	0.400	0.0168	0.725	111
TDN	− 3.551	1.143	0.0090	0.683	125
Secchi depth	0.072	0.036	0.0672	0.725	55
$\log_{10}$(TDP +1)	0.023	0.018	0.2181	0.853	115
FI	− 0.005	0.004	0.1789	0.269	83
pH	− 0.022	0.065	0.7470	0.430	109
$\log_{10}(SO_4)$	− 0.054	0.087	0.5440	0.987	125
Biological responses					
$\log_{10}$(zoo. density + 1)	− 0.269	0.088	0.0136	0.710	55
Zoo. size	0.108	0.044	0.0324	0.866	47
$\log_{10}$(phyto. density + 1)	− 0.142	0.071	0.0690	0.502	102
Phyto. richness	− 0.033	0.032	0.3060	0.078	38
Zoo. richness	− 0.087	0.088	0.3231	0.391	38
Zoo. fecundity	0.077	0.472	0.8700	0.562	55
$\log_{10}$(chl-a + 1)	− 0.006	0.036	0.8677	0.257	109

Influence of elevation on physicochemical responses

Increases in lake elevation were associated with weaker stratification ($\beta_{elevation}$: − 0.063 ± 0.016, $P = 0.0013$, $R^{2c} = 0.60$), colder water temperatures ($\beta_{elevation}$: − 1.09 ± 0.40, $P = 0.02$, $R^{2c} = 0.73$) and lower specific conductance ($\beta_{elevation}$: − 0.145 ± 0.03, $P = 0.003$, $R^{2c} = 0.87$). Concentrations of nutrients and DOC were generally dilute and (with the exception of NO_3) tended to decrease with elevation while water clarity increased (Table 3). Thus, higher elevation lakes had lower concentrations of TDN ($\beta_{elevation}$: − 3.55 ± 1.14, $P = 0.009$, $R^{2c} = 0.68$) and PO_4 ($\beta_{elevation}$: − 0.014 ± 0.004, $P = 0.002$, $R^{2c} = 0.14$) and DOC ($\beta_{elevation}$: − 0.16 ± 0.03, $P = 0.003$, $R^{2c} = 0.97$). Concomitantly with observed patterns for DOC, Secchi depth increased with elevation ($\beta_{elevation}$: 0.07 ± 0.04, $p = 0.067$, $R^{2c} = 0.73$) while capacity to attenuate PAR (K_{PAR}) decreased ($\beta_{elevation}$: − 0.06 ± 0.01, $P = 0.001$, $R^{2c} = 0.36$). In contrast, concentrations of NO_3 were greater in higher elevation lakes ($\beta_{elevation}$: 0.20 ± 0.05 $P = 0.002$, $R^{2c} = 0.81$). Variation in TDP, SO_4, and pH were not significantly associated with elevation (Fig. 2, Table 3), and interactions between elevation and other predictors were generally non-significant (and removed).

Among a subset of 16 lakes for which we estimated FI, values averaged 1.35, indicative of DOM predominantly derived from plant and soil sources. FI values ranged from 1.30 with some higher values up to 1.49 (standard deviation of 0.041) indicating potential contribution of microbially derived DOM (Table 2). Moreover, we found that FI was negatively associated with lake surface area (β_{SA}: − 0.002 ± 0.001, $P = 0.007$) and positively associated with both lake maximum depth (β_{MD}: 0.003 ± 0.001, $P = 0.012$) and sample depth (β_{EPI}: − 0.005 ± 0.001, $P = 0.034$, $R^{2c} = 0.27$), but unrelated to elevation (Fig. 2; Table 3).

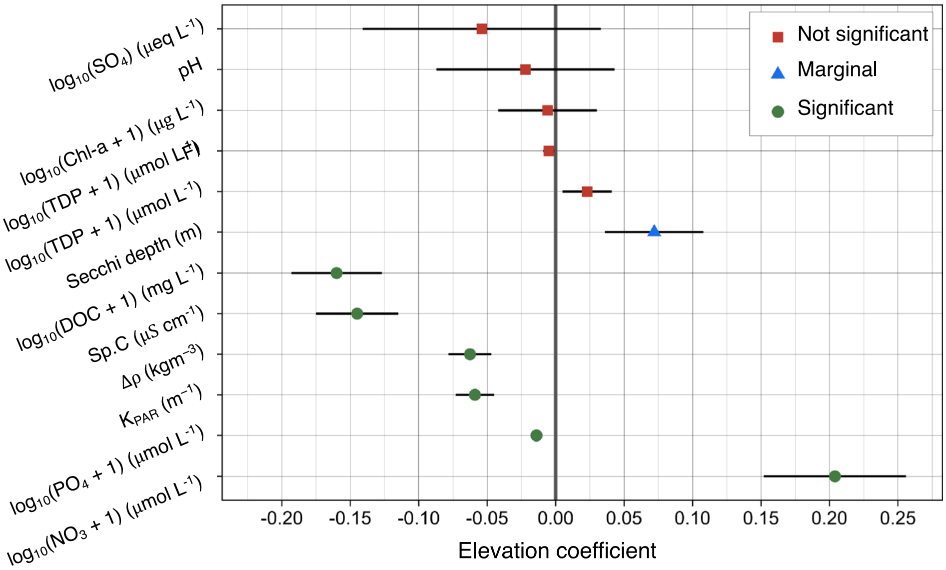

Fig. 2 Beta coefficients of physicochemical responses based on individual GLMMS for transformed TDP, NO_3 and PO_4 in μmol L^{-1}; transformed SO_4 in μeq L^{-1}, transformed DOC in mg C L^{-1}, FI, specific conductance (Sp.C.) in μs cm^{-1}, pH, secchi depth in m, transformed PAR attenuation (KPAR) m^{-1}, thermal stratification (Δ ρ) in kg m^{-3} and elevation (scaled). Point shape corresponds to a significant relationship values for each physiochemical response and horizontal bars represent the standard error. Temperature and TDN were excluded as their range was much larger than the other response variables

Influence of elevation on biological responses

Cumulatively, we found 74, 33, and four morphometrically unique groups of phytoplankton, zooplankton, and other arthropods. Within the zooplankton taxa we found 11 cladocerans, three copepods and 19 rotifers. With respect to phytoplankton at the phylum level we found 23 Bacillariophyta, nine Charophyta, 17 Chlorophyta, four Cryptophyta, four Cyanophyta, two Euglenozoa, three Miozoa, eight Ochrophyta and three unidentifiable unique groups. We also found one protozoan, Ciliophora, in our phytoplankton samples.

Chl-a concentrations exhibited a large range with values as low as 0.4 µg L^{-1} in Upper Diamond Lake to values as high as 22 µg L^{-1} in Lake Albion (Table 2). This broad range of concentrations was observed in lakes both above and below treeline and for all NDVI values for the surrounding watershed. Overall, chl-a concentrations were greater in hypolimnetic samples (β_{EPI}: -0.10 ± 0.05, $P = 0.039$, $R^{2c} = 0.37$), regardless of elevation or other lake characteristics. In contrast, phytoplankton density was lower in higher elevation lakes ($\beta_{elevation}$: -0.15 ± 0.07, $P = 0.058$), but also higher in hypolimnetic samples (β_{EPI}: -0.28 ± 0.07, $P < 0.001$, $R^{2c} = 0.49$). Additionally, we observed no significant increase or decrease in either chl-a concentrations or phytoplankton density with sample date. Elevational increases were associated with decreases in zooplankton density ($\beta_{elevation}$: -0.26 ± 0.09, $P = 0.013$, $R^{2c} = 0.69$) and increases in average zooplankton size ($\beta_{elevation}$: 0.11 ± 0.04, $P = 0.032$, $R^{2c} = 0.87$). Fish presence was also associated negatively with zooplankton size (β_{fish}: -0.62 ± 0.10, $P < 0.001$, $R^{2c} = 0.87$). We also observed a slight increase for zooplankton density from the first to third visits (β_{visit}: 0.085 ± 0.04, $P = 0.040$, $R^{2c} = 0.71$). There was no relationship between elevation and either phytoplankton or zooplankton taxonomic richness or zooplankton fecundity, although zooplankton taxonomic richness and zooplankton fecundity both were significantly associated with lake surface area (richness: β_{SA}:0.18 ± 0.09, $P = 0.048$, $R^{2c} = 0.38$; fecundity: β_{SA}:-0.44 ± 0.22, $P = 0.043$, $R^{2c} = 0.55$) (Fig. 3, see Table 3 for physicochemical and biological model responses to elevation).

Spatial variation in lake community composition

Using data on the combined zooplankton and phytoplankton taxonomic composition of each lake, we found a positive correlation between community dissimilarity and elevational distance ($r = 0.35$, $P = 0.02$), but no significant association between straight-line distance and community dissimilarly ($r = 0.15$, $P = 0.12$, Fig. 4). For instance, average community dissimilarity changed by 18% for every 500 m of elevation distance, while only changing by 4% for 500 m in UTM distance. Overall, lakes above treeline supported fewer total planktonic taxa (gamma diversity = 70) compared with those below treeline (gamma diversity = 109), and beta diversity (for aggregated planktonic taxa) was significantly higher for lakes below treeline ($F(1,12) = 5.82$, $P = 0.033$). In particular, lakes below treeline tended to have zooplankton populations dominated by cyclopoid copepods and greater densities of chydoridae (small cladocerans) as well as high densities of phytoplankton groups such as bacillariophytes, chrysophytes, cyanophytes, and other microeukaryotes euglenophytes and ciliates. In contrast, alpine lakes contained mostly zooplankton and phytoplankton groups dominated by calanoid copepods and chlorophytes.

Discussion

While low-elevation lakes have a long history of limnological study and characterization, considerably less is known about the ecology of alpine aquatic systems. Rapid yet continuous variation in lake characteristics with elevation offer an important opportunity to investigate the role of physical heterogeneity on aquatic chemistry and biology. Our results supported past patterns of elevation driven catchment characteristics (Rose et al. 2009; Moser et al. 2019), where increases in elevation were associated with greater water clarity and higher nitrate concentrations with significant decreases in stratification strength, dissolved organic carbon (DOC), water temperatures, and conductivity. The lower temperatures and shorter growing seasons of high-elevation lakes can limit both ambient water temperatures as well as strengthen the contrast between surface and hypolimnetic temperatures (i.e., stratification strength) (Livingstone 1997; Weyhenmeyer et al. 2004; Kraemer et al. 2017). Lakes above treeline, which in our study were typically surrounded by talus slopes, also had less influx of terrestrially derived sources of dissolved organic material (DOM), helping to account for the progressive declines in DOC concentrations with elevation (Rose et al. 2009; Sadro et al. 2012). The uppermost lakes in mountain catchments also receive the majority of precipitation and are closely linked to cryospheric features like snow fields and permafrost. As a result, these lakes collect the greatest amount of nitrate (NO_3) from both atmospheric deposition associated with human activities (Williams et al. 1997; Baron et al. 2009; Saros et al. 2010). These findings are broadly consistent with patterns reported for other montane and alpine lake ecosystems, including those from European mountain ranges (Reche et al. 2005; Camarero et al. 2009), the Sierra Nevada Mountains of California (Sadro et al. 2012), the Beartooth Mountains of Wyoming and Montana (Williamson et al. 2010; Rose et al. 2015), and the Canadian Rockies (Pinel-Alloul et al. 2013).

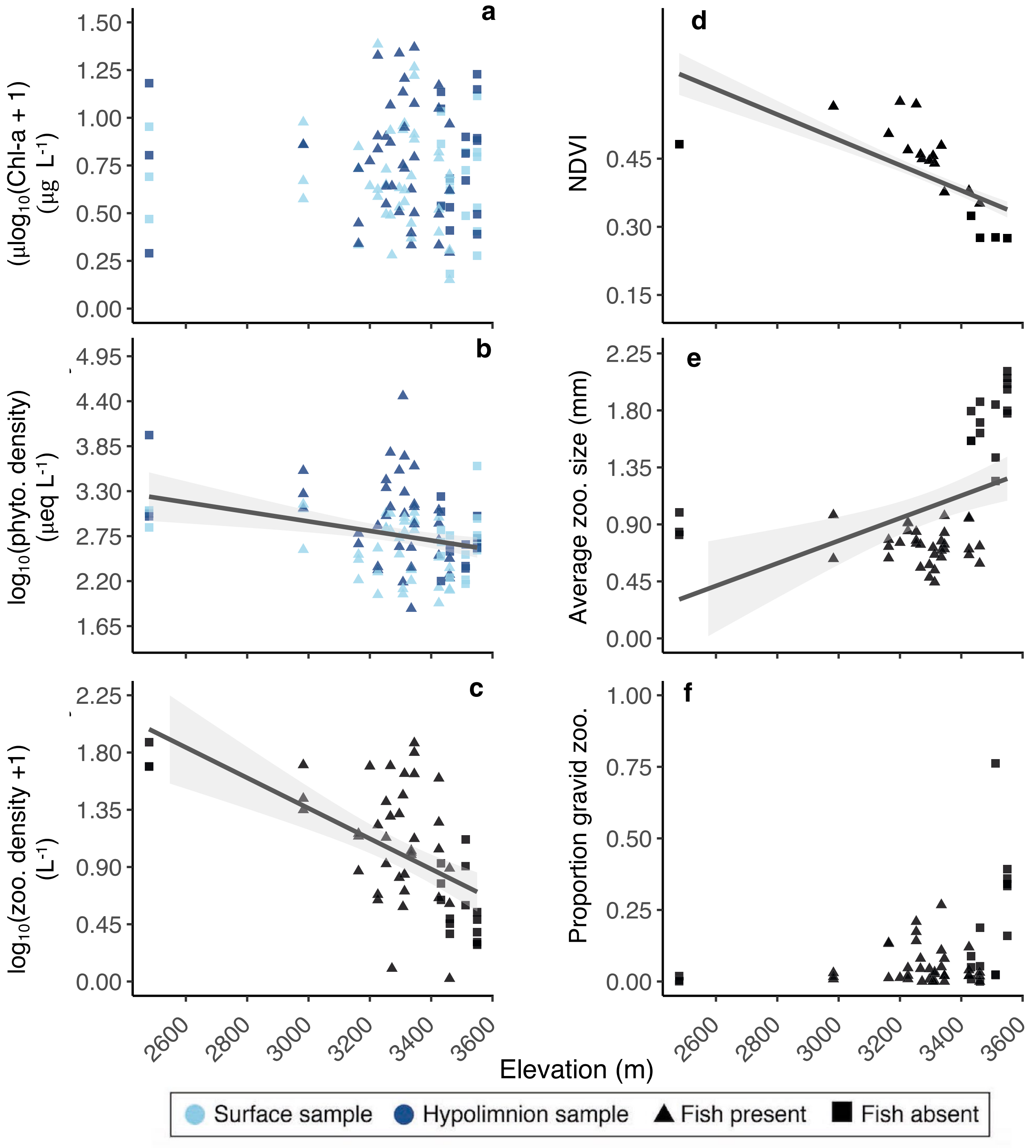

Fig. 3 Correlations of elevation with **a** transformed chlorophyll-a (chl-a) concentrations in μg L^{-1}, **b** transformed phytoplankton (phyto.) density in L^{-1}, **c** transformed zooplankton (zoo.) density in L^{-1}, **d** NDVI **e** average individual zooplankton size in mm and the **f** proportion of gravid zooplankton. Point colors correspond to sample location when relevant for the response. Point shape corresponds to whether the lake was contained by fish. Plots with regressions lines and 95% confidence bands indicate statistically significant linear regressions

Analytically, the use of a mixed-modeling approach allowed us to statistically incorporate the inherent heterogeneity in lake ecosystems by accounting for variation in sample depth, sampling date, and morphometric characteristics, thereby focusing our analyses on how a broad range of responses covaried with elevation. Superimposed upon

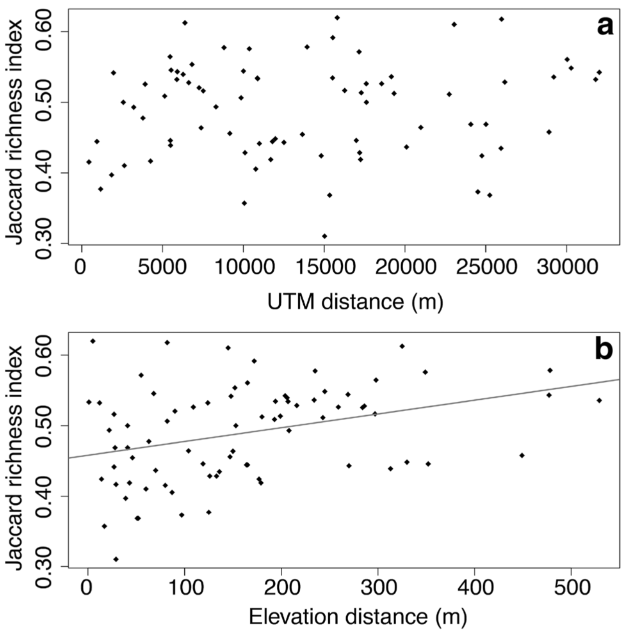

Fig. 4 Plot A and B represent community dissimilarity for three visits for a subset of 15 lakes with complete richness observations. Dissimilarly was calculated using Jaccard's dissimilarity index for observations of occurrence of 111 different taxonomic groups ranging from species to class for both phytoplankton and zooplankton and ranged from 0.620 to 0.310. **a** UTM distance ranged from 427.57 to 36,000.77 m and was not correlated with community dissimilarity (r = 0.101, p = 218). **b** Elevation distance ranged from 1 to 530 m and was positively correlated community dissimilarity (r = 0.347, p = 0.02)

the large-scale influences of elevation are the more local effects associated with the catchment and lake morphometric factors, which can mediate the duration of ice-cover and the dynamics of snowmelt (Sadro et al. 2019). In regards to our biological sampling of multiple planktonic communities this approach revealed clear patterns with respect to elevation and community organization, and density for which there are fewer previous studies on mountain lakes (Stoddard 1987; Catalan et al. 2009; Skála 2015; Lyons and Vinebrooke 2016). We found beta diversity (aggregated across all planktonic groups measured) was higher in lakes below treeline. Similarly, the estimated average density (for all samples collected) of both phytoplankton and zooplankton increased by 60% and 77%, respectively for lakes below treeline. Lower densities are consistent with the potential influences of reduced total nutrient availability, colder temperatures, and shorter water residence times associated with alpine aquatic ecosystems (Williamson et al. 2010; Kissman et al. 2017). Average zooplankton body size also increased by 18% for cladocerans and 41% for copepods for lakes above treeline, even while controlling for the established negative influence of introduced fish (Loewen and Vinebrooke 2016). This pattern was driven mainly by the presence of large-bodied cladocerans (e.g., *Daphnia pulicaria*) and calanoid copepods (e.g., *Hesperodiaptomus shoshone*) in lakes above treeline and could also reflect the tendency of cold-water systems to favor slower-growing, larger-sized, and longer-lived organisms (Dodson 1974; Angilletta et al. 2004). We caution, however, that the uneven distribution of fish—which were less common among the highest lakes—limit opportunities for strong inference.

Elevation was more strongly correlated with planktonic community similarity among lakes relative to measures such as geographic distance. Thus, lakes at similar elevations—even when relatively far apart—shared more similar species of phytoplankton and zooplankton than lakes within the same catchments but at different elevations. Planktonic communities are often considered to be broadly distributed across regional scales and potentially greater scales (Finlay 2002; Filker et al. 2016); but recent efforts to characterize micro-biodiversity have shown that planktonic species often cluster in certain environments regardless of dispersal potential (Martiny et al. 2006; Stomp et al. 2011). Specifically, in 2016 Flicker et al. looked at community composition of small-sized eukaryotes across three separate continents and found clear dissimilarity between communities separated by large scales (> 10,000 km), a high degree of similarity due to regional scale environmental factors in high-mountain lakes. Contextualizing this trend to zooplankton communities; we found that taxa such as the calanoid *Diaptomus* (subgenus: *Hesperodiaptomus*) were only observed in alpine lakes, and past studies have suggested these copepods are high-elevation specialists (Loewen et al. 2019). In part, this may be due to their carotenoid pigmentation and formation of mycosporine-like amino acids (MAAs) which help protect them against harmful UVR (Stoddard 1987; Moeller et al. 2005; Larson et al. 2008; Nevalainen et al. 2015). Similarly, alpine cladocerans tended to exhibit a greater frequency of melanization, which can help protect against UVR but is energetically costly, creating a trade-off between photoprotection and the costs of melanin synthesis (Hessen 1996, 2002; Hessen et al. 1999). This trade-off could help explain why cladocerans tended to have lower abundances than copepods within high-elevation systems (Sommaruga 2001). Overall, these findings contribute to a growing effort to characterize mountain lake community composition at various trophic scales (Oikonomou et al. 2015; Filker et al. 2016; Loewen et al. 2019) and provide evidence that elevation and the physical changes associated with it function as a niche filter, for which the biological communities are more closely associated with their elevational position rather than their geographic position or connectivity with neighboring lakes.

While our results showed distinctive patterns for how biological communities shifted along elevation, they were more ambiguous with respect to chlorophyll-a concentrations and allochthony. Interestingly, we found no relationship between elevation and chlorophyll a (chl-a) values, despite other marginal evidence of increased water clarity and lower standing stocks of phytoplankton. Several past studies in Green Lakes Valley (one of the catchments surveyed here), have shown for multiple summer seasons that FI was greatest in the alpine lakes above treeline, reflecting autochthonous DOM production, and decreased in sub-alpine lakes reflecting greater inputs of DOM derived from plants and soils (Hood et al. 2003a; Miller et al. 2009). Our fluorescence index (FI) data (which did not include Green Lakes Valley lakes) averaged around 1.4, a value slightly higher than 1.3 which is indicative of allochthonous DOM (Cory and McKnight 2005). Notably, higher FI values occurred in hypolimnetic waters, where higher chl-a concentrations also occurred; but these patterns were unrelated to elevation. In general, we observed little precipitation preceding our sampling visits and lakes tended to become more thermally stratified. The stratification pattern combined with the evidence of hypolimnetic chlorophyll-a maximums and autochthonous DOM, indicates that ultraviolet radiation (UVR) could be potentially restricting primary productivity particularly in the high elevation lakes that were strongly stratified (Laurion et al. 2000). This inclination could have been better substantiated with additional sampling visits; however, the sudden and unpredictable occurrence of ice-cover at our survey sites challenged our ability to capture later seasonal variation and limits our current scope of inference (Kolesar et al. 2002). The complex relationship between elevation and lake-wide metabolism make it difficult to disentangle the patterns of DOM concentrations from a strictly comparative sampling design in which lakes vary in exposure to UVR, precipitation and snow melt patterns, basin morphologies, and stratification regimes (Miller et al. 2009; Sadro et al. 2011, 2018).

For instance, the influence of treeline, which is often a relatively abrupt and non-linear transition between forested areas and alpine areas (Humphries et al. 2008), plays a key role in the determining the influence of terrestrial vegetation and organic matter for in-lake processes (Miller and McKnight 2015). One of these processes is the photoprotective role DOC plays in limiting UVR penetration, which for lakes above treeline (with less contact with terrestrial carbon sources) can be a significant factor in regulating biology at multiple trophic levels (Vincent and Roy 1993). Additionally, landscape factors like position of treeline and the associated source of terrestrially derived carbon could have widespread cascading effects on nutrient availability and ecosystem productivity. For example, researchers observed shifts in the bacterial community composition and increased the rate of carbon and phosphorus cycling following experimental treatments of allochthonous carbon (Rofner et al. 2017). Similarly, because mountain lakes have unique biogeochemical patterns often dominated by snow deposition (Ventura et al. 2000; Kuhn 2001), atmospheric nitrogen deposition often leads to greater nitrate concentrations at higher rather than lower elevations (i.e., the Landscape Continuum Model, Seastedt et al. 2004). The ratio of lake productivity to respiration may therefore shift from > 1 (net autotrophic) to < 1 (net heterotrophic) as elevation moves downward toward treeline. This work emphasizes opportunities to develop novel predictive frameworks for capturing the unique physical and biological characteristics of mountain ecosystems.

Although there has been persistent interest in understanding landscape-level controls on lake characteristics (Soranno et al. 2017; Hill et al. 2018), this effort has rarely extended to dynamics within mountain lakes; either along lake chains, elevations, or in regards to their biological communities, despite the fact that these ecosystems represent almost a quarter of the world's lakes (Verpoorter et al. 2014). And while high-elevation aquatic ecosystems are often relatively remote, they are nonetheless vulnerable to contemporary threats such as warming (Preston et al. 2016; Sadro et al. 2019) and nutrient deposition, which have the potential to alter fundamental aspects of their ecology. Alpine lakes along the Front Range of the Colorado Rocky Mountains, for instance, experience high rates of upland inorganic nitrogen deposition (both as nitrate and ammonium) from agricultural and industrial sources (Bowman et al. 2015). Current and future changes in deposition, warming, and treeline movement (Bueno de Mesquita et al. 2018) have the potential to threaten the more unique attributes of alpine lakes and their ability to play an important role in ecosystem services ranging from water provisioning to nutrient cycling (Rhodes et al. 2017).

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