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Understanding Ecosystem and Food Web Processes of Freshwater Lakes

By

CHRISTINE ANN PARISEK
DISSERTATION

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in

Ecology

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OFFICE OF GRADUATE STUDIES

of the

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Abstract

This dissertation explores freshwater lake ecosystems, especially their productivity, vulnerability, and food web architecture, through the lenses of landscape limnology and community ecology. There is a growing necessity to quantify ecosystem productivity (**Chapter 1**), climate change resilience (**Chapter 2**), and the mechanisms that govern lake food web structure and function (**Chapter 3**). Studies on these topics will enable conservation management of lakes at all scales, including adaptation to global environmental change.

The **first chapter** develops five USA reservoir classification systems ranging in complexity to understand the distribution of fish biomass in different reservoir types. This framework is leveraged to predict pools of fish biomass in unsampled reservoirs across the USA. Results provide evidence that reservoirs, while undeniably ecological catastrophes, hold massive pools of freshwater fisheries biomass and may have higher ecological and ecosystem services value than previously realized. Results provide a new vehicle for upscaled estimates of ecosystem productivity, ecological resilience, a snapshot of inland fisheries biomass potentially available for human consumption, and identifies how reservoir biomass changes over time.

The **second chapter** describes velocity of change in heat accumulation rates across high elevation lake landscapes in the contiguous United States. Mountain lake landscapes are sensitive to climate change, yet the velocity at which they are undergoing thermal change is poorly understood. This uncertainty presents challenges for managers interested in building ecological resilience to climate change. Developed velocity of change metrics provide compelling evidence that lower elevation mountain landscapes are undergoing temperature change more rapidly, and that each of the ten primary mountain ranges in the United States exhibit unique trends in velocity of change. Products from this work include climate

vulnerability classifications for mountain lake landscapes across the USA, based on velocity of change, that managers can use in conservation prioritization frameworks.

The **third chapter** uses an extensive field study to test applicability of two critical ecological theories in mountain lakes; that is that food chain length and community niche complexity scales predictably with either ecosystem size or productivity. Using data collected from 36 mountain lake food webs over three summers in the Sierra Nevada, California, USA, patterns of food web complexity in relation to lake volume were directly tested. Overall, there is limited support for the ecosystem size hypothesis, and weak-to-no support for the productive space hypothesis. Rather, food web architecture was highly context-dependent. Aquatic and terrestrial insects dominated contributions of ecological energy flows to consumers in most lakes. Fish consumer diet reliance on key food sources varied along a lake ecosystem size gradient. From small to large lakes, there is apparently increasing reliance on terrestrial insects and periphyton, decreasing reliance on aquatic plants, and constant, but again high, reliance on aquatic insects. These results are useful in assessing how oligotrophic mountain lake ecology differs from other more well-studied regions, and for better managing mountain lake landscapes and ecosystems.

Collectively, these chapters provide novel information on the ecology of North American lakes, with a special focus on mountain landscapes. These science products will aid conservation management of lake landscapes overall. Further, they are important examples of the use of lesser-studied lake types as models for ecological study.

Chapter 1

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Reservoir ecosystems support large pools of fish biomass

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Abstract

Humans increasingly dominate Earth's natural freshwater ecosystems, but biomass availability of modified ecosystems is rarely studied. We estimate potential fish total standing stock in USA reservoirs is 3.4 billion (B) kg, and approximate annual secondary production at 4.5 B kg y⁻¹. We also observe varied and non-linear trends in reservoir fish biomass over time, thus previous assertions that reservoir fisheries decline over time are not universal. Reservoirs are globally relevant pools of freshwater fisheries, in part due to their immense limnetic footprint and spatial extent. This study further shows that reservoir ecosystems play major roles in food security and fisheries conservation. We encourage additional effort be expended to effectively manage reservoir environments for the good of humanity, biodiversity, and fishery conservation.

Significance Statement

Globally, many freshwater fishes and fisheries resources are imperiled and at-risk of collapse. However, previous research largely focuses on freshwater fisheries in natural rivers and lakes, rather than reservoirs. This study provides evidence that novel and reconciled ecosystems, such as reservoirs, hold massive pools of freshwater fisheries biomass and may have higher

ecological value than previously thought. While dams are patently ecological catastrophes, ecosystem services including secondary fish production provided by reservoirs are nonetheless substantial. Indeed, in many locations (e.g., arid regions), reservoirs are the only remaining fisheries resource. We suggest considerable conservation management and systematic considerations are warranted for reservoir fisheries worldwide.

Introduction

Human dominance over freshwater ecosystems highlights the necessity to understand the fragility and biomass availability of these natural resources in response to global environmental change (Embke et al. 2019; Kao et al. 2020). Inland fisheries are especially critical, providing protein to developing countries (McIntyre et al. 2016), cultural value (Nesper 2002), and economic development (Allison et al. 2009). Freshwater fisheries and diversity are under threat from a range of sources including overfishing, pollution, habitat fragmentation, invasive species, and climate change (Ficke et al. 2007; Arlinghaus et al. 2016). These alterations have prompted widespread declines in freshwater fisheries; trends unlikely to abate given current socioecological trajectories (Leidy and Moyle 1998). Furthermore, harvest of marine fisheries stocks has plateaued since 1989 (Worm et al. 2009), suggesting additional fisheries resources will be needed to sustain human societies in the future. And while aquaculture is increasingly filling gaps, cultured fish are not currently scaling sustainably (Naylor et al. 2021). Inland fisheries will continue to be a major food source globally, but many inland fisheries are data-limited, presenting a challenge to conservation (Cooke et al. 2016).

Reservoirs represent potentially overlooked pools of secondary production (hereafter, “production”). Indeed, impoundments of streams and rivers by dams, are increasingly prominent

features over landscapes (Nilsson et al. 2005; Poff et al. 2007). Dams have altered over half of Earth's large rivers, including eight of the most speciose ecosystems (Nilsson et al. 2005). Overall, dams decimate native fish diversity and other freshwater riverine communities (Poff et al. 1997; Liermann et al. 2012). In a sobering assessment, Benke 1990 (Benke 1990) estimated that only 42 high quality free flowing rivers remain in the contiguous USA. Species that persist in reservoirs tend towards remarkably similar faunas composed of resilient species, often characteristic of warm-water lakes (Rypel and Bayne 2009). While reservoirs are of increasing research interest; still relatively little research exists on the distribution, limnology, and ecology of reservoirs (but see (Thornton et al. 1991; Miranda and Krogman 2015; Miranda and Faucheux 2022)). Fisheries biomass and production likely vary across reservoirs that differ in shape, residence time, temperature, depth, and other factors (Michaletz 1998). Further, the fisheries of some reservoirs may have declined as dams and reservoirs have aged towards or beyond expected lifespans (Miranda and Krogman 2015; Miranda and Faucheux 2022). The sheer number of dams on the surface of the Earth (Nilsson et al. 2005; Winemiller et al. 2016) implies that these environments produce ecosystem services that we should study and manage for improved sustainability. For example, understanding the ecological value of reservoirs may be critical for adapting to future climate change and food security challenges.

The primary goals of this research are to: **(1)** Digitize and make publicly available a legacy database containing fish biomass estimates from USA reservoirs. These data were expensive and laborious to collect and are rarely available for researchers. **(2)** Develop a reservoir classification system with broad application for 85,470 USA reservoirs such that any reservoir can be placed within families of similar reservoir types. A nationwide reservoir classification system may help address deficiencies in freshwater research by providing

comparable ecosystem types upon which to examine important ecological patterns. (3) Test the degree to which biomass in individual reservoirs and reservoir types has changed over long time periods; and (4) Generate fish biomass predictions in all USA reservoirs to a standardized point in time and estimate total biomass and annual production rate potential for fish populations across all USA reservoirs. These results aid in explicitly quantifying ecosystem services provided by reservoirs, in addition to stimulating thought on ways to manage reservoirs for improved function.

Methods

Fish Biomass

Empirical measurements of fish biomass are rare (Rypel and David 2017). For most of the last century, it was common practice to use toxicants for sampling fish populations and community biomass, particularly in reservoir environments of southern USA (Carlander 1955; Ploskey and Jenkins 1982). Rotenone – a plant extract, was the primary chemical used in fish poisoning surveys. Rotenone kills fish by blocking oxygen uptake; thus, suffocating fish. While lethal, it is widely recognized in the fisheries literature as being one of the best methods for obtaining empirical fish biomass values (Shelton and Davies 1983). In surveys, block nets are used to isolate coves or other pelagic areas, and the poison pumped at appropriate concentration to kill all fishes present within the water column. During the 1970s, the US Fish and Wildlife Service launched the National Reservoir Research Program (NRRP), which as part of its mission, began collating prior rotenone surveys collected by other state and federal agencies and coordinating future surveys in USA reservoirs. Original physical copies of the data were recently transferred to, and are now permanently stored at, the Center for Watershed Sciences, University

of California Davis, Davis, California, USA. Until now, the data from the NRRP's efforts have only been available on paper.

We digitized the legacy National Reservoir Research Program rotenone (poisoning) fish biomass dataset and make these data publicly available as part of this paper. The biomass data used for this study were generated from once widespread rotenone sampling programs which are now mostly banned (Rypel et al. 2021). For environmental and humane reasons, sampling with toxicants has become rare over time and was never widely used in countries outside the USA. Due to rotenone's efficacy, these rotenone datasets likely represent the best available, and most accurate, data on fish biomass in reservoir ecosystems to date; data of this kind are unlikely to ever be collected again. In total, the digitized dataset contains fisheries biomass data from 1,127 rotenone surveys on 301 USA reservoirs, 1948 – 1978, and spans twenty-two states (AL, AR, FL, GA, IA, IL, IN, KS, KY, LA, MA, MD, MO, MS, NC, NM, OK, SC, TN, TX, VA, WV). Species-specific biomass data are available; however, these data are yet to be entered into this database.

We used previously published data to adjust biomass estimates to account for known biases (underestimates) associated with ineffectiveness of block nets and incomplete recovery of fish (Shelton and Davies 1983). Adjustments involved calculating an average of species recovery values presented in Table 10.1 of Shelton and Davies 1983 (Shelton and Davies 1983), and multiplying all reservoir biomass estimates by this constant (1.773056). This adjustment assists in correcting rotenone biomass data for non-recovered fish. Empirical fish biomass values were joined to the open-access Omernik ecoregion dataset (Omernik and Griffith 2014). At its coarsest, level I, North America is subdivided into 15 ecological regions, level II into 52 regions, and level III into 104 regions. We used Omernik level II resolution for the purpose of this

analysis, however, use of any Omernik level resolution resulted in similar biomass predictions. Finally, our biomass data were joined to the 2018 National Inventory of Dams (NID) (US Army Corps of Engineers : Federal Emergency Management Agency. 2018) containing 91,468 rows of data on large, regulated dams and their reservoirs in the United States. The NID dataset is the most complete dataset on the inventory of dams and their reservoirs known in the USA, though there are numerous (hundreds-of-thousands to millions) of small dams and other structures which are not captured through the NID. NID reservoirs were also joined to Omernik level II ecoregions. During our analyses, we identified some issues with the NID dataset that required action. For example, some larger reservoirs have multiple dams; thus, data were cleaned using coding rules that, to the best of our ability, ensured each reservoir was only being counted once. Also, some of the largest waterbodies in the NID are natural lakes with small dams (e.g., Lake Superior) and needed to be removed prior to analysis. Finally, reservoirs without geographic coordinates, ecoregion assignments, and missing surface area information needed attention prior to analysis. The tidied NID dataset used in this analysis held 85,470 rows. See *Supplementary Text* and supporting R code for details on data cleaning and preparation.

Reservoir Classification System

We developed a series of reservoir classification systems of increasing complexity using reservoir volume, discharge, and Omernik ecoregions. In our most refined classification system, which may be of interest to future researchers of USA reservoirs, we used a hierarchical approach to classification whereby reservoirs were grouped by their membership in Omernik's level II ecoregions. Then for each ecoregion, we ran a k-means cluster analysis using reservoir maximum discharge and storage volume ($\ln(x+1)$ transformed and scaled). Parallel with Rypel et al. (Rypel et al. 2019), our reservoir classification was *a priori* constrained to four clusters for

each ecoregion (i.e., large-slow, large-fast, small-slow, small-fast). K-means data clustering is a technique that scales well to large datasets and offers the advantage of flexibility, guaranteed convergence, tight clusters, and better interpretability for later re-use. We also explored other statistical classification algorithms, but none seemed to greatly augment results; we present here the results of our more straightforward clustering.

Reservoir biomass and production estimates

We developed five different reservoir classification schemas and thus five separate biomass estimates, allowing for some estimation of uncertainty (**Figure S1.1**) (McDonald et al. 2012). Most available empirical biomass data were collected in twenty-two southern USA states, therefore, we calculate summary statistics for the southern USA as a sample-rich region, but also present extrapolations for the contiguous USA, while recognizing there are regional differences in the dynamics of fish biomass production.

Generalized Additive Mixed Models (GAMMs) were first created to examine biomass as a function of reservoir age under each of the five classification methods (Pedersen et al. 2019). GAMMs were fit using restricted maximum likelihood (REML) smoothness selection, Gamma family, and log link function (Wood 2011). The two continuous predictors used in the models, *Reservoir-Age* and *Year-Sampled*, received thin plate spline smooths, the reservoir (*Ecosystem*) name received a random effect smooth, and *Classification* received smooth factor interaction for each of its categorical variables to determine whether smoothed fits varied by subclass. Classes with fewer than five data points were removed prior to running the respective model. Model quality was assessed via model convergence, basis checks, residual and partial residual plots, model summaries, and using second-order Akaike information criterion (**Table S1.1**). While

deviance explained by the model is viewed as a more appropriate goodness-of-fit indicator for non-normal errors in non-gaussian models (Wood 2011), both percent deviance explained and adjusted R^2 are presented in **Table S1.1**.

Each model was used to independently predict fisheries biomass data beyond the final year of empirical biomass data (1978-1993) to standardize for noise resulting from reservoirs having been sampled at different points in time, and to estimate potential change in fisheries biomass within reservoirs over time (**Figure S1.2**). Finally, to assess the model's predictive ability, trends in empirical and predicted fish biomass over time in study reservoirs were examined and validated, as suggested by Pedersen et al. (Pedersen et al. 2019) (**Figure S1.3-S1.4**; see SI for validation techniques). Thus, results from Schema 5's nearest reliable year (1993) were used to create total standing stock and production estimates, and main manuscript figures.

In each calculation method, class-specific averages of fish biomass were assigned as fish biomass estimates for any reservoir of the same class that did not have empirical rotenone data (**Table S1.2**). When no biomass estimates were available for an entire class, we substituted mean biomass across all sampled reservoirs. Once all reservoirs had been assigned a biomass estimate, reservoir biomass (kg ha^{-1}) values were multiplied by the surface area of the reservoir (ha), or approximated surface area if none previously existed, to obtain a total standing stock (kg) estimate for every reservoir in the NID. We then summed total standing stocks across the entire cleaned NID dataset to estimate total standing stock in southern USA and USA reservoirs for that classification approach. Finally, we also summed total standing stock by US state to highlight general geographic patterns. Fish production rates were estimated based on published

production to biomass (P/B) ratios for whole fish communities from the literature (see SI Methods).

Validation

We collated additional data on forty-two independent poisoning surveys for USA reservoirs that were not part of the National Reservoir Research Program legacy dataset as a validation dataset (Hill 1986; Yurk and Ney 1989). A mixed effect regression model using classification method as a random effect showed that total standing stock from independent surveys was strongly correlated with predicted total standing stock values from the same reservoir (**Figure S1.3**). Furthermore, the slope of this model = 0.98 and R^2_c (pseudo- R^2 for both fixed and random effects) = 0.98, expressing a near one-to-one relationship that did not differ significantly from a slope = 1. Further validation showed trends between observed fish biomass as a function of predicted fish biomass also followed a line with slope = 1 and intercept = 0 (**Figure S1.4**).

The following R packages were used for this analysis: {tidyverse} v2.0.0 (Wickham et al. 2019), {sf} v1.0.12 (Pebesma 2018; Pebesma and Bivand 2023), {sp} v1.6.0 (Pebesma and Bivand 2005; Bivand et al. 2013), {ggspatial} v1.1.8 (Dunnington 2023), {tigris} v2.0.3 (Walker 2023), {mgcv} v1.8.42 (Wood 2003, 2004, 2011, 2017; Wood et al. 2016), {MuMIn} v1.47.5 (Bartón 2023), {lmerTest} v3.1.3 (Kuznetsova et al. 2017), {smatr} v3.4.8 (Warton et al. 2012), {fBasics} v4022.94 (Wuertz et al. 2023), {data.table} v1.14.8 (Dowle and Srinivasan 2023), {scales} v1.2.1 (Wickham and Seidel 2022), {patchwork} v1.1.2 (Pedersen 2022), {cowplot} v1.1.1 (Wilke 2020), {LaCroixColor} v0.1.0 (Bjork 2023).

We provide additional details on summary analyses and validation procedures in the supplementary text. All cleaning and analytical code used R software (R version 4.3.0, R Core Team 2023) and is freely available and presented as part of this paper (DOI 10.5281/zenodo.8316696; https://github.com/caparisek/res_biomass_USA) (Parisek et al. 2023a). All data and reservoir classifications are available in the supplement and are also registered on Zenodo (DOI 10.5281/zenodo.8317007) (Parisek et al. 2023b, 2023a).

Results

Fish biomass and production rates in 301 sampled USA reservoirs were highly variable in space and time. Across all sampled reservoirs, total standing stock predicted for the standardized year (1993) ranged 802 kg – 103 million (M) kg with mean standing stock for an average reservoir = 3.14 M kg (+/- 0.47 SE). Similarly, production rates across sampled reservoirs ranged 1,043 kg y⁻¹ – 135 M kg y⁻¹ with mean production for an average reservoir = 4.1 M kg y⁻¹ (+/- 0.61 SE) (Interquartile range of P based on interquartile range of P/B = 1.6 – 5.0 M kg y⁻¹).

Classification Schemas & Model Selection

We created a series of reservoir classification schemas of ascending complexity that placed all USA reservoirs into families of reservoirs with similar underlying characteristics. Our most complex classification system (Schema 5) was highly detailed and combined data on ecoregion, total reservoir storage capacity (m³), and water discharge (m³s) from dams. Out of five Generalized Additive Mixed Models (GAMMs), each of which applied one of the unique classification schemas, Schema 5 yielded the best model for making total standing stock predictions (**Figure 1.1; Figure S1.1-1.2; Table S1.1**). Thus, within any given ecoregion, four different clusters of reservoirs emerged: 1) small volume and low discharge; 2) small volume and

high discharge; 3) large volume and low discharge; and 4) large volume and high discharge (Figure 1.2).

Fish Biomass and Production

By combining empirical biomass data with our highest ranked reservoir classification system, we estimate southern USA reservoirs contain 1.92 billion (B) kg (± 0.09 SE across calculations) of fish mass, and total annual production for the region ranges 2.20 – 2.78 B kg y^{-1} (± 0.12 SE) across calculations (Interquartile range of P based on interquartile range of P/B = 1.11 – 3.46 B kg y^{-1}). Expanding to the entirety of the USA, we estimate total reservoir standing stock is 3.43 B kg (± 0.18 SE across calculations) with production ranging 3.87 – 5.01 B kg y^{-1} (± 0.23 SE) across calculations (Interquartile range of P based on interquartile range of P/B = 2.00 – 6.25 B kg y^{-1}) (Table 1.1; Table S1.2). The top 5 USA states in total standing stock of reservoir fishes included Texas, Arkansas, Oklahoma, Florida, and South Dakota. Most states have reservoir standing stocks <100 M kg (Figure 1.3A); however when states are scaled by surface area, divergent state ranking patterns emerge. For example, Louisiana, Indiana, Alabama, Maryland, and Illinois had the highest mean biomasses, but none of these states were in the top five for total standing stock (Figure 1.3B). Similarly, predicted total standing stock varied widely across Omernik level II ecoregions and when also incorporating reservoir storage and discharge (Figure S1.2).

Trends in reservoir biomass are variable over space and time. For example, we observe patterns of relatively constant biomass, increasing and declining biomass, and spikes in biomass followed by decreases that ultimately return to a baseline. Importantly, documentation of lake-specific trends allowed for standardization of biomass estimation to a given year of interest.

Although we triangulated on one year (1993) for this analysis, this same technique could be applied to standardize biomass estimates to any year of interest, while still accounting for important lake-specific trends. Standing stock estimates from independently acquired surveys correlated strongly with predicted total standing stock values from the same reservoir (**Figure S1.3–S1.4**, *see also Methods for full validation results*).

Discussion

This research develops novel understanding of the biomass and secondary production rates of fishes in reservoirs, with implications for the management of freshwater resources globally. Our estimates suggest reservoirs contain substantial pools of fish biomass comparable to other important values presented in the literature (**Table 1.2**) (Deines et al. 2017; Embke et al. 2020; Food and Agriculture Organization of the United Nations 2022; GLFC (Great Lakes Fishery Commission) 2022). Fish are core to food security and cultures in many nations across the world (Fluet-Chouinard et al. 2018; Embke et al. 2019). While the literature has focused predominantly on the role of marine fisheries in food security, there is a growing recognition that inland fisheries play major and underappreciated roles (Cooke et al. 2016; Lynch et al. 2016; Embke et al. 2020; Kao et al. 2020). In addition, we find non-linear trends in biomass exist both spatially and temporally. This suggests nuance exists in how reservoir production changes with time, and that reservoirs do not necessarily always experience uniform declines in productivity over long time periods. For example, coldwater and coolwater fish habitat in USA reservoirs is predicted to decline with climate change alone by 45% and 30%, respectively (Stefan et al. 2001), and decreased water levels could reduce availability of littoral fish habitats depending on the degree of change to reservoir inflows (Miranda et al. 2020). Future work covering longer time periods is needed to better understand the scope for production declines with reservoir age.

Our final reservoir classification schema provides a useful tool for future reservoir research and conservation. For example, the schema can be applied in an array of ways and is designed such that reservoirs can theoretically shift to different classes over time as flow and volume characteristics change. Fish biomass data comport well with our classification schema, demonstrating that the ecology of reservoirs varies strongly alongside the reservoir classes. While in this study the classification schema was used to understand patterns in fisheries and food security, our classification may have additional applications towards effective reservoir management for the good of humanity, biodiversity, and fisheries conservation. For example, these classifications could be used in the study and management of limnology, food web ecology, and ecosystem dynamics of reservoirs throughout the USA (e.g., respectively, by (1) helping scientists and resource managers make informed conservation management choices based on a reservoir's class and its ecological dynamics, (2) providing a framework to explore how different reservoir classes potentially lend themselves more to certain food web structures and species dynamics, and (3) allowing for the study of broader ecosystem trends in reservoirs over time. A particular advantage is that this classification system can be used at the national (USA) and regional (state or lower) scales, and thus may be of interest to a diversity of managers and scientists. Further, the same framework could also be applied globally or in any region where reservoir discharge and volume data are available.

The implications of large pools of fish biomass in reservoirs are severalfold. Firstly, an abundance of fixed carbon in resident reservoir organisms suggests a major and increasing role for reservoirs in the global carbon and freshwater cycles. Understanding the scope of this effect should attract research attention going forward. Secondly, it is clear from the magnitude of our estimates, that reservoirs (and probably other novel ecosystems) harbor additional sources of fish

protein that are likely already being utilized substantively by societies. Awareness around this topic is highly limited within the ecological and social sciences. Yet without proper management, freshwater populations can quickly deteriorate and even collapse (Embke et al. 2019; Rypel et al. 2021). Therefore, one implication of our findings is that reservoirs globally would benefit from increased management attention, due to these pools of freshwater fisheries being quite large, and generally receiving less systematic management. Without proper management, ecosystem services will be extremely limited, or in worst cases, just collapse. Finally, we note that reservoirs can also represent important habitats for native species, e.g., those resilient to fragmentation by dams (Rypel and Bayne 2009; Beatty et al. 2017), or as potential novel habitat for species vulnerable to collapse in their native range (Perales et al. 2015; Pennock et al. 2020). There may be opportunity to craft reservoir ecosystems into emergency rooms for a subset of native species. However, conservation management of reservoirs to this point has generally not embraced this potential.

Reservoirs occupy a massive geographic footprint on the planet; thus, pools of fisheries biomass within reservoir ecosystems are relevant at all scales. While impoundment of rivers can create short-lived production spikes, these effects notoriously dissipate (Balon 1967; Ploskey and Jenkins 1982), and long-term declines in production is a growing concern (Miranda and Krogman 2015). Similarly, global inland fisheries catch has the potential to either increase or decrease in response to climate change impacts, largely owing to variation in land-use surrounding individual waterbodies (Kao et al. 2020). Yet we observe that these production trends can have substantial spatiotemporal variation. Therefore our method of exploring and quantifying macroecological production patterns can aid in illuminating shifts in productive capacity, which in turn can be useful for conservation practitioners. Further, climate change has

the potential to expedite or slow the rate of functional aging in existing reservoirs, and this topic is of growing interest (Miranda and Faucheux 2022).

Owing to their massive footprint, reservoir ecosystems now support globally relevant pools of fish biomass. Understanding the distribution and dynamics of this pool may be highly relevant from a global carbon standpoint. Relative to potential fish production in USA reservoirs, which we demonstrate is approximately $0.0045 \text{ Pg yr}^{-1}$ of production (i.e., 4.5 B kg yr^{-1}), reservoirs and lakes as a whole comprise $0.28 \text{ Pg C yr}^{-1}$ and $0.11 \text{ Pg C yr}^{-1}$ of the global carbon cycle, respectively (Cole et al. 2007). Although this quantity may appear small, it is on the scale so as to be relevant from a carbon cycle perspective. Furthermore, fish consumers classically exert control over food webs via trophic cascades, such that even a relatively small number of fish, or change in numbers, can play disproportionately impactful roles in carbon flux, nutrient cycling, and energy transfer (Brett and Goldman 1996; Atwood et al. 2013). Indeed our biomass and production estimates may also represent partial indicators of ecological resilience (Moore et al. 1993; Stone et al. 1996), especially when used in conjunction with local-scale functional diversity and food web metrics (Downing and Leibold 2010). Therefore, we encourage future freshwater scientists to make use of the reservoir classification framework and supplementary datasets (**Dataset S3**) developed in this study for other endeavors.

We note our method for estimating fish biomass is only one approach to generating such estimates, and we view these estimates as a valuable preliminary framework. For example, Deines et al. (Deines et al. 2017) utilized remotely-sensed chlorophyll concentrations from 80,012 lakes to approximate global lake fish harvest. In their approach, chlorophyll data were related to empirical estimates of fisheries harvest on a subset of lakes and these relationships were used to extrapolate fish harvest at scale. Similar methods have been used to assess

production of terrestrial plants and other aquatic organisms (Silva et al. 2008). Yet this method involves a key assumption that food web pathways of carbon transfer in aquatic ecosystems are roughly fixed relative to the “greenness” of the water. Increasingly, we understand many aquatic food webs are benthic in their functionality (Vander Zanden and Vadeboncoeur 2020), which presents issues for remotely-sensed models of fish production based solely on “greenness”. We additionally note that while many studies estimating biomass and production rely upon modeling approaches, this study, in contrast, uses empirically-collected biomass data to explore biomass and production relationships; there is less need to model biomass and production when these same data can be empirically-derived and are available (Waters 1992; Rypel et al. 2018). One issue with our method is the limited spatial extent of the biomass surveys – because fish poisoning surveys were so heavily concentrated in southern USA states. Future studies aimed at reconciling fish biomass and production estimates using a variety of methodologies could be valuable. Variability in the assemblage P/B ratio, or by species and across latitudes, is known to a certain degree (Rypel and David 2017). Nevertheless, additional research to acquire assemblage P/B ratios on reservoirs specifically would be interesting and might help advance some key questions on reservoir fisheries ecology. These data would also help further validate the application of P/B in this context.

Ultimately, our estimates of standing stock biomass are probably conservative. The NID database is likely missing millions of smaller impoundments that escape local and federal regulation and thus inclusion in the NID. Small reservoirs, like small lakes, are numerous and notoriously difficult to inventory (Morden et al. 2022). If these values were added, standing stock totals would only increase. However, most of our empirical biomass data were derived from larger reservoir environments, and limnetic extent is one of the primary drivers of the total

standing stock calculation. Therefore it is likely that total standing stock values from these many smaller reservoirs would ultimately be small, even in aggregate (Verpoorter et al. 2014).

Reservoirs are important ecosystems to study further and to sustainably manage at all scales. There is near-complete regulation of the world's rivers by widespread dam installation (Poff et al. 1997; Nilsson et al. 2005). Ecological effects of dams have been overwhelmingly negative and represent one of the principal drivers of freshwater biodiversity loss at all scales (Poff et al. 2007; Tickner et al. 2020). Paradoxically however, little research has occurred on the novel ecosystems and changes to production left in the wake of dams. In many locations, reservoirs and fragmented rivers are the only freshwater ecosystems remaining (Benke 1990); thus improved understanding of the ecology of these environments and their fisheries should be of interest to conservation scientists at all scales. Even though reservoirs are human-dominated environments, their global geographic footprint is testimony to their modern scope of importance. Taking down dysfunctional dams combined with improved management of remaining dams and reservoirs may represent a path towards improved freshwater fisheries, conservation, and food security. We encourage conservation scientists around the globe to rethink the potential for reservoirs to meet human- and conservation-based goals.

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Figures & Tables

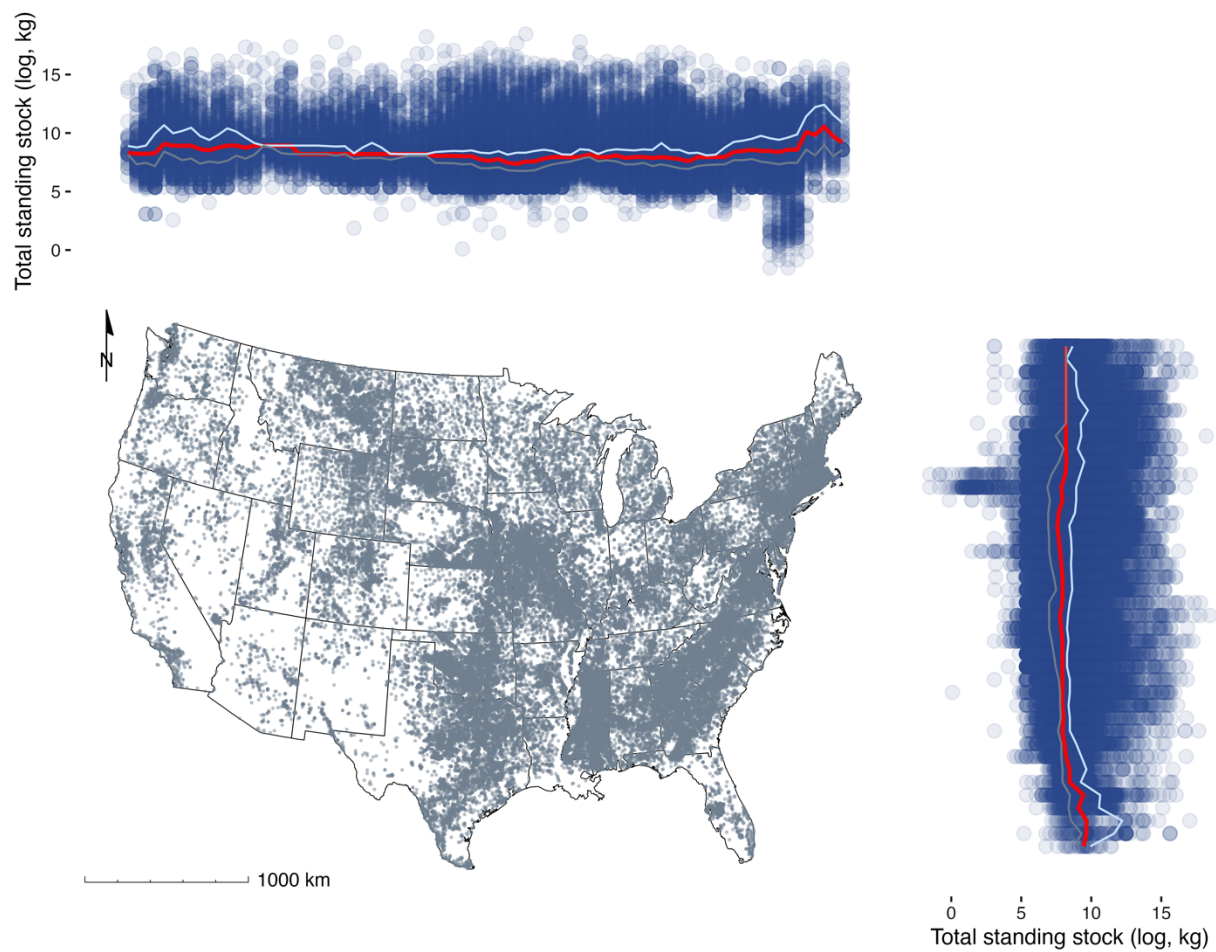


Figure 1.1

Map of contiguous United States representing all NID reservoirs (gray) and estimated total standing stock (log, kg) of those reservoirs by binned longitude and latitude (blue). Median (red), 25% quartile (gray), and 75% quartile (cyan) estimates by binned longitude and latitude total standing stock (log, kg) are overlaid. Map created using R software (R version 4.3.0, R Core Team 2023).



Figure 1.2

Results from k-means analysis by ecoregion using 4-cluster separation on USA reservoir discharge (log, m³ s⁻¹) and storage volume (log, m³) (n = 36,340). Clusters represent reservoirs with small volume and low discharge (light blue), small volume and high discharge (turquoise), large volume and low discharge (medium blue), and large volume and high discharge (dark blue).

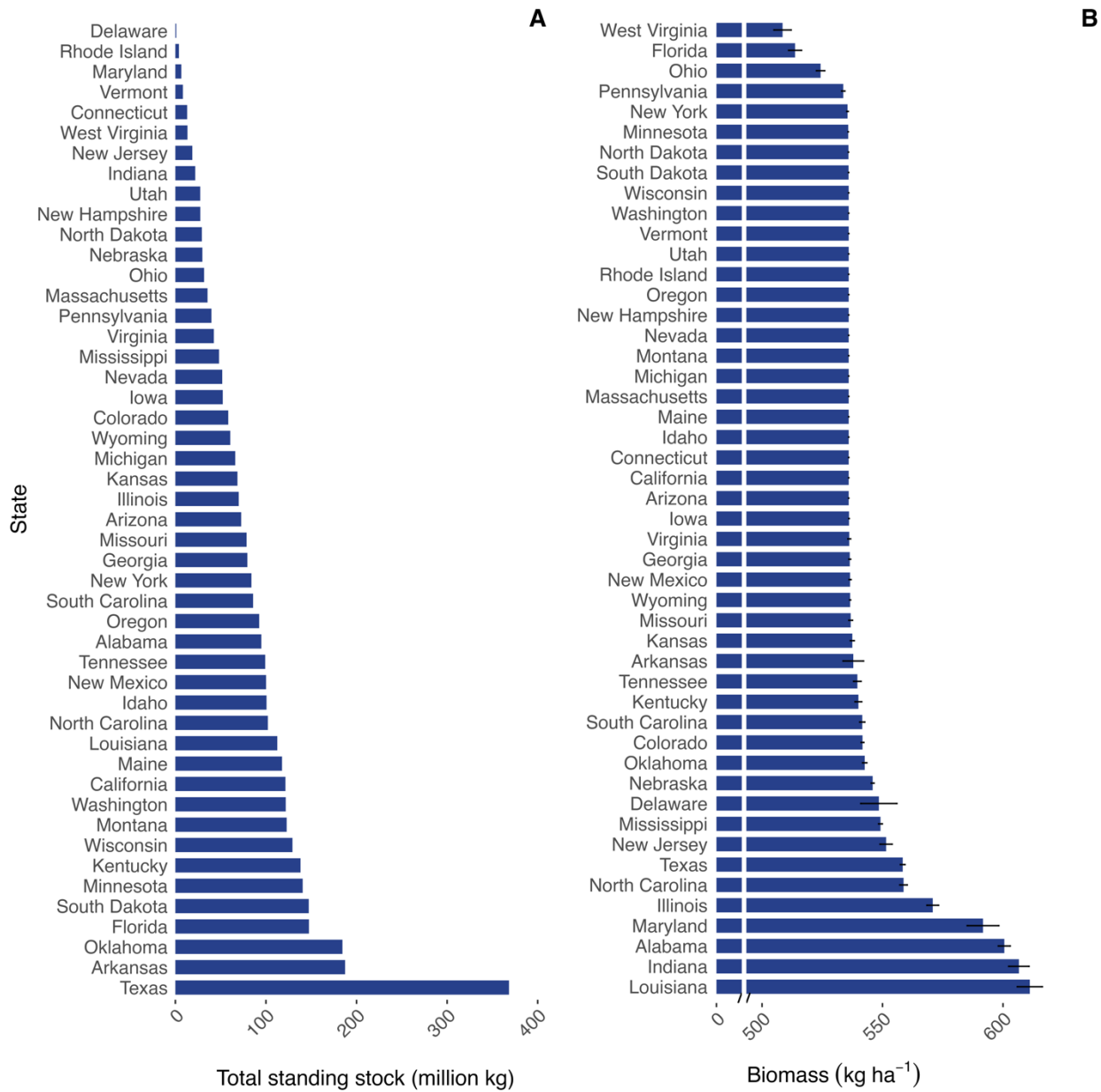


Figure 1.3

Bar plot ranking USA state by total standing stock and biomass. (A) Summary of total standing stock (million kg) estimates by state for reservoirs of the contiguous USA. (B) Mean fish biomass (kg ha⁻¹) for each state which relates total standing stock (Panel A) to relative surface area of water available (ha) in that state; error bars represent the standard error of the mean.











Table 1.1

Total southern and contiguous USA reservoir fish total standing stock.

Schema	Southern USA Total Standing Stock (kg)	USA Total Standing Stock (kg)
1 – Simple Average	1,693,346,335	3,031,693,257
2 – Large & Small	2,001,994,842	3,587,800,617
3 – Size-Flow	1,713,033,098	2,976,459,235
4 – Ecoregion	2,055,598,037	3,689,453,361
5 – Eco-Size-Flow	2,137,464,393	3,855,651,138
Mean	1,920,287,341	3,428,211,522

Table 1.2

Current estimates of fish harvest and capture production from the literature compared with the results of this study.

Location	Production (B kg yr ⁻¹)
 Global (Marine) ¹	78.80
 Global (Inland) ²	11.50
 Global (Inland) ³	* 8.40
 Asia ⁴	7.29
 Africa ⁵	3.21
 South America ⁶	0.34
 North America (Inland) ⁷	0.19
 Laurentian Great Lakes ⁸	0.019
 Wisconsin ⁹	* 0.004
 USA Reservoirs ¹⁰	* 4.46

* Fisheries independent surveys.

¹ Global marine fisheries capture, 2020 (Food and Agriculture Organization of the United Nations 2022)

² Global inland fisheries capture, 2020 (Food and Agriculture Organization of the United Nations 2022)

³ Global harvest of inland fish, 2011 (Deines et al. 2017)

⁴ Asia fisheries capture production, 2020 (Food and Agriculture Organization of the United Nations 2022)

⁵ Africa fisheries capture production, 2020 (Food and Agriculture Organization of the United Nations 2022)

⁶ South America fisheries capture production, 2020 (Food and Agriculture Organization of the United Nations 2022)

⁷ North America inland waters, 2020 (Food and Agriculture Organization of the United Nations 2022)

⁸ Laurentian Great Lakes annual fish harvest, 2020 (GLFC (Great Lakes Fishery Commission) 2022)

⁹ Recreational fish harvest from Wisconsin lakes (Embke et al. 2020)

¹⁰ Production estimates for reservoirs in the contiguous USA, reported in this study.

Supplement

NID Preparation

Data were cleaned using rules to remove duplicate rows representing multiple dams on the same reservoirs in the National Inventory of Dams (NID) dataset (US Army Corps of Engineers : Federal Emergency Management Agency. 2018). We identified the 100 largest reservoirs and manually removed those which were clearly natural water bodies (n = 25; e.g., Lake Superior (MI), Lake Winnebago (WI), Mille Lacs Lake (MN), Clear Lake (CA)), as these would significantly and artificially inflate total standing stock and secondary production (hereafter, “production”) estimates for this reservoirs study.

Reservoirs with no latitude or longitude information (n = 242) in the NID received coordinates for its county’s centroid; of these, reservoirs without county information (n = 16) were manually located using other NID characteristics and supplied with coordinates that associated them with their correct Omernik ecoregion. Likewise, reservoirs whose precise latitude-longitude coordinates fell outside an ecoregion polygon (e.g., was implausibly located in an ocean; n = 27), thus receiving an N/A ecoregion after spatial joining, were manually assigned their correct ecoregion.

Reservoirs without surface area information (n = 18,145) received an approximated surface area decided by the most common surface area for that Omernik level II ecoregion; this was done by taking the *mean(log(surface_area))* and back-transforming (10^{\wedge}). This approximated surface area column was only used in the final step of the total standing stock calculation when converting kg/ha to kg would have resulted in the loss of ~21% of final results,

otherwise, the original NID column was used as needed during analysis and reservoirs with missing surface area data received rules outlined in **Table S1.2**.

Finally, in two instances, empirically sampled reservoirs from the National Reservoir Research Programs (NRRP) had dams relocated or otherwise adjusted such that the same dam NID ID was associated with two unique reservoir ecosystems that were sampled at different points in time. The NID ID for these ecosystems received the suffix *A* or *B* in both the NRRP and NID to complete spatial joining prior to analysis.

Predicted Fish Biomass

We performed several checks to determine an adequate breaking point in fish biomass predictions outside the sampling period such that they remain realistic, while also enabling standardization of reservoir biomass estimates to a common and more recent time period. Estimated mean standard error (SE) of prediction fit was calculated for each year. Predictions were capped at the year whose mean SE was no more than twice that of the last year empirical data had been collected. In this case mean SE in 1978 was 158.2, so predictions did not extend beyond 1993 (mean SE of fit 314.0). Likewise, estimated mean standard deviation (SD) of prediction fit yielded the same breaking point. Finally, a broken-stick (i.e., segmented) regression was performed as a final validation of this decision. Thus project trends are shown for 1978 – 1993 and projected biomass estimates from the nearest realistic year (1993) were used in calculations (**Figure S1.2**).

Validation

We validated biomass predictions of all five models (1993) using an independent dataset, as recommended by Pedersen et al. (Pedersen et al. 2019). The validation dataset consisted of 42 independent reservoir fish rotenone survey biomass estimates (Hill 1986; Yurk and Ney 1989) that were not included in the legacy National Reservoir Research Program database. We matched validation ecosystems to our database and compared observed versus predicted total mass values using a mixed effect regression model where observed total fish mass in reservoirs was the dependent variable, predicted total fish mass (from our classification and biomass value assignment procedures) was the independent variable, and classification method was a random effect (**Figure S1.3**). We tested the slope of this relationship against a value of 1 using a t-test. We also compared the Schema 5's predicted fish biomass for 1993 to NRRP empirical fish biomass to validate predictions (**Figure S1.4**).

Fish production estimation

We estimated fish production based on biomass and fish community production to biomass (P/B) estimates from the literature and associated supplementary data. Secondary production rates in heterotrophic populations and communities are strongly predicted by biomass (Downing and Plante 1993; Rypel and David 2017). The statistical relationship between production and biomass is in fact a descriptor of the P/B ratio, which is mathematically the biomass turnover rate of the population or community (Waters 1969; Rypel 2018). Therefore, biomass can be multiplied by P/B to approximate production with a high degree of certainty (Waters 1992). Based on a meta-analysis of community fish production, biomass, and P/B values presented in Rypel and David 2017 (Rypel and David 2017), we estimate average community

fish P/B for 116 aquatic ecosystems is 1.3 (mean = 1.300, median = 0.975, 25% quartile = 0.520, 75% quartile = 1.620). Therefore, we multiplied our final biomass estimates by 1.3 to approximate annual production of fish communities in USA reservoirs. We also provide the interquartile range of P based on the interquartile range of P/B using Schema 5's final biomass estimate.

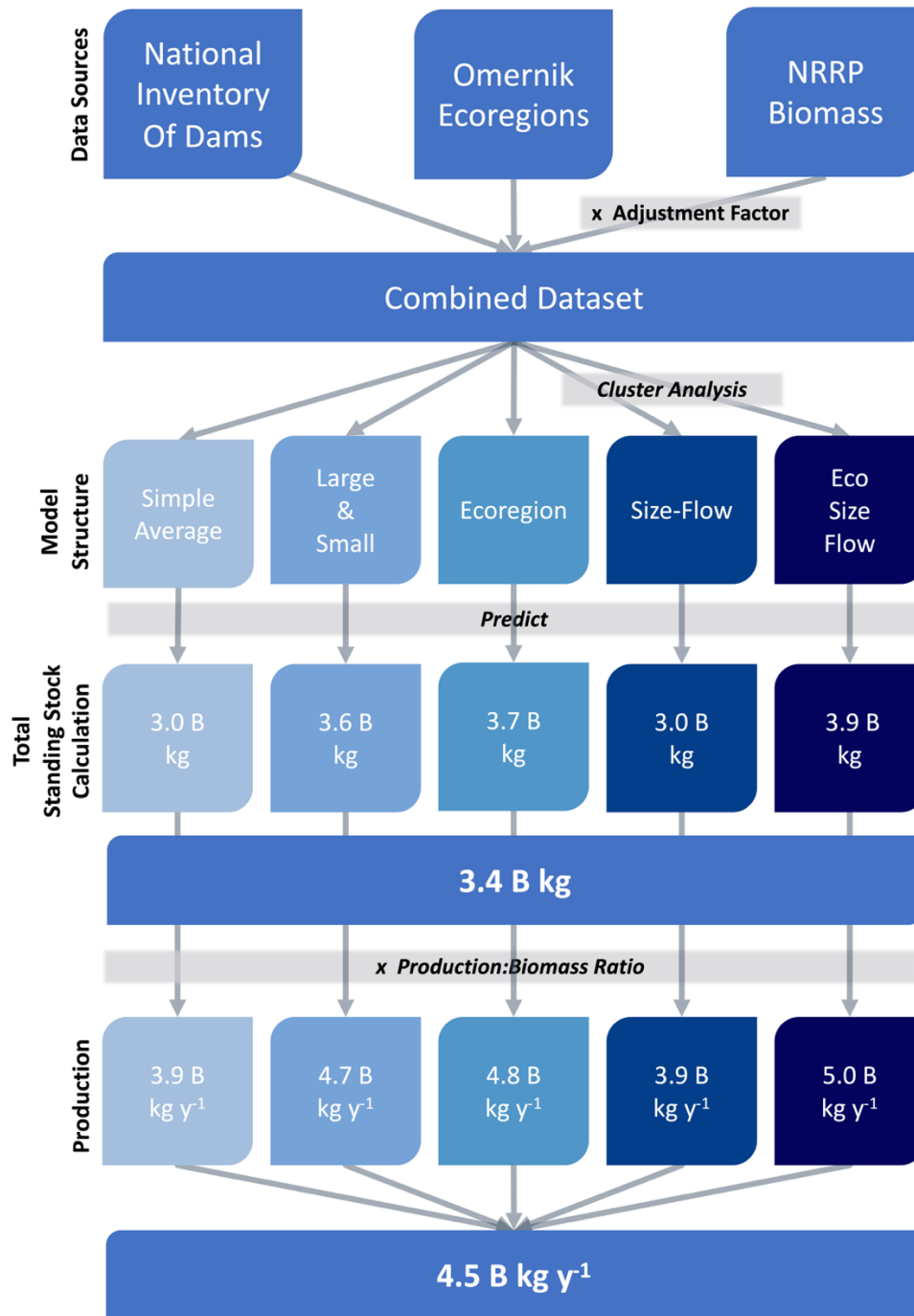


Figure S1.1

Workflow describing the development and processing of different data types in this study. Three data sources were combined to create a combined dataset which was then applied in each of the five schemas (simple average, large and small, ecoregion, size-flow, and eco-size-flow).

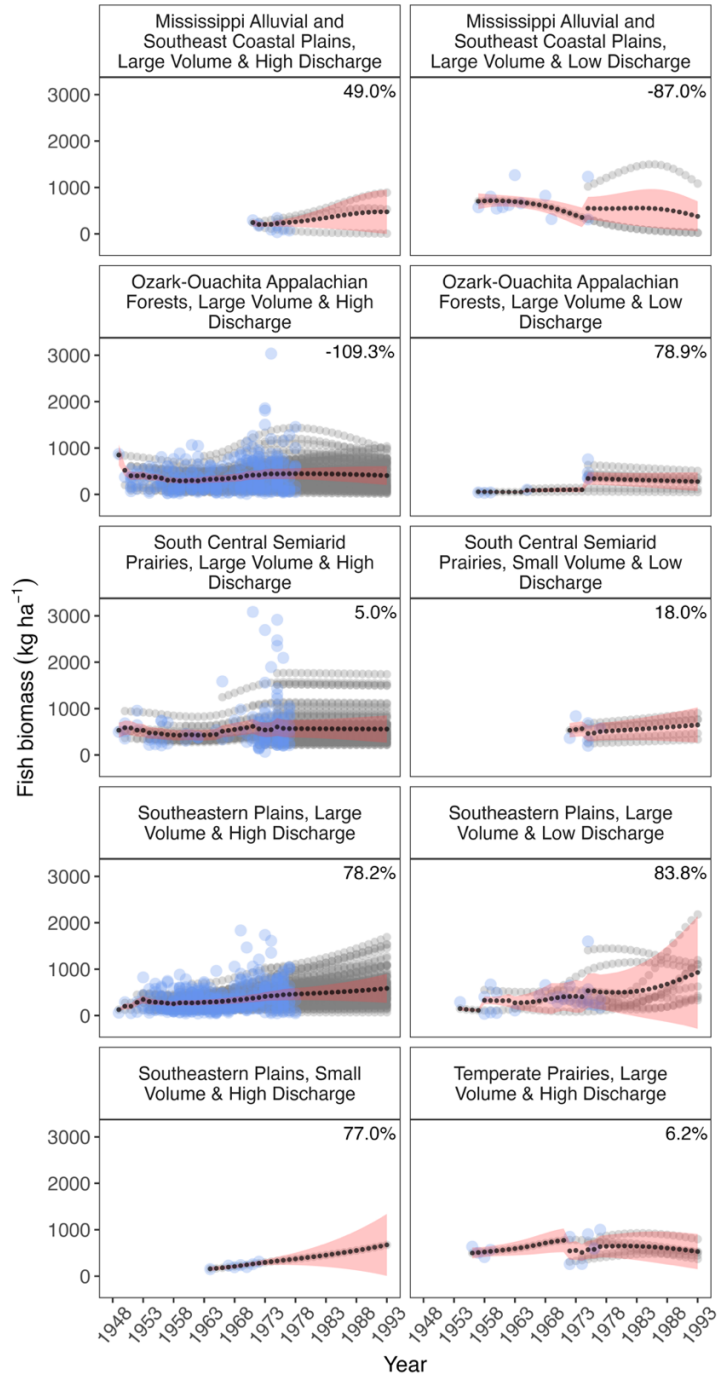


Figure S1.2

Temporal trends in empirical (blue) and predicted (gray) fish biomass over time in study reservoirs. Black line denotes mean of predictions from GAMMs using Schema 5 classification. Red ribbon denotes standard error of the model's predicted fit. Percent change of fish biomass (kg/ha) from the initial year to the final (1993) is denoted in the upper right ($((\text{final year} - \text{initial year}) / \text{final year}) * 100$).

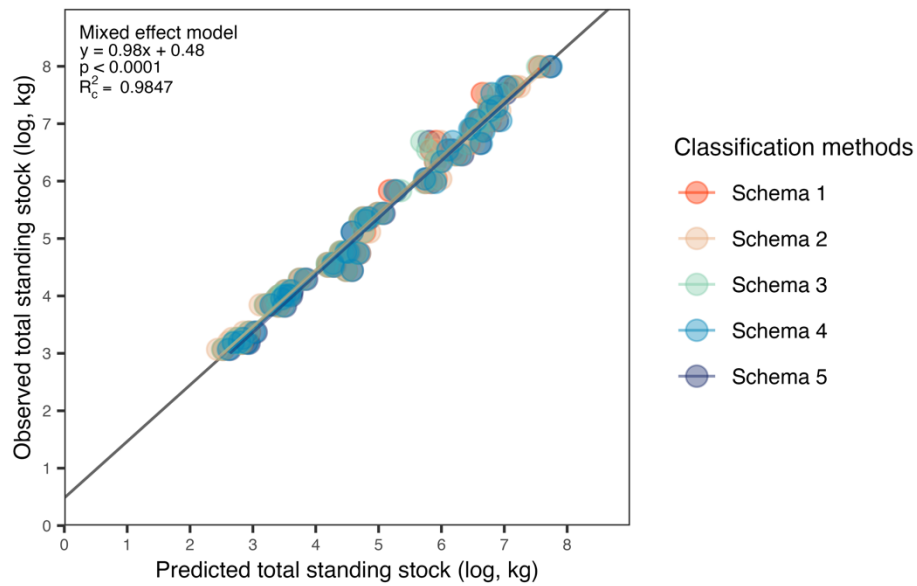


Figure S1.3

Validation analysis comparing predicted biomass values with an independent validation dataset from the literature on the same reservoirs. A mixed effect model was fit to the data with classification method as a random effect. Colored regression lines denote random effects and the thick dark line denotes the overall model regression.

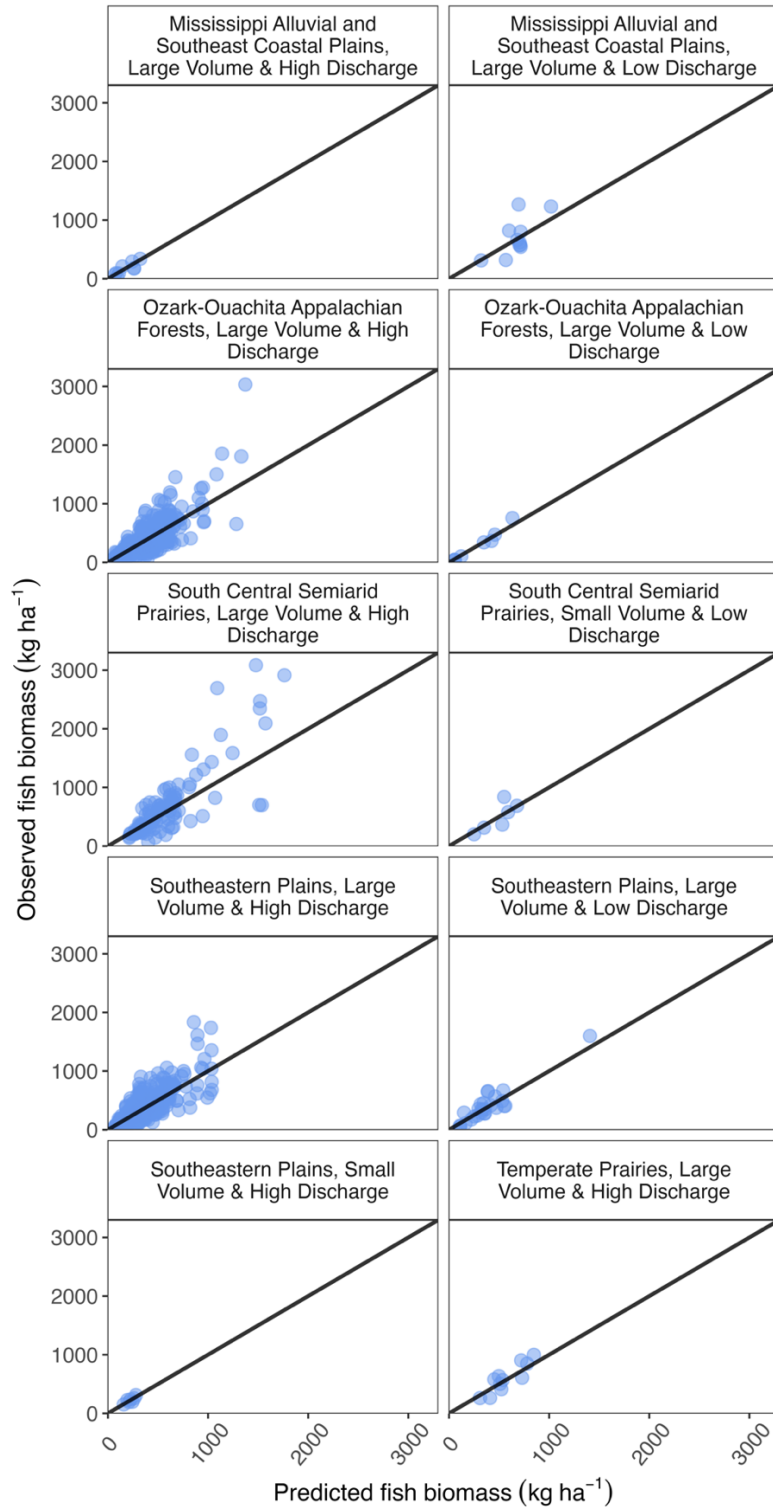


Figure S1.4

Observed fish biomass as a function of its predicted fish biomass. Black line illustrates a trend with slope = 1 and intercept = 0.

Table S1.1

GAMM model structure and summary output used for each of the classifications used for predictions. GAMMs used *Gamma*(*link = log*) and “REML” method. Smoothed variables are denoted within (*s()*). Smoothing is denoted with *bs =*.

Schema	Model Structure	Deviance Explained (%)	Adjusted R-sq.	n	df	AIC
- 1 - Simple Average	Biomass ~ s(Reservoir_Age, bs="tp") + s(Ecosystem, bs="re")+ s(Year, bs="tp")	70.0	0.563	1,127	243.2	14,646.5
- 2 - Large & Small	Biomass ~ s(Reservoir_Age, bs="tp", by=Large_Small) + s(Ecosystem, bs="re")+ s(Year, bs="tp")	69.7	0.557	1,097	236.5	14,274.3
- 3 - Size-Flow	Biomass ~ s(Reservoir_Age, bs="tp", by=Cluster_Volume) + s(Ecosystem, bs="re")+ s(Year, bs="tp")	72.0	0.572	1,007	227.5	13,052.1
- 4 - Ecoregion	Biomass ~ s(Reservoir_Age, bs="tp", by=Ecoregion) + s(Ecosystem, bs="re")+ s(Year, bs="tp")	70.4	0.566	1,115	247.6	14,485.1
- 5 - Eco-Size- Flow	Biomass ~ s(Reservoir_Age, bs="tp", by=Eco_Size_Flow) + s(Ecosystem, bs="re")+ s(Year, bs="tp")	73.6	0.578	990	233.5	12,786.8

Table S1.2

Five reservoir classification methods, ordered top-to-bottom from least complex to most complex.

Schema	Classification methodology
– 1 – Simple Average	A mean fish mass was calculated across all USA reservoirs. Reservoirs with no empirical biomass were given this mean.
– 2 – Large & Small	Reservoirs were grouped into two classes, large and small. Median reservoir surface area for southern impoundments was 4.047 ha, and 4.856 ha for all USA impoundments; thus reservoirs below these thresholds were considered “small” while ones above were “large”. A mean fish mass was calculated for both large and small reservoirs and these values used for reservoirs where no biomass values were available.†
– 3 – Size-Flow	Across all USA reservoirs, a cluster analysis constrained to four clusters was performed using reservoir volume (storage capacity) and maximum discharge. Mean fish mass was calculated across all reservoirs for a given cluster. Cluster mean fish mass values were used to assign a fish mass value to any reservoir missing empirical data. Clustering for the distinct southern and all USA reservoirs was performed separately. †
– 4 – Ecoregion	Omernik level II ecoregions were identified for every reservoir. Mean fish mass was calculated across all reservoirs for an ecoregion. Ecoregion mean fish mass values were used for any reservoir with unknown fish biomass values.†
– 5 – Eco-Size-Flow	Omernik level II ecoregions were identified for every reservoir. Within every ecoregion of the USA, a cluster analysis constrained to four clusters was performed using volume (i.e., storage capacity) and maximum discharge. Mean fish mass was calculated across all reservoirs for a given cluster. We used cluster mean fish mass values to assign a fish mass value to any reservoir missing empirical data.†

†In the event there were no empirical data for a given cluster or ecoregion, the mean value across all USA reservoirs was used.

Chapter 2

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Velocity of climate change and the vulnerability of mountain lake landscapes

Abstract

Freshwater ecosystems in mountain landscapes are increasingly threatened by climate change. Accumulated heat in ecosystems can result in lethal short-term heat exposure, but the velocity of change governs severity and rates of heat exposure in the long-term. Here, we apply a novel and integrative heat accumulation and velocity of change approach to craft an actionable system for classifying climate-vulnerable mountain lake watersheds in the USA. Broadly, our results demonstrate that rates of heat accumulation are increasing steeply across mountain lake landscapes, but this rise is most pronounced at lower elevations. Across the USA, we estimate 19% of mountain lake watersheds are currently at the greatest vulnerability (highest heat accumulation). However, this value is set to jump to 33% by end-of-century. Further, percent change in mean killing degree days (i.e., the mean number of days above 90th percentile) will increase 215 – 254% (mean = 236%) over this same timeframe. Taken together, results indicate heat accumulation will increase substantially over the next 75 years; changes will be experienced most severely in lower elevation lake landscapes and those with the greatest historical velocity of change. This degree of climate change will restructure the distributions of native mountain species. Decision makers and communities can utilize these classifications to understand lake types likely to support desired species and ecosystem services deep into the future, thereby enabling more effective allocation of limited conservation resources.

Significance Statement

Mountain lake landscapes are sensitive to climate change, yet the velocity at which they are undergoing thermal change is poorly understood. This study reports on velocity of change in heat accumulation rates across high elevation lake landscapes in the USA. Results show mountain lake landscapes at lower elevations are undergoing more rapid change, and there is variation amongst ranges in velocity of change. Vulnerability scores for individual watersheds may be useful for managers grappling with allocation of limited resources to combat climate change and engender ecological resilience.

Introduction

Rates of freshwater biodiversity collapse outmatch those of other environments, and protections for freshwater ecosystems are insufficient at almost all scales (Reid et al. 2019; Tickner et al. 2020; Flitcroft et al. 2023). Freshwater ecosystems are in global peril; human domination of the global water cycle has undermined ecosystem stability and disrupted ecological organization (Baron et al. 2002; Woodward et al. 2010; Collen et al. 2014). Climate change is desiccating wetlands, accelerating glacial retreat, and producing cascading consequences to ecosystem regimes, food web structure, and community functions (Carpenter et al. 1992; Ledger et al. 2013; Xu et al. 2019). Indeed, impacts of climate change are triggering disruptions across all levels of organization in freshwater ecosystems (Carpenter et al. 1992; Woodward et al. 2010; Knouft and Ficklin 2017). Climate-driven environmental disruption may be especially important in mountain ecosystems, where terrestrial and freshwater taxa interact and often subsidize one another (Piovia-Scott et al. 2016; Rolla et al. 2018; Parisek 2024).

Mountain species possess narrow thermal tolerances, restricted range distribution, and thus climate adaptation via dispersal is highly limited (Sunday et al. 2019; Viterbi et al. 2020).

Temperature, particularly water temperature, is perhaps the most important ecological variable mediating key ecological processes in aquatic ectothermic species (Magnuson et al. 1979). Understanding the role of temperature in regulating the distribution of organisms is therefore widely recognized as critical for understanding and managing freshwater biodiversity (Lyons et al. 2009; Rypel 2014b; Lusardi et al. 2021). Mountain lake landscapes are already thought to be exceptionally vulnerable to climate change (Ficke et al. 2007; Bonacina et al. 2023; Prather et al. 2023). Therefore, quantifying information on heat accumulation and heat content of these areas is important (Vanderkelen et al. 2020). Nevertheless, nuance in how thermal regimes (i.e., the timing, magnitude, and velocity of temperature change or heat accumulation) holistically respond to climate change is important to quantify and understand (Willis et al. 2021). Velocity of change in particular has been identified as a useful lens through which to understand, not just the magnitude of climate change experienced by organisms, but also the quickening pace of that change (Scheffer 1990; Barnett et al. 2015; Rypel In Revision.). For example, high velocity of change in ecosystems is associated with ecosystem fragility and shifts to alternate stable states (Scheffer and Carpenter 2003; Carpenter et al. 2017; Collins et al. 2018).

The consequences of potential increased velocity of climate change not only impacts aquatic ecosystems within catchments, but also the entire surrounding landscape (Greig et al. 2012; Larsen et al. 2016). Kratz et al. (1997) described the position of a lake within landscapes as a combination of the spatial and ecohydrological contexts of a lake within larger lake districts. Climate-driven niche ranges of many mountain organisms are shifting upslope toward more suitable habitat, such as those of alpine grouse and hares (Schai-Braun et al. 2021), plants

(Inouye 2020; Richman et al. 2020), forest species and forest type (Abbasi et al. 2024), macroinvertebrates (Shah et al. 2012; Suzuki et al. 2024), ungulates (Büntgen et al. 2017), songbirds (Van Tatenhove et al. 2019), and a wide variety of other animals and fungi (Mamantov et al. 2021; Vitasse et al. 2021). Species range shifts in turn spur novel species interactions within native and expanded ranges (Alexander et al. 2015; Shepard et al. 2021; Abbasi et al. 2024) and has the potential to alter or displace species' functional roles within their ecosystems (Bender et al. 2019; Richman et al. 2020; Balik et al. 2023). For lakes specifically, warming temperatures, and the resultant shift in treeline, is influencing algal community composition; lakes are experiencing phytoplankton increases with warming at lower elevations, but phytoplankton decreases once past the treeline (Kuefner et al. 2021). Additionally, changing lake stratification dynamics, and warming water temperatures coupled with increasing prevalence of lake browning is reducing availability of coldwater fish habitat (Jane et al. 2024).

Novel conservation prioritization frameworks will assist practitioners in taking well-informed management action towards adapting to and mitigating increased velocity of change. More specifically, understanding how divergent ecosystems across mountain landscapes will respond to rising rates of heat accumulation anticipated by the end of the century will be important for deciphering which lake landscapes are most vulnerable to these shifts (Adrian et al. 2009). Managers, especially those tasked with conservation prioritization of sensitive aquatic systems, their flora, and their fauna, have relatively few tools or science-based strategies to triage their resources effectively (Tulloch et al. 2015). Therefore, a vulnerability classification of lake landscape regions based on heat accumulation and velocity of change would be of wide appeal within the environmental management community.

In this study, we characterize climate vulnerability for all major USA mountain lake landscapes based on degree to which they have accumulated heat, historically and to end-of-century, as well as their experienced rate of change. Our specific goals were to: (1) Quantify heat, and harmful heat, accumulation across USA mountain lake landscapes over time. (2) Quantify the experienced velocity of thermal change across these same lake landscapes. (3) Provide a mountain lake landscape classification based on heat accumulation such that any mountain lake landscape can be classified into one of three vulnerability types. (4) Quantitatively evaluate how lake landscape vulnerability, and lake classification, change over time under the modest SSP 3 / RCP 7.0 climate scenario.

Methods

Datasets

Spatialized lake polygon data for the United States (USA) were acquired from the National Hydrography Database (NHD) with the {nhdR} package (version 0.6.1) (Stachelek 2019; USGS 2022). The NHD contains comprehensive and standardized spatial distributions of surface waters (e.g., lakes, ponds, streams, rivers, canals) throughout the USA. The NHD was best suited for this study because it best captured mountain lakes, which are often small and miscounted, when compared to other popular databases. Only waterbodies with the “Lake/Pond” designation in the NHD were used in this analysis (0-497 km² in surface area).

Spatial NHD lake data (representing “*Watershed*” locations later joined to air temperature data) were joined to the Omernik Level III ecoregions framework (<https://www.epa.gov/eco-research/ecoregions>) (Omernik 1995; Omernik and Griffith 2014) and cropped to contain mountainous polygons for each of the 10 primary mountain ranges in the contiguous United

States, contemporarily named: Appalachian/Atlantic Maritime Highland (n = 10,467 lake-watershed points), Arizona–New Mexico (n = 1,033 lake-watershed points), Blue (n = 284 lake-watershed points), Blue Ridge (n = 464 lake-watershed points), Cascade (n = 2,165 lake-watershed points), Idaho Batholith (n = 1,035 lake-watershed points), Klamath (n = 245 lake-watershed points), Rocky/Colombia (n = 9,661 lake-watershed points), Sierra Nevada (n = 2,358 lake-watershed points), Wasatch–Uinta (n = 988 lake-watershed points). These coordinates merely represent key locations in the lake landscape, and owing to restrictions of the NHD and size cutoffs do not totally represent an accurate count of lakes on the landscapes themselves. The ecoregions framework supports systematic ecological classification and aided spatially delineating USA mountain ranges. In instances where a lake boundary occurred in multiple ecoregions, and thus duplication occurred, duplicates were removed. Lake watersheds were assigned elevation data with {elevatr} (version 0.99.0) (Hollister et al. 2023).

High resolution (30 arc sec, ~1km) global downscaled air temperature data were acquired from the open access CHELSA climate database (Climatologies at High resolution for the Earth’s Land Surface Areas; Version 2.1) (Karger et al. 2017, 2018, 2020). Mean daily air temperatures (TAS air temperatures at 2 meters from hourly ERA5 data) were acquired for both historical (1979–2019) and projected (2011–2040, 2041–2070, 2071–2100) time periods at the lowest provided resolution (monthly). Projected climatologies data in this study focused only on the most probable climate scenario, SSP 3 / RCP 7.0 (“business as usual” scenario). Historical data were available in unique year–month combinations (e.g., per lake, n = 456), but projected data, as is typical of climatologies, were available only as a conglomerative average across each time period–month for each unique SSP scenario (e.g., per lake, n = 12 for the 2011–2041 time period under SSP 3). The year 1979 was excluded from analysis due to incomplete data. Lake

data were joined to CHELSA data to acquire watershed-level air temperature values at the landscape level; this allowed for fine-scale assessment of landscape temperature change, however the method remains relatively limited in granularity (i.e., a large lake and adjacent pond are not comparable) thus we do not extend our interpretations to the local-scale.

Heat Accumulation

This study applies the Growing Degree Day (GDD) and Killing Degree Day (KDD) thermal metrics to translate changes in temperature in the mountain lake landscape into ecologically meaningful interpretations; as the analysis focuses on the lake landscape, we do not suggest air temperature is a substitute for water temperature nor do result interpretations require it. Both GDD and KDD are heat accumulation measures that have been broadly used for >70 years in ecology and >270 years in agronomy (Barnard 1948; Seamster 1950; Wilsie and Shaw 1954; Neuheimer and Taggart 2007; Butler and Huybers 2015). While GDD and KDD are related, they have divergent ramifications for organisms. GDD measures cumulative heat units above a base threshold temperature, typically a threshold optimal for growth and development (Seuffert et al. 2012; Butler and Huybers 2015; Honsey et al. 2023). In contrast, KDD measures cumulative units over a known lethal temperature threshold and is used to help assess cumulative risk of severe heat exposure to organisms. KDD is a related metric to those used in heatwave studies (e.g., Tassone and Pace 2024) but emphasizes total accumulated heat as opposed to heat pulses. While GDD has long been applied as an ecological indicator in agricultural studies, it is generally underutilized in limnology and the aquatic sciences (Neuheimer and Taggart 2007), but see (Venturelli et al. 2010; Rypel 2014a; Spurgeon et al. 2020; Mushegian et al. 2021). Only relatively recently has the GDD concept been integrated into studies relating to zooplankton and

phytoplankton (Gillooly 2000; Dupuis and Hann 2009; Ralston et al. 2014), macrophytes (Beck et al. 2014), and freshwater bivalves (Watanabe et al. 2021).

This study quantified GDD and KDD metrics for mountain lake landscapes in both historical and projected time periods (**Figure 2.1; Figure S2.2-S2.3**). We calculated GDD for each unique *Lake–Year–Month* combination by adapting the original degree days (DD) formula:

$$DD = \sum_{t=1}^N \frac{T_{min} + T_{max}}{2} - T_0, T_t > T_0$$

or

$$DD = \sum_{t=1}^N T_t - T_0, T_t > T_0$$

where N = number of days, T_{min} and T_{max} = minimum and maximum temperature on day t (when minimum and maximum are not available, T_t = mean temperature on a day t , can replace the entire lefthand side of the equation), and T_0 = threshold temperature beneath which thermal energy is considered negligible toward physiological growth and maturity processes of species in mountain lake landscapes, particularly aquatic species. To fit the structure of the data available for this study, we used the secondary equation and modified the following elements: N = number of months; T_t = mean temperature on a month t .

We used -5, 0, 5, and 10°C as T_0 thresholds to explore trends. Ultimately, a GDD threshold of 0°C was used because this was identified as the most parsimonious base temperature

in general analyses of fish growth (Honsey et al. 2023). We calculated KDD using the same equation but used the 90% quantile for each mountain range (13.25 – 22.85 °C) as the T_0 threshold temperature. KDDs therefore represent lake landscape temperatures that are lethal or near-lethal, at least for native cold-adapted organisms.

In the event negative degree days resulted, these data were converted to zeros as it meant no heat had been accrued above the threshold. Zero degree day data were retained in the dataset for modeling (see Methods “Linear mixed-effect models”), but were removed from figures to improve data visualization. As CHELSA climate data were only available for unique *Year–Month* combinations, these data were expanded to complete the GDD or KDD calculation using mean monthly temperature as the expander for each month. Therefore, each day of a unique *Lake–Year*’s month received the same average temperature for each day of that respective month (Rypel 2012b, 2015). Last, these expanded values were summed for every unique *Lake–Year* to acquire the number of growing or killing degree days for a watershed location in a year.

Velocity of Climate Change

We measured velocity of change using Bayesian mixed effect regression models. In the models, *GDD* for each *Lake–Year* combination was the response variable, *Year* was a fixed effect, and *Lake* was a random effect (**Table S2.2**). The random effect slopes were subsequently interpreted as the velocity of change for each watershed. Overall trends in GDD were plotted with a parent regression line and random effect slopes examined as a function of elevation for each mountain range (**Figure 2.2-2.3**). Using GDD slopes, we additionally show differences in the velocity of change for each mountain range (**Figure 2.4**). A parallel analysis was performed using mean temperature (°C) rather than GDD, and because similar trends resulted, we display

only results from GDD for consistency with KDD analyses (**Figure S2.4-S2.5**). Both model response variables were transformed, GDD $\ln(x+1)$ or temperature $\log(x+10)$, prior to modeling.

Climate Vulnerability Classification

We performed a k-means cluster analyses based on mean historical heat accumulation for a site (Mean GDD, $\ln(x+1)$ transformed) to identify and group lake landscapes within each mountain range based on similar vulnerability properties. K-means is an ideal method for classifying rate of change in climate data as the method is versatile, guarantees model convergence, is scalable and computationally efficient with large datasets, and is simple and readily interpretable (Rypel et al. 2019) (**Figure 2.5; Figure S2.6**). The classification was *a priori* constrained to three clusters (i.e., cold, transitional, or hot). We elected not to cluster based on model slopes, primarily because the variance structure of projected climate data did not match that of the historical datasets. Hence given low sample size of projected data, and because GDD and slope are nearly colinear, we conservatively limited our analyses of slope to only historical data.

Climate Change Projections

We performed Discriminant Function Analyses (DFAs) to predict probability of lake assignment to one of the aforementioned clusters for three future time periods under the SSP 3 (RCP 7.0) climate scenario (**Table 2.1; Table S2.3**). Each lake landscape's mean historic GDD, and its respective cluster assignment, was used to build a predictive model for each mountain range separately. The continuous model variable, GDD, was $\ln(x+1)$ transformed as in the k-means cluster analysis. Projected GDD for each mountain range was used to aid in cluster predictions. Analyses were performed using the linear DFA function from the {MASS} package

(version 7.3-60.0.1) (Venables and Ripley 2002). DFAs used to predict each ranges' future cluster assignments possessed a high degree of accuracy (>94%; **Table S2.3**). Using the above approach, we were able to successfully examine how climate vulnerability classifications changed given probable climate futures.

Data & Code Availability

Data and code to produce the main analysis are available on GitHub (<https://github.com/caparisek>) and will be registered with a DOI upon publication.

Results

Statistical distributions of lakes varied across mountain ranges (**Figure S2.1; Table S2.1**). For example, mountain ranges like the Appalachians and Rockies have numerically many more lakes compared with other ranges. However, while both of these ranges, and also the Sierra Nevada, have more small lakes than larger lakes, ranges like the Appalachians have more low elevation lakes, being a relatively lower mountain range in general. Understanding the distribution of lakes across mountain ranges is limited by capacity of remote sensing tools to detect small lakes, sometimes referred to as “ponds” (Richardson et al. 2022). Nonetheless, lake distributions of all mountain ranges are decidedly right-skewed, with some expressing more or less skew versus others. Trends in kurtosis (i.e., distribution tailedness) also shed light on how rare large lake ecosystems (e.g., Lake Tahoe, 496.2 km²) are across mountain ranges. While all ranges exhibit leptokurtic distributions (i.e., kurtosis > 3, sharp peak in small lakes with long thin tails toward larger lakes), but the degree to which they experience this varies greatly.

Heat Accumulation

In all mountain ranges, mean growing degree days (GDD) and killing degree days (KDD) that lakes were exposed to increased over the years represented by the historical period, and from the historic baseline to 2100 in the projected SSP 3 (RCP 7.0) climate scenario (**Figure 2.1**). Based on downscaled historical climate data, lakes in low elevation watersheds are consistently exposed to a greater number of GDDs than high elevation lakes; this pattern was present in all mountain ranges (**Figure S2.2**). Interestingly, while a range of mid-high elevation sites experience low KDD, sites at lower elevations often had the highest KDDs. In some cases, there was a tight relationship between elevation and KDD (e.g., Sierra Nevada, Blue Ridge), but in others, the relationship was more heterogenous (e.g., Cascades, Rockies). Similar heat accumulation trends, and an increase in KDD over time, are also evident in the future (**Figure S2.3**). Quantiles derived from historical climate data illustrate the distributions of air temperatures within these diverse lake landscapes (Median = 4.75°C, Interquartile Range = -3.15 – 12.95°C).

Velocity of Climate Change

Mixed-effect models examining relationships between historical year and GDD (heat accumulation) revealed increasing trends in every mountain range ($R^2_c > 0.89$; **Table S2.2**; **Figure 2.2**). This pattern was almost identical for models constructed using temperature (°C) in place of GDD (**Figure S2.4**). Slopes extracted from these models for each site (as random effects), allowed comparisons of velocity of change estimates across sites. For both GDD and temperature models, and across all mountain ranges, velocities of change correlated significantly with elevation (**Figure 2.3**; **Figure S2.5**; Pearson's R Correlations: all correlations -0.48 – -0.95,

all p-values < 0.0001). Thus, lake landscapes with the highest velocity of climate change tended to be those distributed at lower elevations.

Boxplots examining GDD-modeled slope as a function of mountain range indicate which lake landscapes experience faster rates of change than others. For example, the ranges of Wasatch-Uinta, Idaho Batholith, Arizona-New Mexico, and Sierra Nevada are changing most quickly, while the ranges of Blue Ridge, Klamath, and Appalachians appear to be changing relatively slower (**Figure 2.4**).

Climate Vulnerability Classification

We built a climate change vulnerability classification using hindcasted air temperature heat accumulation data spanning a 38 y time series. Thus, every modeled mountain lake landscape was identified and subsequently its lake-watershed sites clustered into one of three classes of climate vulnerability: (1) cold, (2) transitional, or (3) hot (**Figure 2.5; Figure S2.6**). Across all mountain ranges 1980–2018, 19% of sites hold characteristics consistent with high heat and fast rates of heat accumulation, 42% of sites remain colder with slow rates of change, and 39% of sites are classified as transitional (**Table 2.1**). The percentage of watersheds assigned to each of these categories varied for each mountain range, such that historically the Sierra Nevada had 68% of its watersheds classified as cold, and Idaho Batholith, Wasatch-Uinta, and the Appalachians had 48%, 47%, and 45%, respectively. In contrast, ranges such as Blue Ridge and Arizona-New Mexico had 22-25% of watersheds classified as cold. However, these proportions change dramatically over time with probable climate projections (*see DFA results below*).

Climate Change Projections

Discriminant Function Analyses (DFAs) for each mountain range performed exceptionally well (> 94% accuracy, $p < 0.0001$; **Table S2.3**). DFAs revealed that by the end of the century just 8% of sites across all ranges will be classified as cold, 33% of sites will likely be classified as hot, and 59% of sites will be transitional (**Table 2.1**). This represents a -82%, 80%, and 51% change, respectively, from the historical baseline. Specifically, ranges such as Blue Ridge, Idaho Batholith, and Klamath, are anticipated to have just 1% of “cold” lake landscapes left by the end of the century, with the Appalachians, Cascades, Rockies, and Wasatch-Uinta having just 8%, 7%, 7%, and 6% of cold landscapes remaining (**Figure 2.4**).

Discussion

Landscape differences in geology, latitude, and longitude promote differences in the ecology of lakes; indeed, those ranges with higher elevation lakes likely contain a wider diversity of microclimates. In this study we (i) quantify heat accumulation and velocity of change in mountain lake landscapes in the USA, and (ii) create a climate change vulnerability framework to assist decision makers in allocation of limited conservation efforts towards these environments. Additionally, we believe this work is the first to (iii) exercise the agro-climate thermal time indicator, *killing degree days*, specifically to watersheds and aquatic ecosystems.

Heat Accumulation

Thermal extremes in freshwaters are increasing in frequency and threaten aquatic organisms and ecological processes as end-of-century approaches (Becker et al. 2018; Till et al. 2019; DuBose et al. 2019). In high-altitude ecosystems especially, snowpack is diminishing and

ice-cover on lakes is reducing rapidly; the ramifications of which alter water security downstream and wreak havoc on thermal regimes in these coldwater habitats (Viviroli et al. 2011; Sadro et al. 2019; Moser et al. 2019; Jane et al. 2024). Higher heat accumulation in lakes is also known to increase disease susceptibility (Marcogliese 2008), favor phytoplankton blooms (Piccioni et al. 2021), modify lake stratification dynamics (Woolway et al. 2021), and reduce oxygen levels in lakes (Blumberg and Di Toro 1990; Bukaveckas et al. 2023), all of which could disrupt or rewire food webs (Bartley et al. 2019). Taxa, like some lake-dwelling mountain aquatic insects, may be able to mitigate risk of heat exposure in lakes by tolerating migration to cool streams if required (Birrell et al. 2020; Parisek et al. 2023).

In this study, we observe mountain lake landscapes that previously supported more favorable coldwater habitats will experience more days with higher temperatures, greater accumulated heat, and an amplification of killing heat. Where lake landscapes newly experience greater growing degree days, these warmer temperatures may open up new habitats suitable to support optimal growth and development in the future. However, we also predict these landscapes will experience 215 –254% (mean = 236%) increases in heat accumulation exceeding the 90th percentile of that observed historically. Our findings suggest that across USA mountain ranges, watersheds positioned at lower elevations are consistently exposed to higher rates of heat accumulation. This latter point, despite being based on air temperature data, is also supported by observed trends in surface water temperature from other mountain ranges, such as the Pyrenees, as demonstrated by 59 mountain lakes along an elevation gradient (Sabás et al. 2021). The accumulated heat (i.e., degree-day) metric is a valuable tool for assessing changing heat content dynamics (Choiński et al. 2015; Christianson et al. 2019). In freshwater systems generally, increased heat accumulation extends the duration of the growing season and can enhance

maturation rate in fishes (Venturelli et al. 2010; Uphoff et al. 2013), however, some fish populations have a reduced tolerance and perform less well (McDermid et al. 2013; Feiner et al. 2016). Indeed research suggests ecological response to increased heat accumulation is nonlinear, as it is also known to be ecosystem-specific and heavily associated with changes in latitude (Rypel 2012a; Richard and Rypel 2013; Rypel and David 2017; Spurgeon et al. 2020). It is unknown how fishes and other aquatic organisms respond to heat accumulation along an elevation gradient. For instance, organisms may attempt to migrate or else attempt to tolerate warming temperatures. Relatedly, climate change may simultaneously increase primary productivity and thereby improve food resources for higher order taxa in the food web.

Velocity of Climate Change

Quantifying geographically-distinct velocities of climate change provides critical insight and nuance on the uneven impacts of climate change. For example, we observe that velocity of climate change varies considerably by mountain range (i.e., some ranges experience greater velocities of change through time, while others have relatively slower rates of heat accumulation). This finding provides key insight on the fragility of certain regions and lakes to ecosystem state shifts (Scheffer 1990; Scheffer and Carpenter 2003; Butitta et al. 2017). Individual species and ecosystems possess different thresholds for how they will react to higher heat accumulation; however the pace at which they can acclimatize to the rapidity of these changes is also important. Species with less time to adjust to rapidly increasing temperatures (e.g., long-lived and less mobile organisms), are likely to struggle in climates whose heat accumulation occurs at a higher velocity (Pacheco-Riaño et al. 2023; Rypel 2023). However a slow rate of change can also be dangerous, especially in regions where climate variance has historically been low (Kraemer et al. 2015).

While GDD and velocity of change are closely linked, the relationships are apparently often curvilinear (e.g., Appalachians, Cascades, Sierra Nevada; **Figure 2.5**). Therefore, velocity of change actually slows once high heat accumulation is reached. This pattern is consistent with expectations from regime shift theory, where the highest rates of change are more frequently observed in systems undergoing a state shift (Butitta et al. 2017). Combined, the empirical patterns in velocity of thermal change suggests these landscapes have likely been rapidly shifting for some time, so much so that the rate of change is actually beginning to slow. These important relationships also highlight how heat accumulation or velocity of change alone produce similar, but fundamentally different assessments of vulnerability (Hamann et al. 2015; Woolway and Maberly 2020; Woolway 2023). Some of our study mountain ranges showed parallel results in their heat accumulation and velocity of climate change (e.g., Wasatch-Uinta Mountains) while others were completely different (e.g., Klamath Mountains). Therefore, conservation applications based on just one or the other may come to divergent conclusions. Coupling velocity of change with heat accumulation provides a richer portrait of vulnerability, which may be of interest in future climate change assessments efforts going forward.

A limitation of our analysis is the lack of available water temperature data, a problem that is exasperated by the lack of study in mountain systems more generally. These data are not yet feasible to acquire at scale, and so here we used air temperature data to explore changing patterned in accumulated heat in the lake landscape. We note, however, that lake surface water temperatures are reported to correspond closely with air temperatures (Armitage 2023) and thus can still be a useful proxy for non-taxa-specific landscape level temperature-based analyses. While lake surface water cannot serve as a proxy for lake temperature at depth, and attaining lake depth temperature estimates at scale remains elusive to scientists, this information still

provides valuable insights into microclimates experienced in mountain lake watersheds. On the whole, the use of air temperature to assess accumulated heat and identify occurrence of extremes provides meaningful information about which regions and lake watersheds are more likely to be at risk of exposure to repeated extreme temperatures (Armitage 2023). Future work could build from this study by forging models on well-studied lakes that generate hindcasted and forecasted lake temperatures (Read et al. 2019; Willard et al. 2021) rather than just lake landscapes.

It is worth noting that lake themselves do not necessarily show the same temperature trends as their watersheds, and thus these results should only be interpreted as landscape-level trends. As demonstrated by **Figure S2.1** and **Table S2.1**, while most mountain ranges are indeed skewed toward having smaller waterbodies, large outlier lakes are also present (e.g., Lake Tahoe, Sierra Nevada). Factors contributing to the lake heat budget, such as lake morphology, and exposure to solar radiation, cloud cover, and albedo effects, play key roles in making lake warming not a geographically consistent phenomena (O'Reilly et al. 2015). Additionally, while high elevation mountain lakes may experience greater elevation-dependent warming throughout the day, reduced snow cover and greater solar radiation drives convective cooling (i.e., night time heat loss) which plays a large role in the actual water temperatures in mountain lakes. Seasonal effects, such as the ice-free season leading to more warming in the summer and ice and snow cover enhancing colder temperatures in the winter also play significant roles in mountain lake temperatures. Finally, we note the relationship between lake surface area and elevation is quite varied across the ranges (**Figure S2.1, Panel D**). This variation would likely present differences in lake heat budgets as well. This area of research would benefit from having the ability to tease apart nuances such as lake volume, maximum depth, morphology, and convective

cooling, as these could all reasonably influence the speed at which lakes accumulate heat as landscape temperatures rise (Sabás et al. 2021).

Climate Vulnerability Classification

Ecosystem vulnerability schematics are core to advancing conservation activities at all scales. The goal of our proposed climate change classification is to help identify, across multiple mountain ranges, the vulnerability of individual mountain lake landscapes to increasing heat accumulation. The three clustering tiers are delineated by (1) low heat accumulation, often with sites from high-elevation; (2) transitional, often with sites from mid-elevation; and (3) high heat accumulation, often with sites from lower elevation ranges. Combined, the classification schema shows lower-elevation mountain lakes are experiencing more rapid landscape-level thermal change across all USA mountain ranges. These lakes are also most likely to first experience increased killing degree days as end of the century approaches. Further, our findings suggest particular conservation consideration should be given to watersheds where cold-adapted endemic species have fewer than 5% of cool landscape available to them by the end of the century (e.g., Appalachians, Blue Ridge, Idaho Batholith, Klamath).

Accelerating change in freshwater systems will force managers to strategically select where they can reasonably work for maximal impact. The vulnerability schema provided here provides an initial tool to help. Global lake thermal regimes are already undergoing worldwide shifts at increasing velocities (Maberly et al. 2020; Woolway and Maberly 2020). No study exists, however, which classifies lake landscape vulnerability in mountain regions for anticipated heat accumulation and rates of change. Previous accepted frameworks for lake thermal classification exist, although they emphasize mixing regimes and require specific data to perform

multi-dimensional lake models (Hutchinson and Löffler 1956; Lewis Jr. 1983; Woolway and Merchant 2019). To assess lake landscape vulnerability at scale, however, these data are not available and thus limits exploration. Numerous assessments have sought to quantify vulnerability of lakes, depending on the focal need of the assessment, including through change in eutrophication (Giuliani et al. 2019), pollution resilience (Wu et al. 2012), water balance (Bracht-Flyr et al. 2013), and invertebrate-based temperature reconstructions (Eggermont et al. 2010). Some studies have concluded high-elevation lakes to be most vulnerable to change when specifically focusing on changes in ice dynamics, which low elevation lakes do not frequently experience (Gađek et al. 2020; Råman Vinnå et al. 2021). However assessments using the accumulated degree-day approach supports our finding that low-elevation watersheds are indeed highly sensitive to warming trends (Thompson et al. 2005; Sabás et al. 2021).

There are several potential uses for our mountain lake landscape classification framework. Many of the most well-studied mountain lakes are located at relatively high elevations. Results from this study suggest managers should increasingly monitor coldwater lakes at lower-to-mid elevations. Further, while shallow versus deep lakes would be affected on the lake landscape differently, these watershed locations still are mostly likely to experience the greatest accumulated landscape heat. Regional managers can use our classification to identify specific watersheds of greatest threat to loss of endemic species. Further, the classification provides an initial ability to better understand types of challenges these species are uniquely facing (e.g., fast change or a “slow boil”) and thus provides an ability for managers to take early action in watersheds undergoing the greatest volume of threats. Yet whereas climate change itself is unmanageable at a local scale, conservation practitioners must find ways of building resilience into ecosystems using the levers that they do have control over (Rypel and Magnuson

2019). For some watersheds, this might mean reduced harvest limits or improved in-lake or shoreline habitats (Carpenter et al. 2017). In other ecosystems, it may entail improved management of the watershed, land use and nutrient loading (Jacobson et al. 2016; Lau et al. 2022; Jane et al. 2024). We therefore encourage managers to use the information provided here to plan resource allocation, funding needs, and decision making towards climate change resilience.

Freshwater biodiversity is increasingly challenged by the scope and extent of global climate change and human domination of the world's water cycle. This analysis provides an initial attempt and novel perspective to understand lake landscape vulnerability across USA mountain ranges. Our results show how vulnerable mountain lakes are experiencing unprecedented exposures to heat accumulation, especially at low elevations. Increased velocities of change are also fundamentally reshaping the structure and function of these ecosystems and increasing their frailty. Conservation managers need tools to triage their time, energy, personnel, and budget. In providing this classification and vulnerability analysis of the USA mountain lake landscapes, we hope to deliver one useful tool for aiding in complicated decision-making processes. Overall, our results may call attention to the wide ways in which mountain lake landscapes are likely to change in the next 75 years.

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Figures & Tables

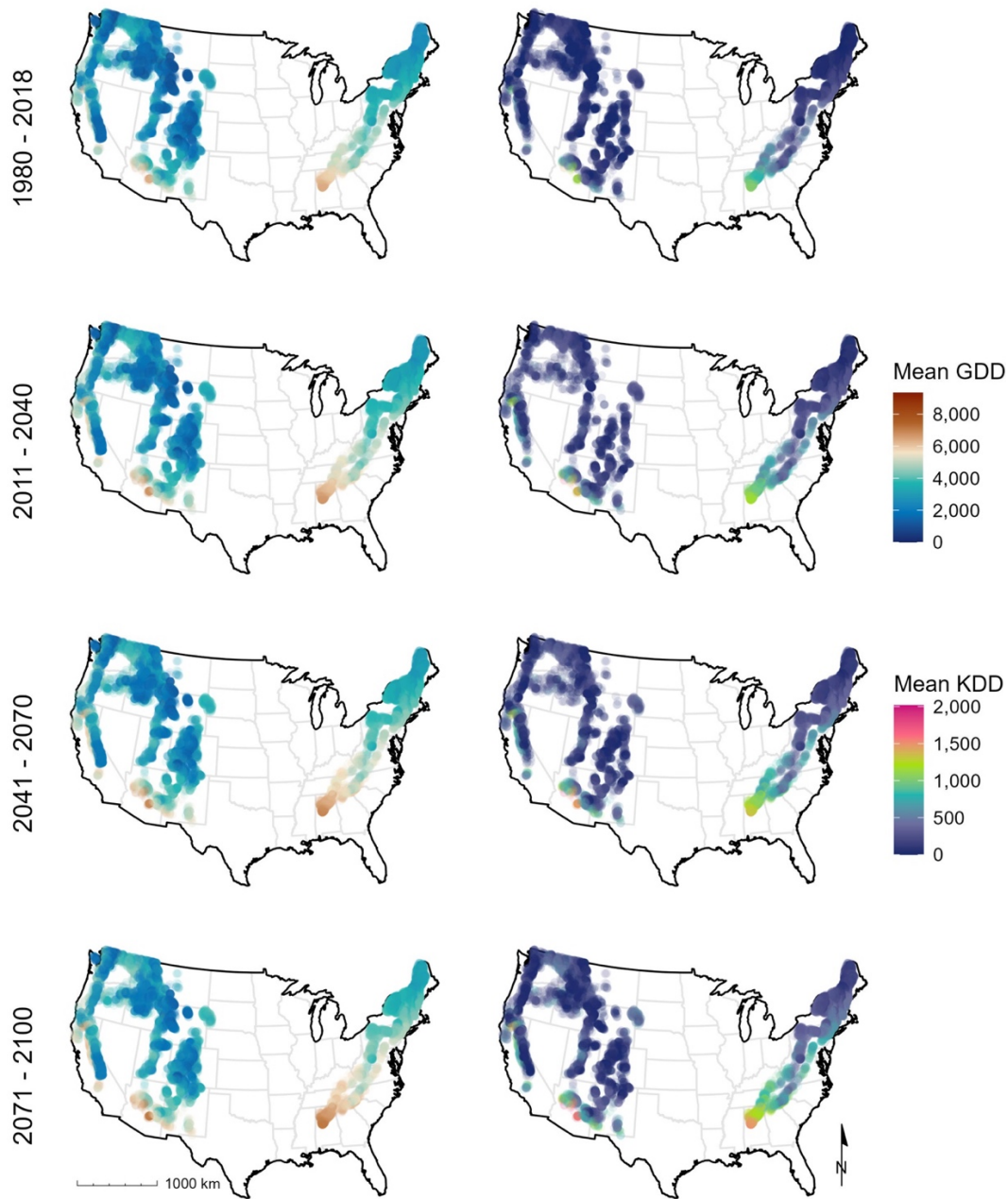


Figure 2.1

Mean Growing Degree Days (GDD; left panel) and Killing Degree Days (KDD; right panel) across mountain lake landscapes in the contiguous USA for the time periods: 1980–2018, 2011–2040, 2041–2070, 2071–2100.

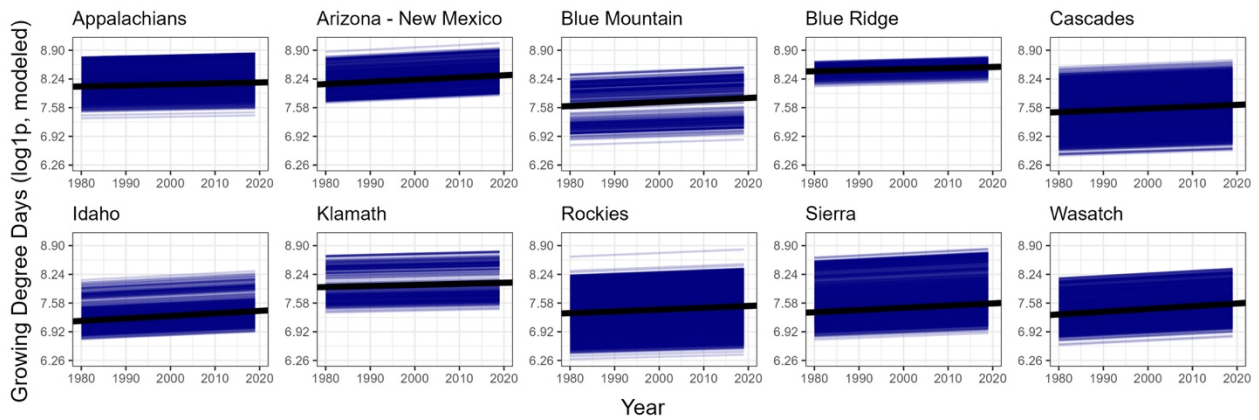


Figure 2.2

Long-term trends in GDD for mountain lake landscapes in 10 mountain ranges across the USA as assayed using random slope and random intercept linear mixed effect models. Dark parent line denotes overall trend for each region.

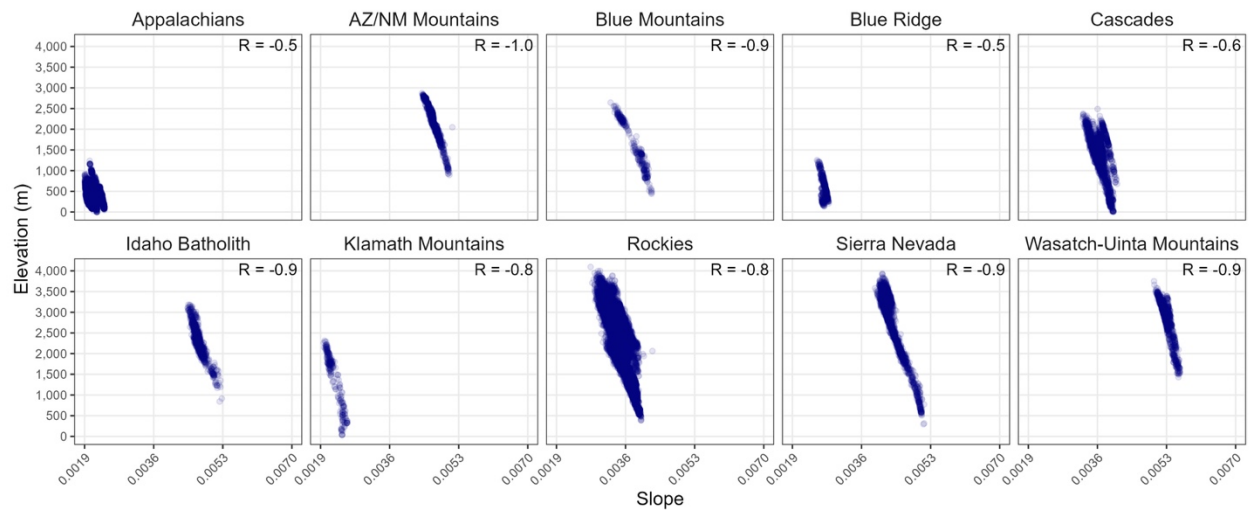


Figure 2.3

Velocity of climate change (assayed as random slopes extracted from the random slope and random intercept linear mixed effect model) plotted against elevation of mountain lakes. Pearson correlation coefficient (R) is shown in upper right of each plot.

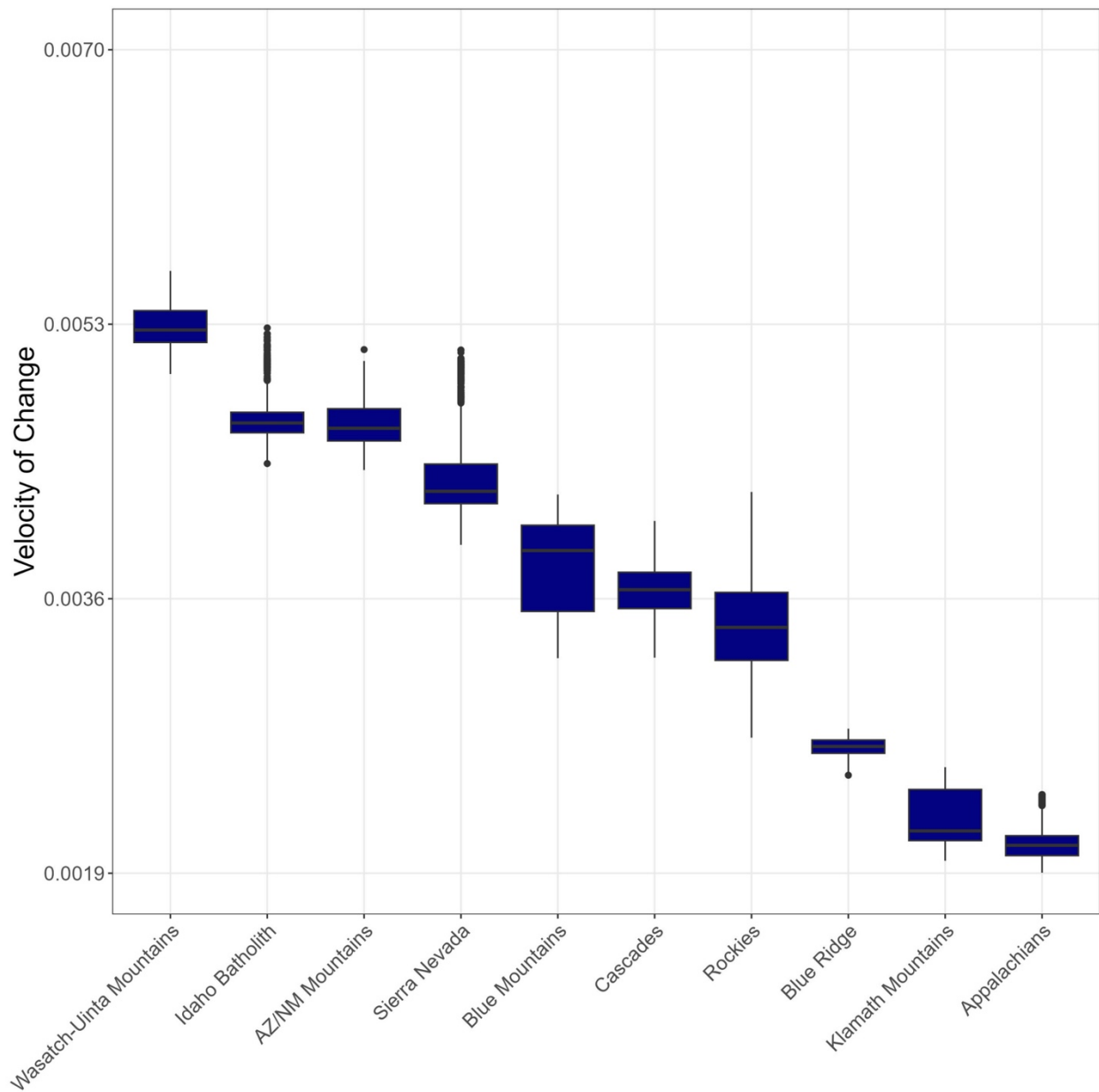


Figure 2.4

Box plots showing the range of observed velocities of change (random effect slopes) in each focal mountain range. Each box represents the median value and interquartile range, and error bars denote the 95% confidence interval.

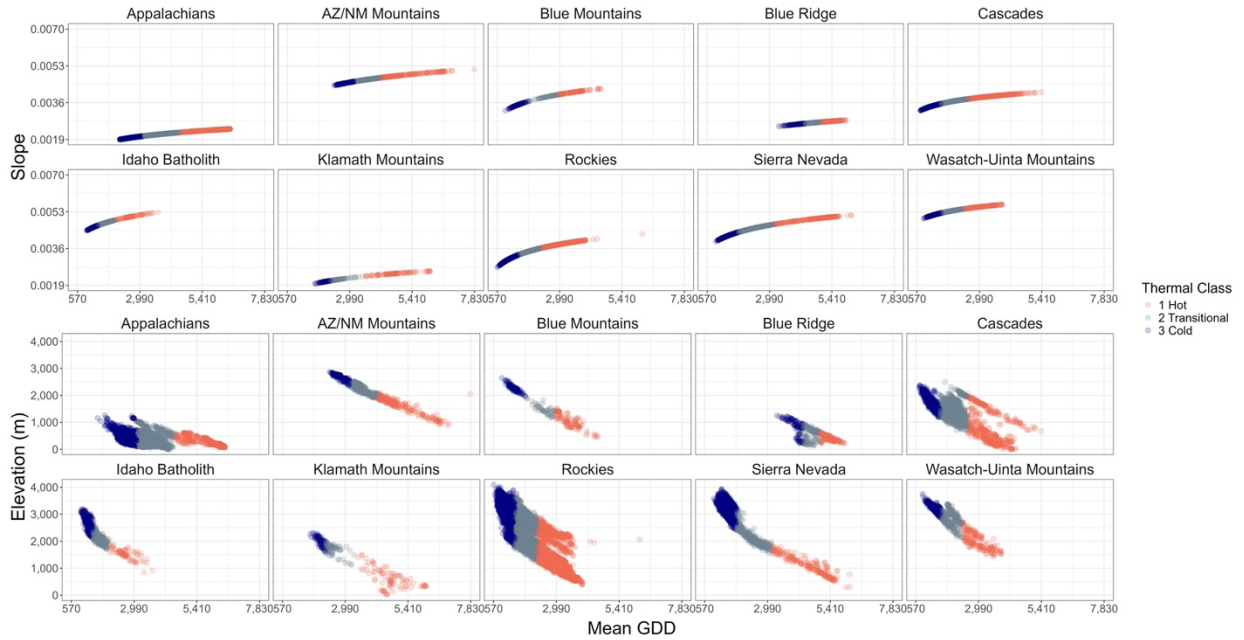


Figure 2.5

Relationship of velocity of change (random effect slopes) and elevation as a function of mean GDD for each lake in 10 major mountain ranges in the USA. In each plot, each unique lake landscape is identified by its membership in each of the three climate vulnerability classes.

Table 2.1

Summary of membership totals (historical and future) in each of three climate vulnerability classes for major mountain ranges in the contiguous United States, including percentage of lakes (non-bold) and percent change (bold) from the historic time period.

Region	Time Period (1980–)	Percentage of Lakes & Percent Change from Historic Baseline		
		Cold	Transitional	Hot
All	2018	42	39	19
	2040	25 (-40)	52 (34)	22 (21)
	2070	16 (-62)	57 (46)	26 (43)
	2100	8 (-82)	59 (51)	33 (80)
1. Appalachians	2018	45	44	10
	2040	26	63	11
	2070	15	72	13
	2100	5	75	19
2. Arizona–New Mexico Mountains	2018	25	45	30
	2040	37	47	37
	2070	42	51	42
	2100	55	44	55
3. Blue Mountains	2018	40	19	41
	2040	38	12	50
	2070	36	12	52
	2100	23	21	56
4. Blue Ridge	2018	22	44	33

	2040	8	38	54
	2070	4	30	66
	2100	1	15	84
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	2018	28	48	24
5. Cascades	2040	17	55	28
	2070	13	56	32
	2100	7	51	42
<hr/>				
	2018	48	44	8
6. Idaho Batholith	2040	11	80	10
	2070	4	82	15
	2100	1	75	24
<hr/>				
	2018	30	33	38
7. Klamath Mountains	2040	9	52	39
	2070	3	57	40
	2100	1	57	42
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	2018	38	35	27
8. Rockies	2040	22	44	33
	2070	15	46	40
	2100	7	47	46
<hr/>				
	2018	68	24	9
9. Sierra Nevada	2040	54	36	11
	2070	42	46	12
	2100	26	61	14
<hr/>				
	2018	47	33	20
10. Wasatch-Uinta Mountains	2040	23	50	27
	2070	14	53	32
	2100	6	56	38

Supplement

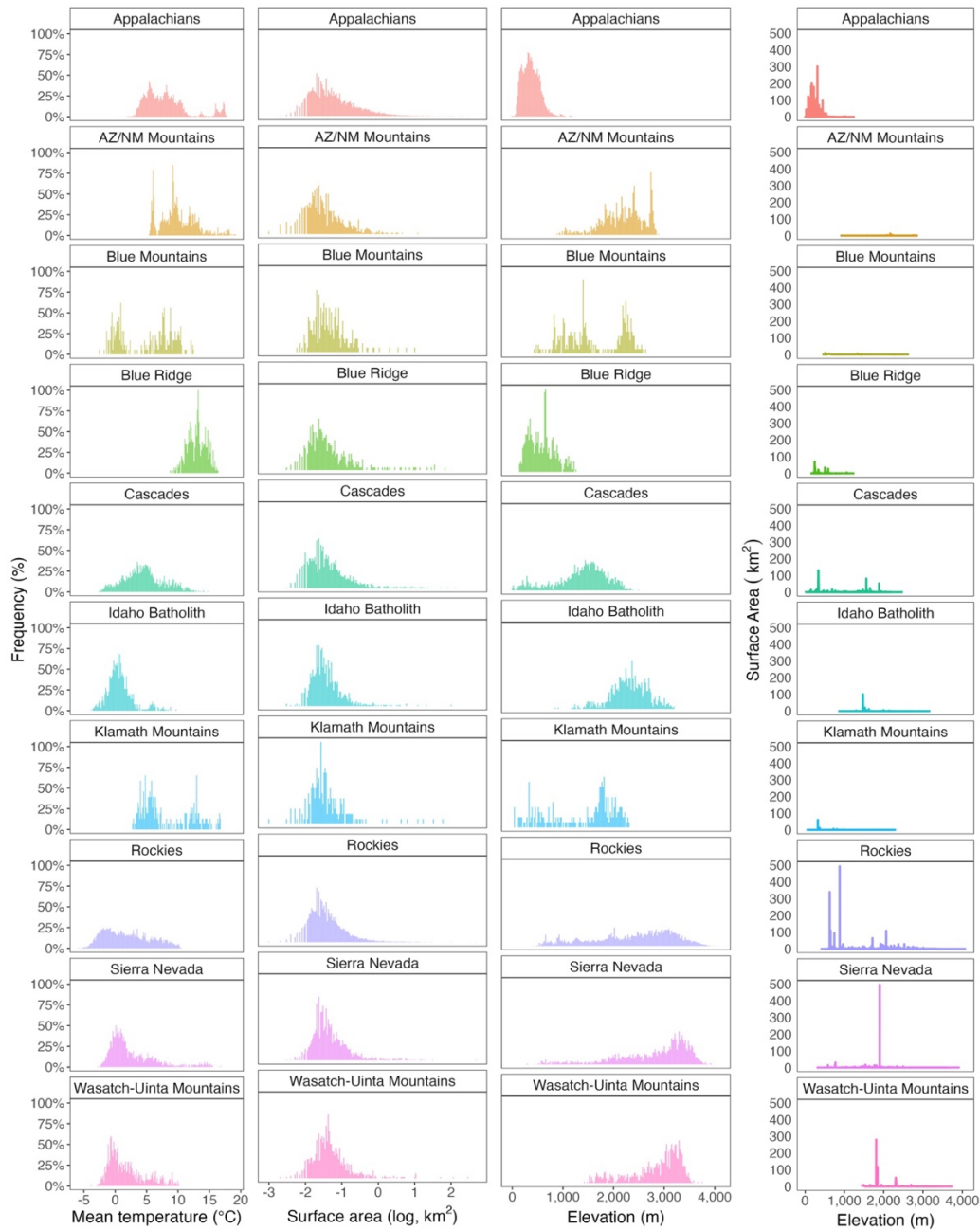


Figure S2.1

Frequency histograms for temperature (°C), lake surface area (log, km²), and elevation (m) for lakes in 10 USA mountain ranges. Surface area as a function of elevation is shown to provide context and highlight lake diversity across ranges. Data were obtained from the National Hydrography Database and CHELSA Database.

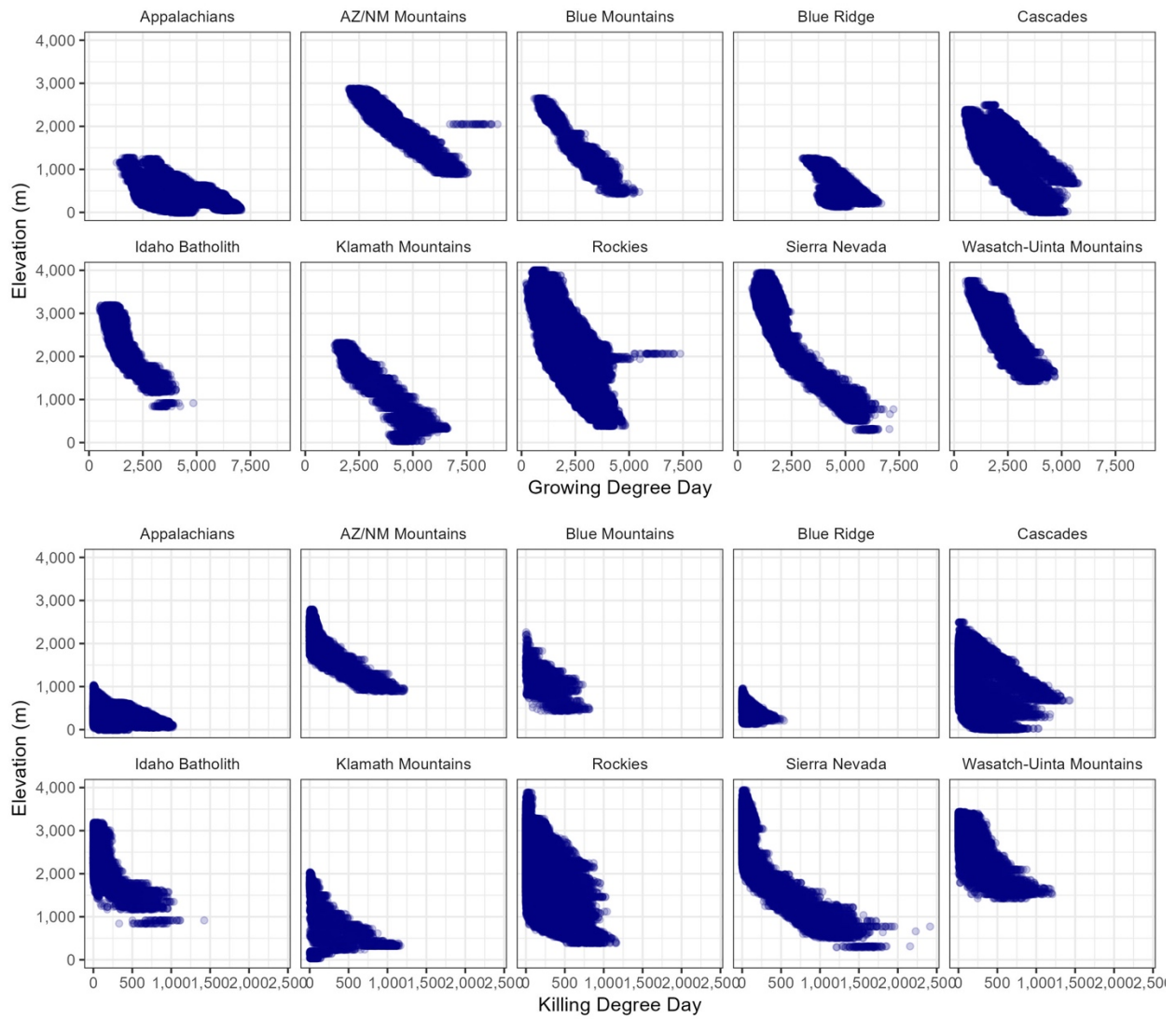


Figure S2.2

Historical sum of growing degree day and killing degree day as a function of elevation. Each point represents a unique *Lake–Year* combination.

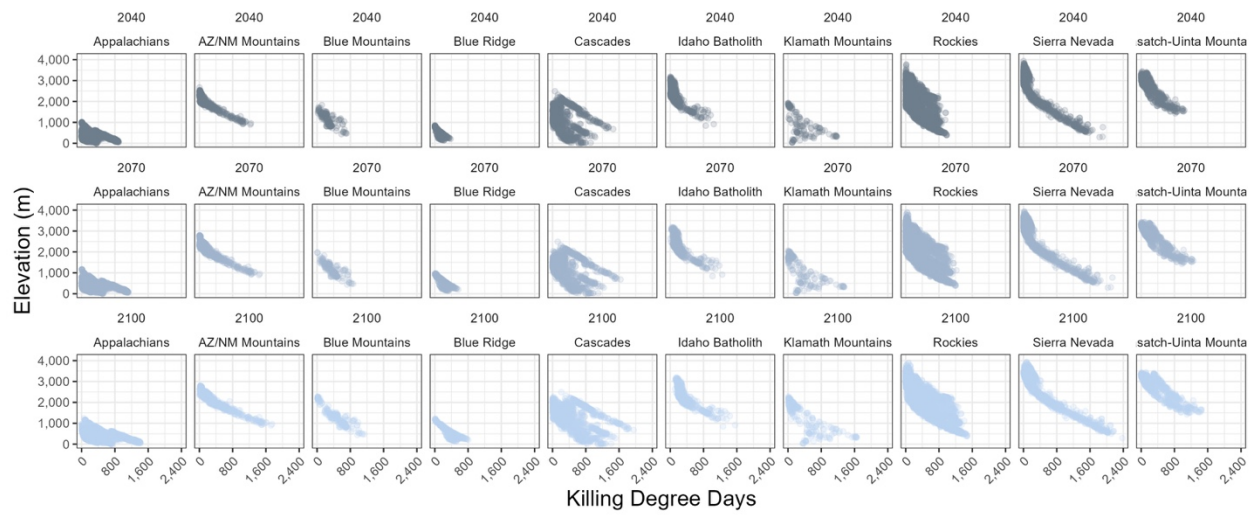


Figure S2.3

Projected killing degree days as a function of elevation. Each point represents a unique *Lake–Year* combination.

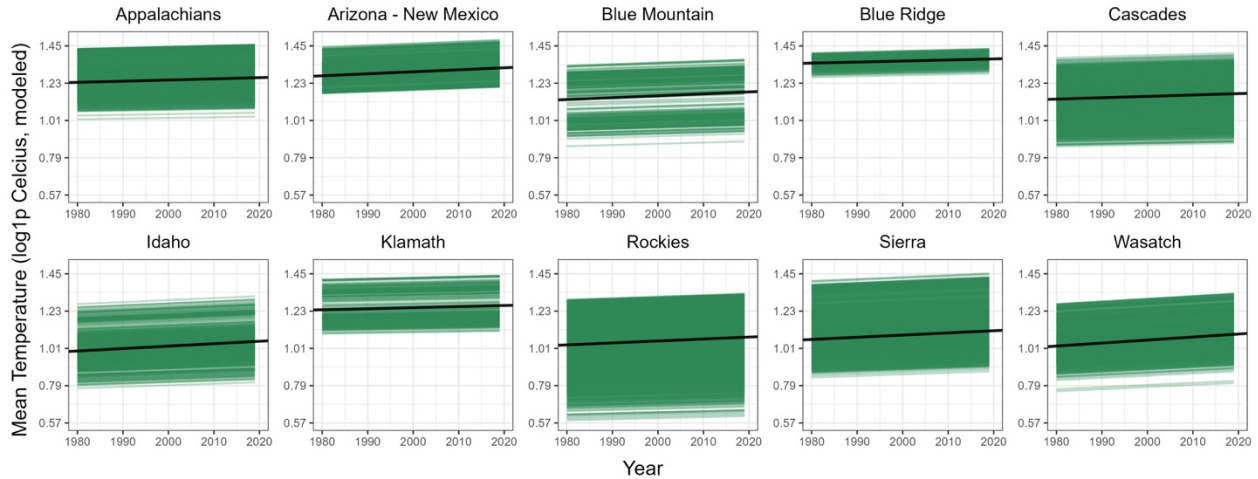


Figure S2.4

Long-term trends in temperature for mountain lake landscapes in 10 mountain ranges across the USA as assayed using random slope and random intercept linear mixed effect models. Dark parent line denotes overall trend for each region.

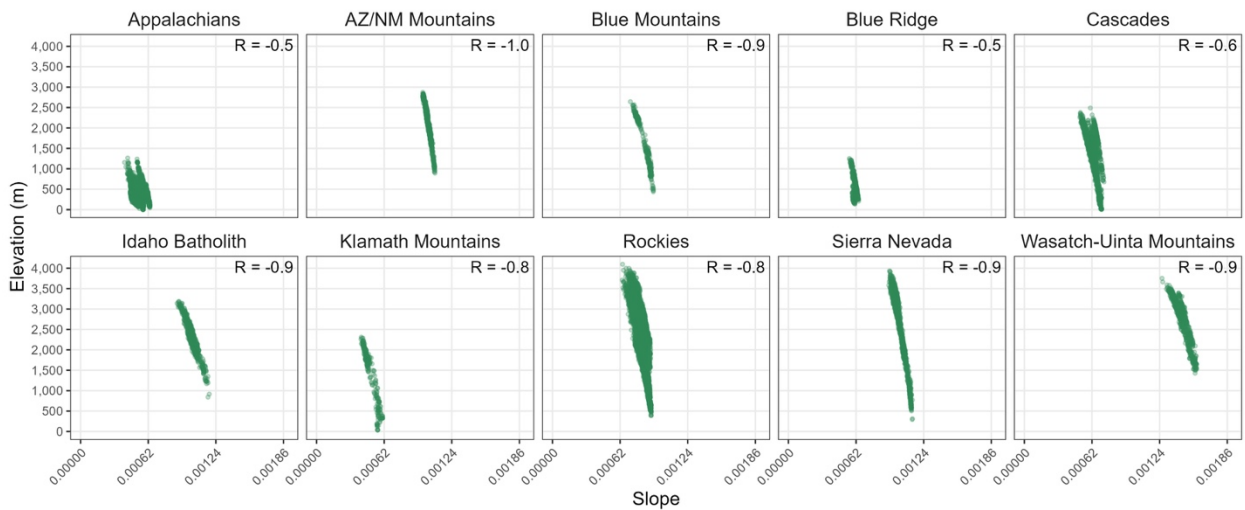


Figure S2.5

Velocity of temperature change (assayed as random slopes extracted from the random slope and random intercept linear mixed effect model) plotted against elevation of mountain lakes. Pearson correlation coefficient (R) is shown in upper right of each plot.

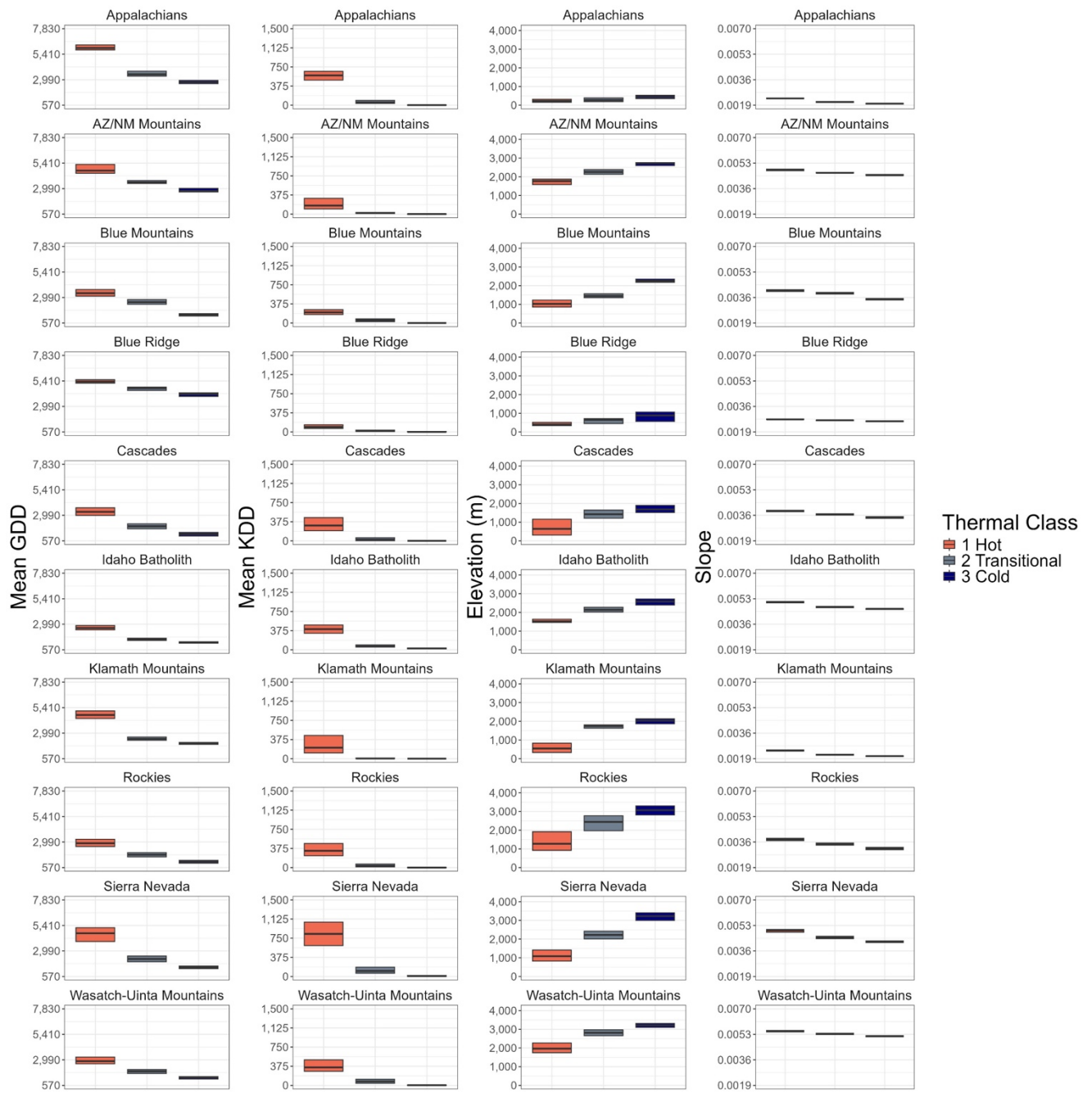


Figure S2.6

Boxplots of mean GDD, mean KDD, elevation, and velocity of change (random effect slopes) in each lake landscape and climate vulnerability category. In each plot, boxes represent the median and interquartile range.

Table S2.1

Descriptive statistics of statistical moments for the distributions of surface area (km²) and elevation (m) for each studied mountain range.

Mountain Range	Lake Abundance (n)	Surface Area (km ²)			Elevation (m)		
		Skew	Kurtosis	Mean	Skew	Kurtosis	Mean
1. Appalachians	10,467	32.2	1,258.7	0.5	0.7	4.0	368
2. Arizona–New Mexico Mountains	1,033	17.7	414.8	0.1	-0.6	3.2	2,188
3. Blue Mountains	284	15.7	258.0	0.4	0.0	1.6	1,602
4. Blue Ridge	464	9.4	103.1	1.2	0.5	2.5	585
5. Cascades	2,165	20.3	487.6	0.5	-0.7	2.9	1,348
6. Idaho Batholith	1,035	27.1	806.4	0.3	-0.5	3.6	2,307
7. Klamath	245	9.0	87.3	0.9	-0.4	1.7	1,336
8. Rockies	9,661	44.4	2,189.7	0.4	-0.5	2.3	2,361
9. Sierra Nevada	2,358	44.8	2,110.5	0.5	-1.1	3.7	2,774
10. Wasatch-Uinta	988	24.8	672.5	0.7	-1.0	3.0	2,842

Table S2.2

Summary statistics for linear mixed-effect models from which velocity of climate change metrics were extracted.

Mountain Range	Pseudo R ²	Parent Intercept	Parent Slope	Model Slope (Year Effect)		
				df	t-value	p-value
Growing Degree Days (1980–2018)						
1. Appalachians	0.97	3.48	0.0023	1,142	370	<0.0001
2. Arizona–New Mexico Mountain	0.96	-1.86	0.0050	37,799	226	<0.0001
3. Blue Mountains	0.97	-1.53	0.0046	2,120	70	<0.0001
4. Blue Ridge	0.89	3.56	0.0025	8,434	93	<0.0001
5. Cascades	0.95	-0.79	0.0042	10,022	150	<0.0001
6. Idaho Batholith	0.86	-4.21	0.0057	39,612	132	<0.0001
7. Klamath Mountains	0.97	3.07	0.0025	1,858	39	<0.0001
8. Rockies	0.95	-0.82	0.0041	371,846	297	<0.0001
9. Sierra Nevada	0.96	-2.62	0.0050	6,879	201	<0.0001
10. Wasatch-Uinta Mountains	0.94	-5.14	0.0063	18,566	159	<0.0001
Temperature (1980–2018)						
1. Appalachians	0.96	-0.14	0.0007	135,980	313	<0.0001
2. Arizona–New Mexico Mountain	0.96	-1.06	0.0012	94,82	188	<0.0001
3. Blue Mountains	0.97	-1.09	0.0011	10,920	58	<0.0001
4. Blue Ridge	0.89	0.12	0.0006	9,618	93	<0.0001

5. Cascades	0.96	-0.47	0.0008	77,688	132	<0.0001
6. Idaho Batholith	0.90	-1.85	0.0014	6,367	116	<0.0001
7. Klamath Mountains	0.97	-0.01	0.0006	1,882	43	<0.0001
8. Rockies	0.96	-1.25	0.0012	44,117	274	<0.0001
9. Sierra Nevada	0.96	-1.49	0.0013	91,413	182	<0.0001
10. Wasatch-Uinta Mountains	0.95	-2.50	0.0018	13,220	157	<0.0001

Table S2.3

Summary statistics of Discriminant Function Analyses (DFAs) predicting lake landscape membership into each of three climate vulnerability classes.

Mountain Range	DFA models using 80% as training and 20% as testing dataset		Coefficients of Linear Discriminants
	Accuracy (%)	p-value	
1. Appalachians	100	<0.0001	12.30
2. Arizona–New Mexico Mountains	95	<0.0001	10.90
3. Blue Mountains	96	<0.0001	8.35
4. Blue Ridge	96	<0.0001	21.94
5. Cascades	96	<0.0001	6.44
6. Idaho Batholith	99	<0.0001	10.87
7. Klamath Mountains	94	<0.0001	9.25
8. Rockies	99	<0.0001	6.81
9. Sierra Nevada	97	<0.0001	7.44
10. Wasatch-Uinta Mountains	98	<0.0001	8.30

Chapter 3

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Testing the ecosystem size and productive space hypotheses using multidimensional food web data

Abstract

Empirical tests of theory are important for building improved understanding of ecosystems. This study evaluates two long-standing and still-competing hypotheses for what regulates the architecture of food webs – ecosystem size or productivity. We test hypotheses using a classic measure of food web complexity (food chain length), and also new multidimensional isotopic niche space measures, in 36 mountain lakes. We also examine diet proportions among six distinct food sources for higher level fish consumers in these same ecosystems. We demonstrate both hypotheses may not be solely predictive, but rather appear context-dependent. Across lakes ranging widely in volume (8,773 – 3,999,753 m³), food chain length and all six multidimensional isotopic space niche measures showed positive trends with ecosystem size. However only three measures of complexity (trophic area, niche centroid distance, and $\delta^{13}\text{C}$ range) scaled significantly. There were no significant relationships between lake productivity (ranging 0 – 26.7 $\mu\text{g/L}$) and any of the six community niche metrics (e.g., trophic area, centroid distance, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ range, and mean and standard deviation of nearest neighbor distance). Aquatic insects supported fish consumers across all lakes, showing the importance of aquatic insects to mountain lakes overall. However, reliance of consumer fishes on terrestrial insects and periphyton increased significantly and non-linearly with lake size, while reliance on aquatic plants showed opposite trends. These results expand upon our understanding

of the biogeography of food webs, including the context and situations where food web complexity and consumer sourcing is mediated by ecosystem size and productivity. Furthermore, our work highlights the connected aspect of mountain lakes within lake landscapes, revealing how land use change likely affects lake ecosystems overall.

Significance Statement

This study critically tests two pervasive hypotheses for the determinants of food chain length – the ecosystem size and productive space hypotheses. We found all food web complexity metrics scaled positively with ecosystem size, but few relationships were actually significant. There were no significant relationships between food web complexity and lake productivity. Fish consumer diets scaled along an ecosystem size gradient, and showed consistent reliance on aquatic insects, potentially increasing reliance on periphyton and terrestrial insects, and potentially decreasing reliance on aquatic plants (though none were apparently significant). Our findings refine the contexts with which food chain length and food web architecture scale with ecosystem size and productivity gradients.

Introduction

The twin effects of ecosystem size and productivity have long intrigued ecologists as fundamental drivers of community assembly, expression of life-histories, and food web architecture (MacArthur and Wilson 1967; Schoener 1989; Young et al. 2013; Rypel 2023). In a landmark paper, Post et al. (2000) presented compelling evidence that food chain length was primarily driven by ecosystem size, and not productivity, at least in large Adirondack lakes. Yet for a range of reasons, including the difficulty of measuring food chain length (Sabo et al. 2009), challenges related to omnivory (Sprules and Bowerman 1988), and defining ecosystem

boundaries (Post et al. 2007), testing the predictors of community assembly across ecosystem types and biomes remains elusive. Indeed, these hypotheses have now been evaluated in a series of contexts, but with mixed findings (Spencer and Warren 1996; Kaunzinger and Morin 1998; Vander Zanden et al. 1999a; Post 2002; Jake Vander Zanden and Fetzer 2007; Takimoto et al. 2008; McHugh et al. 2010; Young et al. 2013; Takimoto and Post 2013)

While food chain length specifically has long fascinated ecologists (Elton 1927; Hutchinson 1959; Yodzis 1980; Sterner et al. 1997; Sabo et al. 2009), it is ultimately just one response variable for studying complexity. Following the proliferation of stable isotopes as a tool for quantifying and visualizing food webs, Layman et al. (2007) proposed a series of community-wide metrics for assessing trophic structure and complexity. These metrics provide holistic and comparable information on the structure and function of food webs and can be used to study the role of environmental factors in shaping food web patterns (Quevedo et al. 2009; Britton et al. 2010; Nagelkerken et al. 2020). Food web complexity metrics can be similarly applied at an intraspecific level to understand how species niche width responds to disturbance (Layman et al. 2007). Yet few studies have examined how community-wide metrics, which heighten understanding of novel elements to food web architecture and community dynamics, are influenced by ecosystem size or productivity (but see O'Neill and Thorp 2014; Wang et al. 2016; Maitland and Rahel 2023).

Lakes have an especially rich history of being useful for developing ecological theory, especially related to food web ecology (Forbes 1887; Carpenter et al. 1985; Vander Zanden et al. 1999a; Scheffer and van Nes 2007). Classically, Lindeman (1942) conceptualized and provided the first attempt at generating a quantitative food web in a small Minnesota bog lake, including the role of the detrital web in energy flow transfer. Assembly rules for biotic communities can be

readily elucidated by quantifying colonization and extinction dynamics as a product of isolation and dispersal (Magnuson et al. 1998; Arnott et al. 2006). And lakes are generally understood to be excellent sentinels for understanding the effects of climate change on freshwater environments more generally (Sharma et al. 2009; Till et al. 2019; Woolway et al. 2022).

Mountain lakes have been somewhat neglected in ecological studies of lentic ecosystems. Rather, limnology as a field has focused more on north-temperate lake environments (e.g., Midwestern USA, Canada, Europe) (Schupp 1992; Kalff 2002; Emmerton et al. 2007; Wehrly et al. 2012; Rypel et al. 2019). Here, previous research suggests a high contribution of benthic metabolism to whole-lake metabolism (Vadeboncoeur and Steinman 2002). However, results from work in high elevation Sierra lakes, where littoral zones are small with little vegetation cover, show incongruent patterns (Sadro et al. 2011). And even though 90-95% of total freshwater surface area may be attributed to only 145 large lakes globally (Herdendorf 1982; Kalff 2002; Jenny et al. 2020), small lakes, including those in high elevation mountain landscapes, are some of the most numerous and poorly studied freshwater environments on Earth (Kalff 2002; Downing et al. 2006; Hanson et al. 2007; Downing 2010; McDonald et al. 2012; Verpoorter et al. 2014; Holgerson and Raymond 2016; Vlah et al. 2017). Small waterbodies differ dramatically from large lakes in physical, biogeochemical, and ecological characteristics (Cole and Caraco 2001; Cole et al. 2011; Read et al. 2012), and therefore play important roles in nutrient cycling, material processing, carbon sequestration (Hanson et al. 2007; Downing 2010; Read and Rose 2013; Holgerson and Raymond 2016; Biggs et al. 2017; Woolway et al. 2020).

Ecological subsidies are critical for lakes, but may also vary across landscapes and lake types (Gratton et al. 2008; Epanchin et al. 2010; Piovia-Scott et al. 2016; Schindler and Smits 2017; Vander Zanden and Vadeboncoeur 2020).. In lotic environments, there is strong

experimental and empirical evidence of arthropods dominating food sources to consumers, especially in headwater streams (Wipfli 1997; Nakano et al. 1999c, 1999a, 1999b). Empirical studies, again in north temperate regions, but focused on small lakes, estimated as much as 40% of zooplankton diet may be of terrestrial origin (Cole et al. 2011). In general, terrestrial organic carbon subsidies decrease with lake size, owing to less terrestrial organic matter being present farther from the shoreline (Vander Zanden and Gratton 2011). Similarly, fluxes of aquatic insects tend to be higher from lakes, owing to greater surface area relative to streams (Gratton and Zanden 2009; Bartrons et al. 2013). Cross-boundary subsidies are therefore important when studying lake food webs, but in many biomes these patterns are rarely examined.

In this study, we examine food webs from 36 high-elevation mountain lakes. We use field-collected stable isotope information to generate multidimensional food webs, and examine two competing hypotheses (the ecosystem size and productive space hypotheses). The specific goals of this study were to (1) Identify patterns in food chain length, food web structure and function, and community niche dynamics in mountain lakes across an ecosystem size and productivity gradient. And (2) Quantify fish consumer reliance on sources obtained from benthic and pelagic pathways along an ecosystem size gradient.

Methods

Research Area

This study is based on multiple field expeditions to comprehensively sample 36 unique mountain lake food webs in the Sierra Nevada, California, USA. Lakes were sampled once, each during the ice free season, May–October of 2014, and 2019–2021 (2014, n = 12; 2019, n = 7; 2020, n = 10; 2021, n = 8; **Table 3.1**). Lake volume was used as a surrogate for lake ecosystem

size, and was calculated as mean depth multiplied by surface area; where mean depth was not available, volume was calculated as a hyperbolic sinusoid ($0.43 \times \text{surface area} \times \text{maximum depth}$), similar to other studies (Post et al. 2000; Rypel 2023).

Field procedures

Representative sampling took place in littoral zones, vegetated aquatic habitat, and open limnetic waters to capture autochthonous and allochthonous inputs. Particulate organic matter (POM) and tissues from primary producers (e.g., aquatic plants, phytoplankton, periphyton), primary consumers (e.g., macroinvertebrates, zooplankton), and secondary-tertiary consumers (e.g., predatory invertebrates, fishes) were collected for stable nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotope food web analysis. Potential allochthonous resource subsidies were also collected (e.g., terrestrial insects and plants) along the riparian zone of the lakes. Identifying information of key food web taxa groups are in **Table S1**.

Lake bathymetry was approximated using GPS coordinates and a handheld depth finder while paddling back and forth across the lake; these data were used to calculate mean lake depth. Each lake received a point-measured vertical profile at its deepest point using a handheld YSI to measure temperature and dissolved oxygen at 1m-depth increments. Using these data, a sketch of the lake's thermocline was created to estimate the lake's epilimnion, metalimnion, and hypolimnion. We also used these data to calculate the temperature at which dissolved oxygen was 3 mg L^{-1} (TDO3). The depth of the thermocline was identified in the field using temperature and dissolved oxygen trends by lake depth to enable sampling from within the epilimnion and the top of the hypolimnion, where the deep chlorophyll maxima (DCM) is typically found in clear water lakes (Camacho 2006; Leach et al. 2018).

Fish – In the field, fish were collected via experimental gill nets (Knapp and Matthews 1998) with the goal of collecting 15 fish per species per lake, where possible. Fish were humanely euthanized, given a unique identification number, photographed, weighed, and measured. While historically fishless, fish consumers were ultimately present in all sampled lakes. Lakes in Sequoia & Kings Canyon National Park contained brook trout (*Salvelinus fontinalis*). Lakes in the Cottonwood Basin were historically stocked with golden trout (*Oncorhynchus mykiss aguabonita*) and rainbow trout (*Oncorhynchus mykiss*) yet now only have self-sustaining golden trout populations (Curtis 1934). Lakes within Caribou Wilderness contain rainbow trout (presumably Eagle Lake *Oncorhynchus mykiss aquilarum*), speckled dace (*Rhinichthys spp.*), tui chub (*Siphateles bicolor*), and brown bullhead catfish (*Ameiurus nebulosus*). Lakes within the Lakes Basin contain brook trout, rainbow trout, speckled dace, brown bullhead catfish, golden shiner (*Notemigonus crysoleucas*), Lahontan redband (*Richardsonius egregius*), and Sacramento sucker (*Catostomus occidentalis*). In all cases, no more than 1-3 fish species were present per lake. Only one study lake (Shotoverin) was stocked during a field season prior to sampling; food web sampling at this site took place at least one month after the stocking date so that their tissues would have time to assimilate their new lake diet (Heady and Moore 2013).

Zooplankton – Vertical zooplankton tows were performed in the lake epilimnion using a closed 63µm mesh plankton tow net with a choke band. Sampling occurred at dawn or dusk to account for zooplankton diel vertical migration patterns (Lampert 1989; Cooke 2019; Doubek et al. 2020; Conroy et al. 2020; Ríos-Escalante et al. 2020). When dried sample weight allowed, zooplankton isotope samples were separated into Copepods and Cladocera and analyzed separately.

Particulate Organic Matter (POM) – Samples were collected on pre-combusted (500°C for 4 hours) Whatman GF/F (0.7 µm nominal) glass microfiber filters after pre-filtering through a 63µm mesh to remove zooplankton. In the field, water was collected at two discrete depths (i.e., epilimnion and top of hypolimnion, where the chlorophyll-max typically develops) using a horizontal PVC Van Dorn water sampler from the deepest area of the lake.

Terrestrial and aquatic plants – The littoral zone was visually searched for all unique aquatic vegetation. Aquatic plants in the depths of the pelagic zone were collected using a D-Net or Van Dorn sampler. In the terrestrial zone, at least five dominant plant species around each lake were collected. For each plant sample, tissues were taken from the same part of the plant (e.g., only leaves, not stem or flower) and, if aquatic, rinsed using lake water in the field. Tissues with minimal damage, medium age (i.e., not too young or aged), and low insect presence were preferred.

Terrestrial and Aquatic Insects – Insects were collected using a combination of techniques (i.e., D-net, minnow net, terrestrial insect net, handpicking). Aquatic macroinvertebrates were searched for along the shoreline and in different littoral habitats. Terrestrial insects were searched for around the margin of the lake and water surface.

Other aquatic algae, diatoms, and sponges – epilithic algae, diatoms, and sponges in the lake littoral zone were collected by pinch or scrape sampling from rocks or other submerged substrates and plants.

Sample handling – All organismal and particulate samples were frozen in the field and stored on dry ice for transport back to the University of California, Davis. Samples were stored in a regular -18°C freezer for no more than one year, otherwise they were transferred to a -80°C

freezer for longer-term storage to prevent $\delta^{13}\text{C}$ signature decay (Sweeting et al. 2004; Wolf et al. 2016; Hogsden and McHugh 2017).

Lab procedures

Samples were cleaned and identified to the lowest possible taxonomic resolution (**Table S3.1**) before they were prepared for stable isotope analysis. Samples were dried in a drying oven at 60°C for at least 24 hours, finely ground, and a weighed portion corresponding to the sample type was packed into a tin capsule per guidelines issued by the University of California Davis Stable Isotope Facility. Samples were sent to the UC Davis Stable Isotope Facility for processing on a mass spectrometer.

Data analysis

Food chain length (i.e., maximum trophic position; **Figure 3.1**) was calculated as

$$\left(\lambda + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{base of food web}}) / 3.4 \right)$$

where λ = trophic position of organism used to estimate $\delta^{15}\text{N}_{\text{baseline}}$ (i.e., here, for zooplankton, = 2.8), $\delta^{15}\text{N}_{\text{consumer}}$ = the highest consumer group's mean $\delta^{15}\text{N}$ in a lake, and $\delta^{15}\text{N}_{\text{base of food web}}$ = mean $\delta^{15}\text{N}$ of zooplankton in a lake (Post et al. 2000). Mean concentration of chlorophyll-*a* ($\mu\text{g/L}$) was used as a proxy for productivity, similar to the way in which total phosphorus ($\mu\text{g/L}$) was used as a proxy for productivity in Post et al. (2000). These chlorophyll-*a* values were often taken from the top of the hypolimnion (presumed chlorophyll-max) of the lake. We note that chlorophyll-*a* can vary seasonally within these systems (Melack et al. 2020), thus all samples were taken during summer months. Six additional community niche metrics (Layman et al. 2007) were calculated to assess other aspects of food web complexity: trophic area (TA; **Figure**

3.2) measures trophic diversity and realized food web niche size, mean distance from centroid (CD) measures the degree of diet diversity and is particularly useful if outliers are present, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ range, respectively, vertical and horizontal heterogeneity in isotopic signals, and mean and standard deviation of nearest neighbor distance are metrics assessing trophic redundancy, evenness of trophic niche distribution, and niche packing.

The U.S. Geological Survey's StreamStats online program was used to acquire basin characteristics for each of the 36 unique lake sites. A correlation matrix was performed to assess relatedness of these variables to ecosystem size, chlorophyll-*a* concentration, food chain length, and the six isotope-based food web complexity metrics; none of the physical characteristics, such as percentage of area covered by forest, percent of area above 6000 ft, mean basin elevation, mean basin slope, and the ratio of watershed-area-to-surface-area, were correlated >60% and were thus not further explored in the analysis.

Random slope and random intercept linear mixed effect models were used to test relationships between each food web complexity variable of interest and ecosystem size. Using the `{lmerTEST}` R package (version 3.1-3) (Kuznetsova et al. 2017), the models used ecosystem size as the independent variable, food web complexity metrics as dependent variables, and region (i.e., Caribou Wilderness, Cottonwood Basin, Lakes Basin, Southern Sierra) as a random effect (**Figure 3.3; Table S3.2**). We used a parallel model to test the effect of productivity on food chain length (**Figure 3.1**). All independent and dependent variables in the linear mixed effect models were Log_{10} -transformed prior to analysis.

Stable isotope mixing models used the `{MixSIAR}` package (version 3.1.12) (Moore and Semmens 2008; Parnell et al. 2013; Stock and Semmens 2016; Stock et al. 2018) to calculate the proportion of source contribution to fish consumers in each food web. Fish consumers were

applied to the model as the “mix” data, and “source” data included submerged aquatic plants, emergent aquatic plants, submerged algae, particulate organic matter, aquatic insects, terrestrial insects, and zooplankton; these sources were simplified into six categories – “Aquatic Plant”, “Algae/Periphyton”, “Particulate Organic Matter”, “Aquatic Invertebrates”, “Terrestrial Invertebrates”, and “Zooplankton”. Miscellaneous food web sources (e.g., snakes, frogs, mushrooms) were excluded in this portion of the analysis, as were diatom samples scraped directly from rocks, terrestrial plants, and aquatic detritus; this was due to either small sample sizes, inconsistencies in the way they were obtained across the sites, or the limitation that a mixing model should not contain >6 sources (Stock et al. 2018). For this portion of the analysis, all lakes from 2014, Pear and Emerald 2019, and Trail, Shotoverin, and Betty 2020, were not included due to insufficient separation of model end members or ineffective mixing/source data. Trophic discrimination factor (TDF) mean and standard deviation were calculated as

$$TDF\ Mean = (Mean\ \delta^{13}C_{Mix}) - (Mean\ \delta^{13}C_{Source})$$

$$TDF\ SD = \sqrt{(SD\ \delta^{13}C_{Mix})^2 + (SD\ \delta^{13}C_{Source})^2}$$

consistent with the recommendations of the R package. The mixing model for each lake was performed separately. Isospace biplots, posterior density plots depicting diet proportion, process diagnostics, and summary statistics were examined prior to proceeding with the analysis. Mixing model isospace bi-plots confirmed fish consumers were appropriately within the six source polygons in most cases, and there was enough separation in either $\delta^{13}C$ and/or $\delta^{15}N$ to distinguish the six sources from one another. The 95.7% quantile from the scaled posterior density statistics was used to analyze fish consumer diet in relation to the six primary sources (**Figure 3.4**).

Finally, generalized additive mixed effect models (GAMMs) were performed on each food web source; models were structured so that the 95.7% credible interval for diet proportion was the dependent variable, ecosystem size was the independent variable, and region was a random effect (**Table S3.3**). Models used the restricted maximum likelihood (REML) approach and quasibinomial family distribution. With the "logit" link function. All continuous variables were Log_{10} -transformed prior to the analysis, with the exception of diet proportion. All cleaning and analytical code used R software (version 4.4.0) (R Core Team 2024).

Data & Code Availability

Data and code to produce the main analysis are available on GitHub (<https://github.com/caparisek>) and will be registered with a DOI upon publication.

Results

The 36 mountain lakes sampled in this study ranged 5,000–228,977 m² in surface area, 1–31.3 m in maximum depth, ~8,700–1,969,000 m³ in volume, 1,554–3,559 m in elevation (**Table 3.1**).

Out of a total of 1,817 stable isotope samples across 2014–2021, $\delta^{13}\text{C}$ ranged -39.72 – -2.44 (mean -25.24) and $\delta^{15}\text{N}$ ranged -11.73 – 10.74 (mean 2.06).

Food Chain Length

Food chain length varied considerably across lakes, ranging 0.84–3.13. For example, food chain length in Silver Lake was 2.75, but in a nearby lake, Snag, was as low as 1.66. Food chain length showed a positive trend with increasing ecosystem size ($p = 0.09$; **Figure 1A, Table S1**). Food chain length showed a decreasing trend as chlorophyll-*a* concentration, a proxy for productivity,

increased and there were significant regional differences ($p = 0.07$ and 0.0003 , respectively; **Figure 3.1, Table S3.2**).

Food Web Complexity

Six community niche food web metrics were examined to determine food web structure. Trends in food web trophic area (i.e., food web size; $p = 0.03$), centroid distance (i.e., diet diversity; $p = 0.004$), and $\delta^{13}\text{C}$ range (i.e., carbon source diversity; $p = 0.01$), increased significantly with lake ecosystem size, while the range in $\delta^{15}\text{N}$, mean nearest neighbor distance, and standard deviation of the nearest neighbor difference did not show significant change (**Figure 3.2-3.3; Table 3.2; Table S3.2**).

Consumer Diet Sourcing

Results from food web mixing models indicated proportion of fish consumer diets for any of the size sources did not change significantly along the ecosystem size gradient (**Figure 3.4, Table S3.3**). Fish consumer diets relied consistently, and in greatest proportion, on aquatic insects as a food source, and again these proportions were relatively consistent across lakes ($p = 0.3$). Fish consumers next greatly relied upon terrestrial insects as part of their diet, and while there was an increasing trend with ecosystem size, it was not significant ($p = 0.16$). Aquatic plants and particulate organic matter show decreasing but non-significant trends with ecosystem size ($p = 0.20$ and 0.21 , respectively). Periphyton contributions were also mostly stable across lakes ($p = 0.55$). Finally, zooplankton show a variable trend of value ($p = 0.25$). Aquatic plants and particulate organic matter showed significant differences in fish consumer diet source contributions by region ($p = 0.006$ and 0.04 , respectively), but none of the other sources did.

Discussion

This study used field data from 36 mountain lakes to critically assess two dominant hypotheses for food chain length – ecosystem size and the productive-space hypotheses. Additionally, we extended the use of food chain length to also include community-niche isotope metrics that aid in determining food web architecture and function and refined understanding of food web architecture and food chain length in the mountain lake ecosystem context. We also examined variation in fish consumer diet sourcing for six food resources along an increasing ecosystem size gradient. We found food chain length, and nearly all six community niche metrics (with the regional exception of $\delta^{15}\text{N}$ range), increased with ecosystem size. We found largely neutral or positive relationships for the six community metrics along an increasing chlorophyll-*a* concentration gradient (i.e., a proxy for productivity), and a decreasing trend with food chain length. Our results support context-dependency as an overarching explanation for varying outcomes along environmental gradients, food chain length, and food web complexity.

Food Chain Length

A long-standing goal in ecology is understanding whether ecosystem size, productivity, or other gradients play strong roles in determining food chain length and community assembly (Elton 1927; Briand and Cohen 1987; Hairston and Hairston 1993; Sterner et al. 1997; Post et al. 2000; Sabo et al. 2009). Food chain length influences critical ecosystem processes, such as energy flow and biomass distribution, community structure, and resilience (Schindler et al. 1997; Post 2002; Takimoto and Post 2013). Operationally, longer food chains suggest more nodes exist between primary producers and top consumers in the food web; thus species interactions are more complex. Conversely, shorter food chains suggest simpler interactions and potentially

higher energy efficiencies, because energy transfers between trophic levels are inefficient to a degree (Ward and McCann 2017). Using north temperate lakes, Post et al. (2000) provided compelling support that ecosystem size, not productivity, was the primary driver of food chain length. Yet others observe that food chain length can be more affected by resource availability, i.e., the productive space hypothesis (Kaunzinger and Morin 1998; Vander Zanden et al. 1999b; Wang et al. 2016), perhaps especially when resources are scarce (Post 2002). Recent work generally shows that these patterns are variable depending on the system of interest (Spencer and Warren 1996; Jake Vander Zanden and Fetzer 2007; Takimoto et al. 2008; McHugh et al. 2010; Young et al. 2013).

Our results show that neither lake volume nor multiple proxies of productivity appreciably drive food chain length in our mountain lake systems. These environments differ in some fundamental ways from others that have been studied. First, fish consumers in these lakes are non-native, and apparently feed at relatively low trophic positions (e.g., on aquatic invertebrates as indicated in our sourcing results). The fishes analyzed in the Post et al. 2000 were native species. Therefore, species introductions and invasions may interfere with natural patterns in food chain length (Woodward and Hildrew 2001; Byrnes et al. 2007; Detmer and Lewis Jr. 2019). Additionally, our study lacked food web data collected from very large lakes, and in doing so may have excluded large apex predators (e.g., trophic level 4) needed to generate long food chain length measures. Even in Post et al. 2000, the trend in maximum trophic position appears weaker when lake volumes are $\sim 10^8$ m³ or less. These differences point to a problem of pattern and scale that should be considered more closely in future work on this topic (Levin 1992; Rypel and David 2017; Chase et al. 2018). Ultimately, our initial findings suggest food chain length patterns in lakes are context-dependent, consistent with other recent research (Ward

and McCann 2017; Detmer and Lewis Jr. 2019). However other measures of food web complexity were related to lake volume.

Food Web Complexity

Food chain length is one measure of food web complexity, but there are many others. For instance, food web connectivity or “connectance webs” (May 1972) once dominated ecology (Warren 1990; Pimm et al. 1991; Martinez 1992; Dunne et al. 2002). Others emphasize quantitative food webs where carbon and energy flows are quantified (Benke and Wallace 1980, 1997; Winemiller et al. 2001; Layman et al. 2012), sometimes to show energy flow responses to disturbance or restoration actions (McHugh et al. 2010; Lu et al. 2016; James et al. 2020). While food chain length has been of long-standing interest to ecologists, newer food web complexity metrics based on stable isotope data (Layman et al. 2007) are increasingly used in research (Okuzaki et al. 2009; Schalk et al. 2017). This study expands the long-standing question of whether food chain length is determined by ecosystem size or productivity, by also examining the relationships of additional food web complexity metrics, and the ecosystem context in which these trends appear. The static nature of these metrics pose challenges, notably the assumption that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are relatively stable across space and time (Hoeinghaus and Zeug 2008). Nonetheless, an expanded toolbox of complexity metrics increases our ability to understand multidimensional changes in food webs. Thus while food chain length might respond clearly to one driver, other complexity metrics may show an opposite trend.

We observe that while food chain length and $\delta^{15}\text{N}$ range do not scale with ecosystem size, food web trophic diversity and occupied niche space of the food web (i.e., trophic area and mean distance from centroid metrics) do. These results therefore provide some support for

existing theory attempting to blend aspects of island biogeography with food web ecology (Holt 1996, 2009; Gravel et al. 2011). Results also show how one measure of food web complexity can support the ecosystem size or productive space hypotheses, while others may not. Lack of significant change in $\delta^{15}\text{N}$ suggests little vertical variation in food web and fewer trophic levels across lakes; other community metrics also did not show a trend. However, total niche area (i.e., occupied space of the food web) and centroid distance (i.e., diet diversity) did increase significantly with lake volume, suggesting lake food webs became more complex with increasing ecosystem size. Variation in $\delta^{13}\text{C}$ range suggests basal resources changed across this size gradient as well. Furthermore, even our food chain length measures, while not significant, approached significance ($p = 0.09$). Taken together, we interpret these results as showing that important changes in food webs are occurring over our ecosystem size gradient, thereby providing limited support for the ecosystem size hypothesis. However, the trends are weak overall, similar to other studies (Spencer and Warren 1996; Jake Vander Zanden and Fetzer 2007; McHugh et al. 2010; Young et al. 2013; Detmer and Lewis Jr. 2019), and certainly more variable than some (Post et al. 2000; Takimoto et al. 2008). Our multidimensional tests of food web complexity help reveal where these trends are strongest and weakest. These results in general comport with Ward and McCann (2017) who used theory to suggest context-dependency as a broad explanation for varying outcomes exploring environmental gradients and food chain length. Further, our tests of the multidimensional responses of food webs only deepens our understanding of lake ecology.

Defining ecosystem size is ostensibly a simple task, but ultimately subjective and difficult (Post et al. 2007). External landscape processes interact with and influence internal ecosystem dynamics, and many of these processes are highly scale-dependent (Nakano et al.

1999c; Post et al. 2007; Rypel 2021). This study, not unlike previous work (Post et al. 2000; Doi 2009; Baho et al. 2017), defines ecosystem size simply as the volume of a lake. Depending on the question however, ecosystem size could be estimated in multiple different ways, including by lake area, watershed area, watershed volume, habitat size (e.g., littoral and pelagic areas and/or volumes), and potentially other permutations. We discovered that, especially in lakes with larger volumes, external source inputs (e.g., terrestrial insects) appear to be important. Therefore, alternate ways of estimating ecosystem size could strengthen or weaken results presented in this study. Going forward, further research on different methods of defining ecosystem size, and scale dependence will be useful for advancing tests of the ecosystem size and the productive space hypotheses.

Consumer Diet Sourcing

Freshwater ecosystems are operationally and energetically coupled with their watersheds (Vannote et al. 1980; Schindler 2009). The ecological subsidy framework proposes that energetic resources generally flow from productive (i.e., donor) to less productive (i.e., recipient) systems, resulting in crucial increases in local productivity that considerably influences community structure, ecosystem stability, and food web dynamics (DeAngelis 1980; Vannote et al. 1980; Polis et al. 1997; Huxel and McCann 1998; Nakano and Murakami 2001). Lakes therefore can be dominated either by autochthonous or allochthonous resources, and the context with which one will outweigh the other is both important and variable (Rautio et al. 2011; Fenoglio et al. 2015; Neres-Lima et al. 2016).

Fish consumer diets were constantly dominated by aquatic insects, regardless of lake ecosystem size. Meanwhile, reliance on terrestrial insect subsidies increased along our lake

ecosystem size gradient, though not significantly, suggesting terrestrial subsidies may be of increased importance in mountain lakes with great volumes. This pattern contrasts with the prediction that larger waterways tend to be dominated by autochthonous production (Vannote et al. 1980), including even in large lakes, where terrestrial subsidies are often considered negligible (Quinlan et al. 2003; Doi 2009).

Diet sourcing of fish consumers appears to vary along the ecosystem size gradient, and though not significant still reveals some important patterns. The lack of a pattern with respect to ecosystem size or productivity is consistent with our finding that food chain length and complexity do not change appreciably along an ecosystem size gradient in these systems. In general, aquatic insects were by far the most common part of consumer diets, and terrestrial insects were clearly the second most important item. Even though they show little relationship with either of our study gradients, plants and periphyton do appear to be important prey for consumers in certain lakes, particularly Lower Sardine and Cottonwood 4 (43% and 44% reliance, respectively). Overall though, the production of plants and algae may be greatly limited by the short duration of the summer growing season (Pechlaner 1971) and low nutrient concentrations (Vadeboncoeur and Steinman 2002; Murphy et al. 2010). Shallow water bodies are known to be highly productive biogeochemical hotspots (Rabaey et al. 2024), therefore they are important to study further. However, it appears the basic consumer structure of our mountain lake food webs is relatively consistent at the lake-wide scale. Future analyses that quantify bathymetry of mountain lakes might assist in examining whether these same patterns remain consistent after standardizing for available area of the littoral and pelagic habitats of lakes.

Conclusion

In conclusion, we find weak support for either the ecosystem size or productive space hypotheses in mountain lake landscapes. While these hypotheses could have been rejected with more simple analyses of food chain length alone, the additional food web complexity variables strengthened our understanding of ecological patterns overall. Therefore, these variables provide a useful complement to food chain length during tests of food web centric hypotheses. In this study, we also provide some evidence that ecological patterns in one region may differ greatly from those observed in another. The state of the ecosystem size and productive space debate is unlikely to fully resolve quickly, as the focus of this debate has turned toward identifying what contexts these, and other, competing hypotheses influence food chain length. Scale-dependence, topography of lake ecosystems, and watershed ecology all have a strong influence on how we measure and understand ecosystem function (Sadro et al. 2012; Lapierre et al. 2018). Future work in alpine landscapes would likely benefit greatly from long-term study, as slow change in ecological communities and food web interactions often eludes our senses and may block deeper ecological understanding (Magnuson 1990; Turner et al. 2003; Sabo et al. 2009). Long-term data has been critical for advancing understanding of north-temperate lakes (Blanchfield et al. 2009; Rypel et al. 2016; Rohwer et al. 2023) and similar studies would benefit understanding and conservation of alpine lake landscapes. These ecosystems are clearly more poorly studied, operate in different ways, and need more intense research focus.

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Figures & Tables

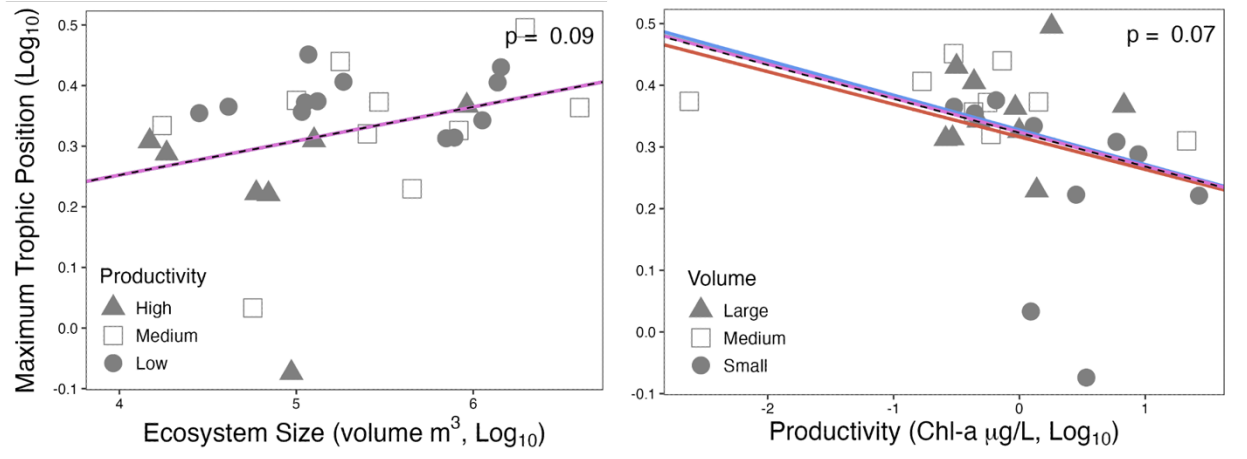


Figure 3.1

Food chain length as a function of ecosystem size and productivity. Lines denote regional random effect: Caribou Wilderness (coral), Cottonwood Basin (green), Lakes Basin (blue), and Southern Sierra (purple).

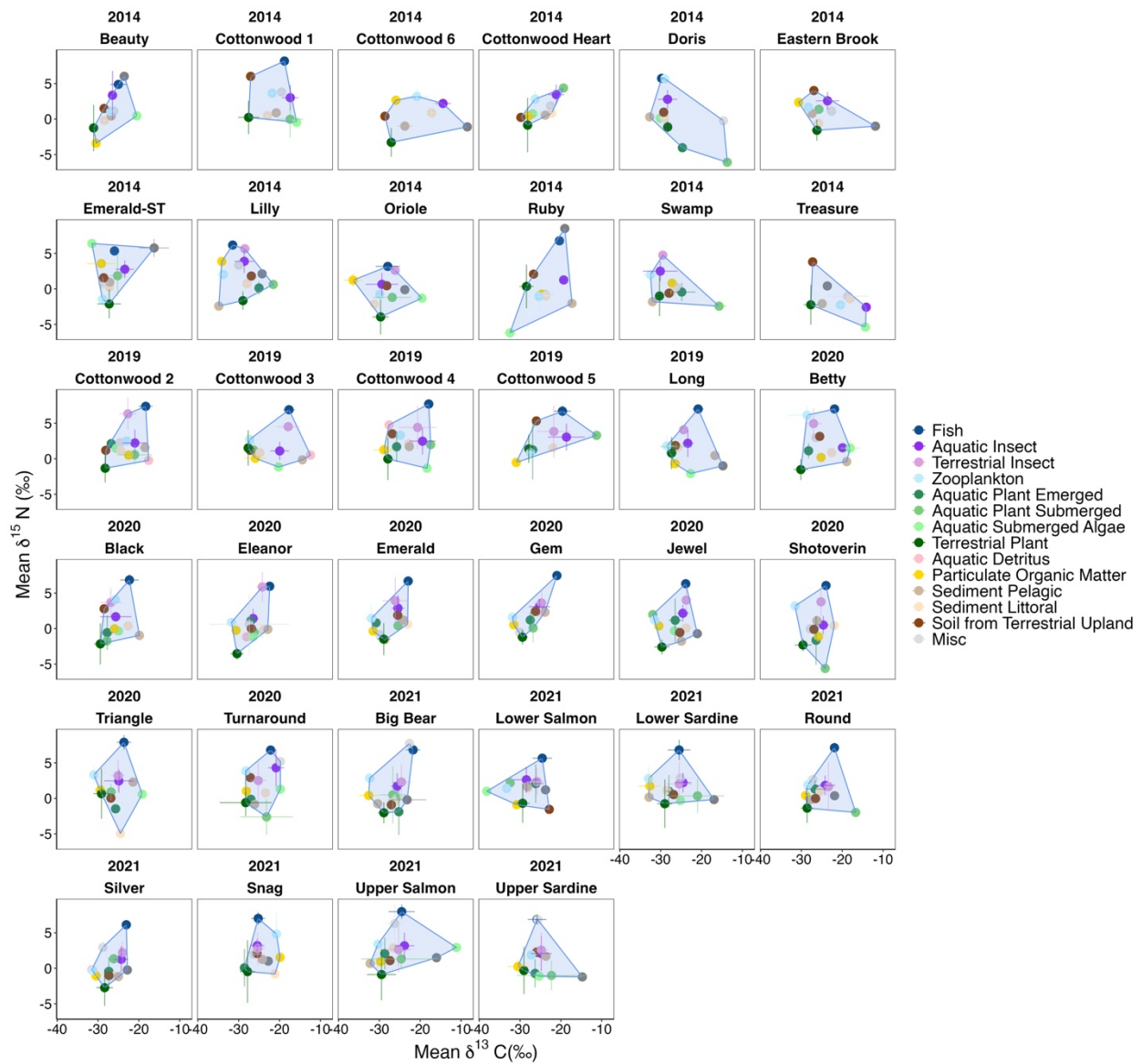


Figure 3.2

Stable isotope food web bi-plots of $\delta^{15}\text{N}$ values versus $\delta^{13}\text{C}$ values for different food web components. The convex hull (trophic area) of each food web is shaded in blue. Error bars represent the standard deviation.

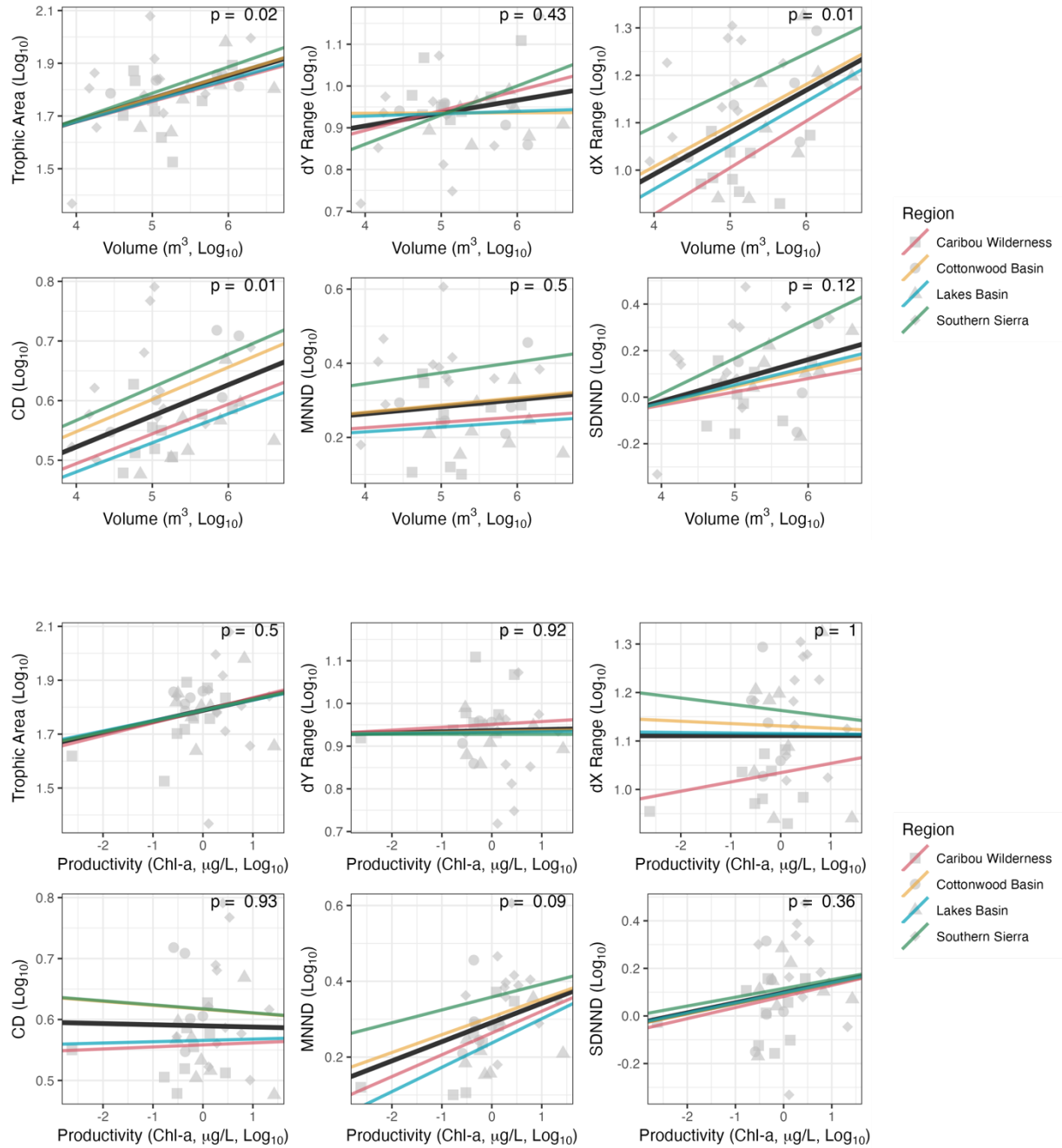


Figure 3.3

Mixed effect model results for six isotope-based food web complexity metrics as a function of ecosystem size (i.e., volume) and lake productivity (i.e., chlorophyll-*a* concentration).

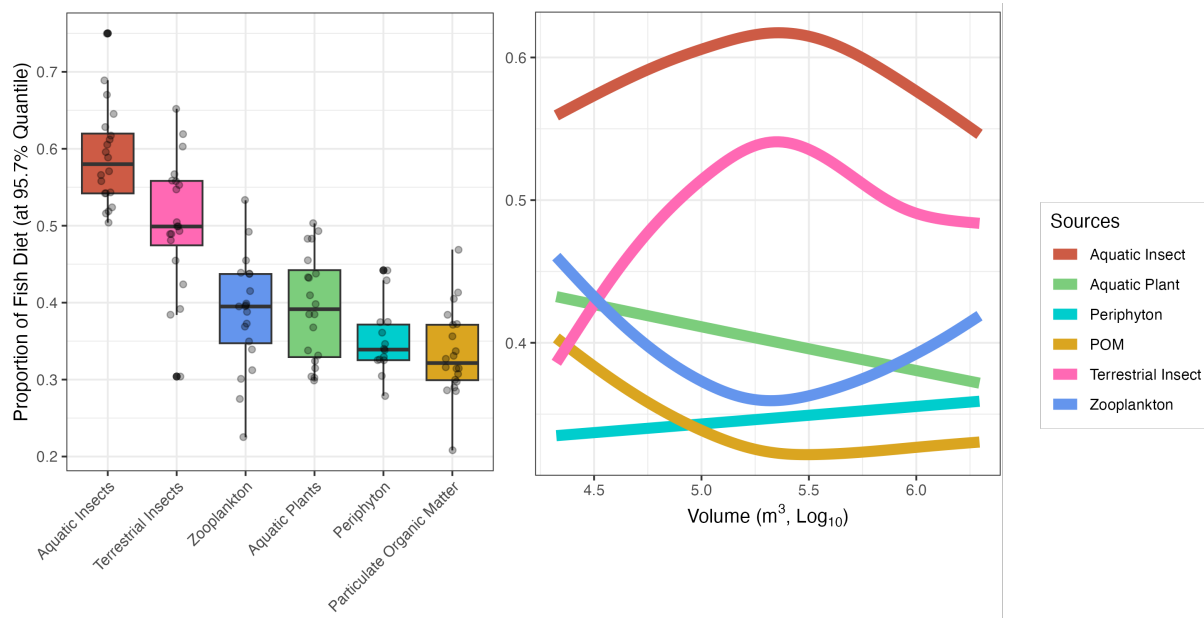


Figure 3.4

Proportion of fish consumer diet by source; one point represents one lake (Left). Generalized additive mixed effect model results for proportion of fish diet as a function of ecosystem size (Right).

Table 3.1

Characteristics of 36 mountain lakes and their sampled food webs.

Year	Lake	Latitude	Longitude	Surface Area (m ²)	Max Depth (m)	Elevation (m)	Volume (m ³)	Productivity (Mean chl- <i>a</i> , µg/L)
Southern Sierra								
2014	Cottonwood Heart	36.5	-118.2	20,402	1.0	3,389	8,773	1.3
2014	Oriole	36.5	-118.7	5,001	6.9	1,722	14,838	5.9
2014	Cottonwood 1	36.5	-118.2	33,761	1.2	3,362	17,421	1.3
2014	Beauty	38.9	-120.2	21,496	2.0	2,148	18,487	8.8
2014	Treasure	37.4	-118.8	24,878	7.3	3,407	78,092	1.9
2014	Doris	37.3	-119.0	25,658	8.5	2,088	93,780	3.4
2014	Cottonwood 6	36.5	-118.2	19,856	12.5	3,559	106,726	2.5
2014	Emerald-ST	36.6	-118.7	27,206	10.0	2,800	116,986	0.3
2014	Lilly	38.9	-120.1	31,843	9.2	1,996	125,971	21.3
2014	Eastern Brook	37.4	-118.7	44,039	7.4	3,154	140,132	2.8
2014	Swamp	38.0	-119.8	60,403	19.2	1,554	498,687	1.9
2014	Ruby	37.4	-118.8	146,187	31.3	3,397	1,967,531	1.8
Cottonwood Basin								
2019	Cottonwood 2	36.5	-118.2	24,528	2.0	3,368	21,094	0.4
2019	Long	36.5	-118.2	33,693	8.0	3,405	115,904	0.6
2019	Cottonwood 4	36.5	-118.2	123,161	14.0	3,419	741,429	0.3
2019	Cottonwood 3	36.5	-118.2	105,903	20.0	3,379	910,766	1.0
2019	Cottonwood 5	36.5	-118.2	140,087	19.0	3,423	1,144,511	0.4
2019	Emerald-SQ	36.6	-118.7	27,206	10.0	2,800	116,986	NA

2019	Pear-SQ	36.6	-118.7	73,163	25.0	2,906	786,502	NA
Caribou Wilderness								
2020	Trail	40.5	-121.2	38,267	2.1	1,996	34,555	NA
2020	Eleanor	40.5	-121.2	18,811	4.7	2,113	38,017	0.3
2020	Betty	40.5	-121.1	37,652	3.1	1,973	50,190	1.2
2020	Shotoverin	40.5	-121.1	40,730	2.9	1,995	50,790	2.8
2020	Jewel	40.5	-121.2	22,760	9.8	2,112	95,421	0.7
2020	Black	40.5	-121.2	45,626	5.4	2,158	106,336	0.4
2020	Emerald	40.5	-121.2	20,884	12.8	2,115	114,946	0.0
2020	Gem	40.5	-121.2	41,175	11.6	2,128	205,381	0.2
2020	Turnaround	40.5	-121.2	130,033	13.0	2,154	725,766	1.4
2020	Triangle	40.5	-121.2	183,206	14.9	2,150	1,173,801	0.5
Lakes Basin								
2021	Snag	39.7	-120.6	81,985	2.0	2,032	70,507	26.7
2021	Silver	39.7	-120.7	40,704	9.0	2,036	157,524	0.7
2021	Lower Salmon	39.7	-120.6	132,689	4.0	1,942	228,225	0.6
2021	Round	39.7	-120.7	61,302	14.0	2,050	369,038	1.4
2021	Big Bear	39.7	-120.7	105,449	21.0	1,976	952,204	0.3
2021	Upper Salmon	39.7	-120.7	165,344	15.0	1,984	1,066,469	6.8
2021	Lower Sardine	39.6	-120.6	160,815	20.0	1,762	1,383,009	0.3
2021	Upper Sardine	39.6	-120.6	228,977	20.0	1,828	1,969,202	0.9

Table 3.2

Food web complexity metrics for 36 mountain lake food webs. Table is sorted by Trophic Area.

Year	Lake	Food Chain Length (Max. Trophic Position)	Trophic Area (TA)	$\delta^{15}\text{N}$ Range	$\delta^{13}\text{C}$ Range	Centroid Distance (CD)	Mean Nearest Neighbor Distance (MNND)	Standard Deviation of Nearest Neighbor Distance (SDNND)
2014	Cottonwood Heart	No Fish	23.3	5.2	10.4	3.3	1.5	0.5
2020	Gem	2.5	33.5	8.7	10.9	3.0	1.3	1.4
2021	Silver	2.8	37.8	8.9	8.5	3.0	1.5	0.8
2020	Emerald	2.4	41.6	8.3	9.0	3.3	1.3	1.0
2021	Snag	1.7	45.2	7.8	8.7	3.0	1.6	1.2
2020	Eleanor	2.3	50.4	9.5	9.4	3.1	1.3	0.7
2019	Cottonwood 2	2.3	50.7	8.7	9.9	3.4	1.9	0.9
2014	Eastern Brook	No Fish	51.4	5.6	18.8	3.9	2.7	2.9
2014	Beauty	1.9	51.4	9.4	10.6	3.4	1.9	1.6
2020	Black	2.3	52.2	9.0	9.6	3.3	1.8	1.0
2020	Jewel	2.4	57.4	8.9	10.9	3.4	1.5	0.8
2021	Lower Salmon	2.1	58.0	7.2	15.3	3.5	1.6	1.4
2021	Big Bear	2.1	59.3	8.9	10.9	3.5	1.7	0.7
2014	Treasure	No Fish	60.1	9.2	13.6	4.8	2.5	1.3

2014	Swamp	No Fish	60.7	7.2	16.8	3.7	2.2	2.4
2020	Turnaround	1.7	60.8	9.6	9.0	3.8	2.1	0.7
2021	Round	2.4	63.6	9.1	12.3	3.3	2.0	1.7
2019	Cottonwood 3	2.1	63.8	8.1	13.3	4.5	2.0	1.4
2014	Oriole	2.0	63.9	7.1	16.8	3.8	2.5	1.5
2019	Cottonwood 5	2.5	64.8	7.2	19.7	5.1	2.9	2.1
2021	Upper Sardine	2.3	67.6	8.1	15.8	3.4	1.8	1.8
2020	Shotoverin	1.7	68.3	11.7	9.6	3.2	2.3	1.6
2014	Emerald-ST	2.8	69.2	8.5	15.2	3.7	2.4	1.9
2014	Lilly	2.0	69.3	8.6	13.3	4.2	2.2	0.9
2019	Long	2.4	69.3	9.1	13.7	4.0	1.6	1.1
2019	Cottonwood 4	2.1	70.3	9.0	11.5	4.1	2.0	1.5
2021	Lower Sardine	2.7	71.0	7.6	16.0	4.0	1.8	1.3
2014	Cottonwood 1	2.2	73.0	8.6	11.7	4.2	2.9	1.5
2020	Betty	1.1	74.4	8.5	12.1	4.2	2.4	1.1
2020	Triangle	2.2	78.1	12.8	11.9	3.9	1.9	1.4
2014	Cottonwood 6	No Fish	82.7	6.5	20.2	6.2	4.0	1.2
2021	Upper Salmon	2.3	95.5	8.9	21.1	4.6	2.3	1.3
2014	Doris	0.8	97.9	11.8	19.0	5.2	2.9	3.0
2014	Ruby	3.1	99.0	14.7	15.2	4.9	2.4	2.2

Supplement

Table S3.1

Order, family, and genus identities for key taxa collected and identified from the lake food webs.

Year	Lake	Sample Type	Order	Family	Genus
2014	Beauty	Aquatic Insect	Diptera	Chironomidae	NA
2014	Beauty	Aquatic Insect	Hemiptera	Gerridae	NA
2014	Beauty	Aquatic Insect	Megaloptera	Sialidae	NA
2014	Beauty	Aquatic Insect	NA	NA	NA
2014	Beauty	Aquatic Insect	Odonata	Aeshnidae	NA
2014	Beauty	Aquatic Insect	Odonata	Libellulidae	NA
2014	Beauty	Aquatic Submerged Algae	NA	NA	NA
2014	Beauty	Fish	NA	NA	NA
2014	Beauty	Misc	Veneroida	Pisidiidae	NA
2014	Beauty	Terrestrial Plant	NA	NA	NA
2014	Cottonwood 1	Aquatic Insect	Diplostraca	Chydoridae	NA
2014	Cottonwood 1	Aquatic Insect	Diptera	Chironomidae	NA
2014	Cottonwood 1	Aquatic Insect	Ephemeroptera	Baetidae	NA
2014	Cottonwood 1	Aquatic Insect	Hemiptera	Corixidae	NA
2014	Cottonwood 1	Aquatic Insect	NA	NA	NA
2014	Cottonwood 1	Aquatic Insect	Odonata	Coenagrionidae	NA
2014	Cottonwood 1	Aquatic Plant Submerged	NA	NA	NA
2014	Cottonwood 1	Aquatic Submerged Algae	NA	NA	NA
2014	Cottonwood 1	Fish	NA	NA	NA

2014	Cottonwood 1	Misc	Veneroida	Pisidiidae	NA
2014	Cottonwood 1	Terrestrial Plant	NA	NA	NA
2014	Cottonwood 6	Aquatic Insect	Coleoptera	Dytiscidae	NA
2014	Cottonwood 6	Aquatic Insect	Diptera	Chironomidae	NA
2014	Cottonwood 6	Aquatic Insect	Hemiptera	Corixidae	NA
2014	Cottonwood 6	Aquatic Insect	Trichoptera	Limnephilidae	NA
2014	Cottonwood 6	Terrestrial Plant	NA	NA	NA
2014	Cottonwood Heart	Aquatic Insect	Coleoptera	Dytiscidae	NA
2014	Cottonwood Heart	Aquatic Insect	Diplostraca	Chydoridae	NA
2014	Cottonwood Heart	Aquatic Insect	Diptera	Chironomidae	NA
2014	Cottonwood Heart	Aquatic Insect	Ephemeroptera	Baetidae	NA
2014	Cottonwood Heart	Aquatic Insect	Hemiptera	Corixidae	NA
2014	Cottonwood Heart	Aquatic Insect	Hemiptera	Notonectidae	NA
2014	Cottonwood Heart	Aquatic Insect	Megaloptera	Sialidae	NA
2014	Cottonwood Heart	Aquatic Plant Submerged	NA	NA	NA
2014	Cottonwood Heart	Aquatic Submerged Algae	NA	NA	NA
2014	Cottonwood Heart	Misc	Veneroida	Pisidiidae	NA
2014	Cottonwood Heart	Terrestrial Plant	NA	NA	NA
2014	Doris	Aquatic Insect	Amphipoda	Hyalellidae	NA
2014	Doris	Aquatic Insect	Ephemeroptera	Baetidae	NA
2014	Doris	Aquatic Insect	Odonata	Coenagrionidae	NA
2014	Doris	Aquatic Insect	Odonata	Libellulidae	NA
2014	Doris	Aquatic Plant Emerged	NA	NA	NA
2014	Doris	Aquatic Plant Submerged	NA	NA	NA
2014	Doris	Aquatic Submerged Algae	NA	NA	NA
2014	Doris	Fish	NA	NA	NA

2014	Doris	Misc	NA	NA	NA
2014	Doris	Terrestrial Plant	NA	NA	NA
2014	Eastern Brook	Aquatic Insect	Amphipoda	Hyalellidae	NA
2014	Eastern Brook	Aquatic Insect	Coleoptera	Gyrinidae	NA
2014	Eastern Brook	Aquatic Insect	Diptera	Chironomidae	NA
2014	Eastern Brook	Aquatic Insect	Ephemeroptera	Baetidae	NA
2014	Eastern Brook	Aquatic Insect	Hemiptera	Corixidae	NA
2014	Eastern Brook	Aquatic Insect	Hemiptera	Gerridae	NA
2014	Eastern Brook	Aquatic Insect	Hemiptera	Notonectidae	NA
2014	Eastern Brook	Aquatic Insect	Megaloptera	Sialidae	NA
2014	Eastern Brook	Aquatic Insect	Odonata	Aeshnidae	NA
2014	Eastern Brook	Aquatic Insect	Odonata	Coenagrionidae	NA
2014	Eastern Brook	Aquatic Plant Submerged	NA	NA	NA
2014	Eastern Brook	Misc	Veneroida	Pisidiidae	NA
2014	Eastern Brook	Terrestrial Plant	NA	NA	NA
2014	Emerald-ST	Aquatic Insect	Diptera	Chironomidae	NA
2014	Emerald-ST	Aquatic Insect	Megaloptera	Sialidae	NA
2014	Emerald-ST	Aquatic Insect	NA	NA	NA
2014	Emerald-ST	Aquatic Insect	Odonata	Aeshnidae	NA
2014	Emerald-ST	Aquatic Insect	Odonata	Coenagrionidae	NA
2014	Emerald-ST	Aquatic Plant Submerged	NA	NA	NA
2014	Emerald-ST	Aquatic Submerged Algae	NA	NA	NA
2014	Emerald-ST	Fish	NA	NA	NA
2014	Emerald-ST	Misc	NA	NA	NA
2014	Emerald-ST	Misc	Veneroida	Pisidiidae	NA
2014	Emerald-ST	Terrestrial Plant	NA	NA	NA

2014	Lilly	Aquatic Insect	Decapoda	NA	NA
2014	Lilly	Aquatic Insect	Ephemeroptera	Baetidae	NA
2014	Lilly	Aquatic Insect	Hemiptera	Corixidae	NA
2014	Lilly	Aquatic Insect	Hemiptera	Notonectidae	NA
2014	Lilly	Aquatic Insect	NA	NA	NA
2014	Lilly	Aquatic Insect	Odonata	Aeshnidae	NA
2014	Lilly	Aquatic Insect	Odonata	Coenagrionidae	NA
2014	Lilly	Aquatic Insect	Odonata	Libellulidae	NA
2014	Lilly	Aquatic Plant Emerged	NA	NA	NA
2014	Lilly	Aquatic Plant Submerged	NA	NA	NA
2014	Lilly	Fish	NA	NA	NA
2014	Lilly	Misc	Veneroida	Pisidiidae	NA
2014	Lilly	Terrestrial Insect	NA	NA	NA
2014	Lilly	Terrestrial Plant	NA	NA	NA
2014	Oriole	Aquatic Insect	Ephemeroptera	Baetidae	NA
2014	Oriole	Aquatic Insect	Hemiptera	Gerridae	NA
2014	Oriole	Aquatic Insect	Odonata	Coenagrionidae	NA
2014	Oriole	Aquatic Plant Submerged	NA	NA	NA
2014	Oriole	Aquatic Submerged Algae	NA	NA	NA
2014	Oriole	Fish	NA	NA	NA
2014	Oriole	Terrestrial Insect	NA	NA	NA
2014	Oriole	Terrestrial Plant	NA	NA	NA
2014	Ruby	Aquatic Insect	Diptera	Chironomidae	NA
2014	Ruby	Aquatic Insect	Megaloptera	Sialidae	NA
2014	Ruby	Aquatic Submerged Algae	NA	NA	NA
2014	Ruby	Fish	NA	NA	NA

2014	Ruby	Misc	NA	NA	NA
2014	Ruby	Misc	Veneroida	Pisidiidae	NA
2014	Ruby	Terrestrial Plant	NA	NA	NA
2014	Swamp	Aquatic Insect	Amphipoda	Hyaellidae	NA
2014	Swamp	Aquatic Insect	Coleoptera	Dytiscidae	NA
2014	Swamp	Aquatic Insect	Coleoptera	Hydrophilidae	NA
2014	Swamp	Aquatic Insect	Decapoda	NA	NA
2014	Swamp	Aquatic Insect	Diptera	Chironomidae	NA
2014	Swamp	Aquatic Insect	Ephemeroptera	Baetidae	NA
2014	Swamp	Aquatic Insect	Hemiptera	Corixidae	NA
2014	Swamp	Aquatic Insect	Hemiptera	Gerridae	NA
2014	Swamp	Aquatic Insect	Hemiptera	Notonectidae	NA
2014	Swamp	Aquatic Insect	Megaloptera	Sialidae	NA
2014	Swamp	Aquatic Insect	Odonata	Aeshnidae	NA
2014	Swamp	Aquatic Insect	Odonata	Coenagrionidae	NA
2014	Swamp	Aquatic Insect	Odonata	Libellulidae	NA
2014	Swamp	Aquatic Plant Emerged	NA	NA	NA
2014	Swamp	Aquatic Plant Submerged	NA	NA	NA
2014	Swamp	Misc	Basommatophora	Lymnaeidae	NA
2014	Swamp	Misc	NA	NA	NA
2014	Swamp	Terrestrial Insect	NA	NA	NA
2014	Swamp	Terrestrial Plant	NA	NA	NA
2014	Treasure	Aquatic Insect	Diptera	Chironomidae	NA
2014	Treasure	Aquatic Submerged Algae	NA	NA	NA
2014	Treasure	Misc	NA	NA	NA
2014	Treasure	Misc	Veneroida	Pisidiidae	NA

2014	Treasure	Terrestrial Plant	NA	NA	NA
2019	Cottonwood 2	Aquatic Insect	Diptera	NA	NA
2019	Cottonwood 2	Aquatic Insect	Hygrophila	Planorbidae	Gyraulus
2019	Cottonwood 2	Aquatic Insect	Megaloptera	Sialidae	Sialis californica
2019	Cottonwood 2	Aquatic Insect	Rhynchobdellida	Glossiphoniidae	Helobdella
2019	Cottonwood 2	Aquatic Insect	Trichoptera	Limnephilidae	NA
2019	Cottonwood 2	Aquatic Insect	Trichoptera	Odontoceridae	NA
2019	Cottonwood 2	Aquatic Plant Emerged	Poales	NA	NA
2019	Cottonwood 2	Aquatic Plant Submerged	Alismatales	Potamogetonaceae	Potamogeton
2019	Cottonwood 2	Aquatic Plant Submerged	Charales	Characeae	NA
2019	Cottonwood 2	Aquatic Plant Submerged	Isoetales	Isoetaceae	Isoetes
2019	Cottonwood 2	Aquatic Plant Submerged	Phylum Bryophyta	NA	NA
2019	Cottonwood 2	Aquatic Submerged Algae	NA	NA	NA
2019	Cottonwood 2	Fish	Salmoniformes	Salmonidae	Oncorhynchus aguabonita
2019	Cottonwood 2	Misc	Class Agaricomycetes	NA	NA
2019	Cottonwood 2	Terrestrial Insect	Diptera	NA	NA
2019	Cottonwood 2	Terrestrial Insect	Hymenoptera	Formicidae	Formica
2019	Cottonwood 2	Terrestrial Insect	Trichoptera	Limnephilidae	Hesperophylax
2019	Cottonwood 2	Terrestrial Plant	Asterales	Asteraceae	NA
2019	Cottonwood 2	Terrestrial Plant	Ericales	Primulaceae	Primula
2019	Cottonwood 2	Terrestrial Plant	Malpighiales	Salicaceae	Salix
2019	Cottonwood 2	Terrestrial Plant	Pinales	Pinaceae	Pinus
2019	Cottonwood 3	Aquatic Insect	Coleoptera	Dytiscidae	Leconectes
2019	Cottonwood 3	Aquatic Insect	Diptera	Chironomidae	NA
2019	Cottonwood 3	Aquatic Insect	Diptera	Simuliidae	Parasimulium

2019	Cottonwood 3	Aquatic Insect	Trichoptera	Limnephilidae	Dicosmoecus
2019	Cottonwood 3	Aquatic Insect	Trichoptera	Limnephilidae	Ecclisomyia
2019	Cottonwood 3	Aquatic Plant Submerged	Phylum Bryophyta	NA	NA
2019	Cottonwood 3	Aquatic Plant Submerged	Poales	NA	NA
2019	Cottonwood 3	Aquatic Submerged Algae	NA	NA	NA
2019	Cottonwood 3	Fish	Salmoniformes	Salmonidae	Oncorhynchus aguabonita
2019	Cottonwood 3	Terrestrial Insect	Megaloptera	Sialidae	Sialis californica
2019	Cottonwood 3	Terrestrial Insect	Odonata	Coenagrionidae	Enallagma
2019	Cottonwood 3	Terrestrial Plant	Malpighiales	Salicaceae	Salix
2019	Cottonwood 3	Terrestrial Plant	Pinales	Pinaceae	Pinus contorta var. murrayana
2019	Cottonwood 3	Terrestrial Plant	Poales	Cyperaceae	Carex
2019	Cottonwood 4	Aquatic Insect	Coleoptera	Dytiscidae	Hygrotus
2019	Cottonwood 4	Aquatic Insect	Coleoptera	Dytiscidae	Leconectes striatellus
2019	Cottonwood 4	Aquatic Insect	Diptera	Chironomidae	Chironomus
2019	Cottonwood 4	Aquatic Insect	Diptera	Chironomidae	NA
2019	Cottonwood 4	Aquatic Insect	Diptera	Chironomidae	Tanypodinae
2019	Cottonwood 4	Aquatic Insect	Diptera	Muscidae	NA
2019	Cottonwood 4	Aquatic Insect	Diptera	Simuliidae	Parasimulium
2019	Cottonwood 4	Aquatic Insect	Megaloptera	Sialidae	Sialis californica
2019	Cottonwood 4	Aquatic Insect	Trichoptera	Limnephilidae	Ecclisomyia
2019	Cottonwood 4	Aquatic Insect	Trichoptera	Limnephilidae	Lenarchus
2019	Cottonwood 4	Aquatic Insect	Trombidiformes, Infraorder Hydrachnidia	NA	NA

2019	Cottonwood 4	Aquatic Plant Emerged	Phylum Bryophyta	NA	NA
2019	Cottonwood 4	Aquatic Plant Emerged	Poales	Cyperaceae	Carex
2019	Cottonwood 4	Aquatic Plant Submerged	Isoetales	Isoetaceae	Isoetes
2019	Cottonwood 4	Aquatic Submerged Algae	NA	NA	NA
2019	Cottonwood 4	Fish	Salmoniformes	Salmonidae	Oncorhynchus aguabonita
2019	Cottonwood 4	Terrestrial Insect	NA	NA	NA
2019	Cottonwood 4	Terrestrial Insect	Hymenoptera	Formicidae	Complex Formica fusca
2019	Cottonwood 4	Terrestrial Plant	NA	NA	NA
2019	Cottonwood 4	Terrestrial Plant	Fabales	Fabaceae	Lupinus
2019	Cottonwood 4	Terrestrial Plant	Malpighiales	Salicaceae	Salix
2019	Cottonwood 4	Terrestrial Plant	NA	NA	NA
2019	Cottonwood 4	Terrestrial Plant	Poales	NA	NA
2019	Cottonwood 4	Terrestrial Plant	Rosales	Rosaceae	Ivesia
2019	Cottonwood 5	Aquatic Insect	Coleoptera	Dytiscidae	Hygrotus
2019	Cottonwood 5	Aquatic Insect	Coleoptera	Dytiscidae	NA
2019	Cottonwood 5	Aquatic Insect	Diptera	Chironomidae	NA
2019	Cottonwood 5	Aquatic Insect	Diptera	Muscidae	NA
2019	Cottonwood 5	Aquatic Insect	Megaloptera	Sialidae	Sialis californica
2019	Cottonwood 5	Aquatic Insect	Trichoptera	Limnephilidae	Lenarchus
2019	Cottonwood 5	Aquatic Insect	Trombidiformes	Lebertiidae	Lebertia
2019	Cottonwood 5	Aquatic Plant Emerged	Phylum Bryophyta	NA	NA
2019	Cottonwood 5	Aquatic Plant Emerged	Poales	Poaceae	Phleum
2019	Cottonwood 5	Aquatic Plant Submerged	NA	NA	NA
2019	Cottonwood 5	Fish	Salmoniformes	Salmonidae	Oncorhynchus aguabonita

2019	Cottonwood 5	Terrestrial Insect	NA	NA	NA
2019	Cottonwood 5	Terrestrial Insect	Diptera	Scathophagidae	NA
2019	Cottonwood 5	Terrestrial Insect	Hemiptera	Cicadellidae	NA
2019	Cottonwood 5	Terrestrial Insect	Hymenoptera	Formicidae	Formica
2019	Cottonwood 5	Terrestrial Insect	Hymenoptera	Formicidae, Subfamily Formicinae	NA
2019	Cottonwood 5	Terrestrial Plant	Ericales	Primulaceae	Primula
2019	Cottonwood 5	Terrestrial Plant	Malpighiales	Salicaceae	Salix
2019	Cottonwood 5	Terrestrial Plant	Poales	NA	NA
2019	Cottonwood 5	Terrestrial Plant	Saxifragales	Crassulaceae	Rhodiola integrifolia
2019	Long	Aquatic Insect	Coleoptera	Dytiscidae	Hygrotus
2019	Long	Aquatic Insect	Coleoptera	Dytiscidae	Leconectes striatellus
2019	Long	Aquatic Insect	Coleoptera	Dytiscidae	NA
2019	Long	Aquatic Insect	Diptera	Chironomidae	NA
2019	Long	Aquatic Insect	Hemiptera	Corixidae	NA
2019	Long	Aquatic Insect	Megaloptera	Sialidae	Sialis californica
2019	Long	Aquatic Insect	Rhynchobdellida	Glossiphoniidae	Helobdella
2019	Long	Aquatic Insect	Subclass Oligochaeta	NA	NA
2019	Long	Aquatic Insect	Trichoptera	Calamoceratidae	Heteroplectron californicum
2019	Long	Aquatic Insect	Trichoptera	Limnephilidae	Ecclisomyia
2019	Long	Aquatic Insect	Trichoptera	Limnephilidae	Lenarchus
2019	Long	Aquatic Insect	Trichoptera	NA	NA
2019	Long	Aquatic Plant Emerged	Phylum Bryophyta	NA	NA
2019	Long	Aquatic Plant Emerged	Poales	Cyperaceae	Carex
2019	Long	Aquatic Plant Submerged	NA	NA	NA

2019	Long	Aquatic Plant Submerged	Spongillida	Spongillidae	NA
2019	Long	Aquatic Submerged Algae	NA	NA	NA
2019	Long	Fish	Salmoniformes	Salmonidae	Oncorhynchus aguabonita
2019	Long	Terrestrial Insect	Coleoptera	Amphizoidae	Amphizoa
2019	Long	Terrestrial Insect	Hymenoptera	Formicidae	Complex Formica fusca
2019	Long	Terrestrial Plant	Ericales	Ericaceae	Phyllodoce
2019	Long	Terrestrial Plant	Liliales	Veratrum	Veratrum californicum
2019	Long	Terrestrial Plant	Malpighiales	Salicaceae	Salix
2019	Long	Terrestrial Plant	Pinales	Pinus	Pinus contorta var. murrayana
2019	Long	Terrestrial Plant	Poales	Cyperaceae	Carex
2020	Betty	Aquatic Insect	Diptera	Chironomidae	NA
2020	Betty	Aquatic Plant Emerged	Alismatales	Alismataceae	Sagittaria cuneata
2020	Betty	Aquatic Plant Emerged	Phylum Bryophyta	NA	NA
2020	Betty	Aquatic Plant Emerged	Poales	NA	NA
2020	Betty	Aquatic Plant Emerged	Poales	Cyperaceae	Carex
2020	Betty	Aquatic Plant Emerged	Poales	Sparganium	Sparganium angustifolium
2020	Betty	Aquatic Submerged Algae	NA	NA	NA
2020	Betty	Fish	Salmoniformes	Salmonidae	Oncorhynchus mykiss
2020	Betty	Misc	Anura	Hylidae	Pseudacris regilla
2020	Betty	Terrestrial Insect	NA	NA	NA
2020	Betty	Terrestrial Insect	Coleoptera	Coccinellidae	Chilocorus
2020	Betty	Terrestrial Insect	Hymenoptera	Formicidae	Camponotus modoc

2020	Betty	Terrestrial Insect	Hymenoptera	Formicidae, Subfamily Formicinae	NA
2020	Betty	Terrestrial Plant	Dipsacales	Caprifoliaceae	Symphoricarpo s
2020	Betty	Terrestrial Plant	Pinales	Pinaceae	Abies magnifica
2020	Betty	Terrestrial Plant	Pinales	Pinaceae	Pinus
2020	Betty	Terrestrial Plant	Poales	Poaceae	NA
2020	Betty	Terrestrial Plant	Rosales	Rosaceae	Spiraea
2020	Black	Aquatic Insect	Coleoptera	Dytiscidae	Coptotomus longulus ssp. longulus
2020	Black	Aquatic Insect	Coleoptera	Gyrinidae	NA
2020	Black	Aquatic Insect	Odonata Anisoptera	Corduliidae	NA
2020	Black	Aquatic Insect	Trichoptera	Limnephilidae	NA
2020	Black	Aquatic Plant Emerged	NA	NA	NA
2020	Black	Aquatic Plant Emerged	Phylum Bryophyta	NA	NA
2020	Black	Aquatic Plant Submerged	Poales	Typhaceae	Sparganium
2020	Black	Aquatic Submerged Algae	NA	NA	NA
2020	Black	Fish	Cypriniformes	Leuciscidae	Rhinichthys osculus
2020	Black	Fish	Cypriniformes	Leuciscidae	Siphateles bicolor
2020	Black	Fish	Salmoniformes	Salmonidae	Oncorhynchus mykiss
2020	Black	Terrestrial Insect	NA	NA	NA
2020	Black	Terrestrial Insect	Araneae	Tetragnathidae	NA- skipped
2020	Black	Terrestrial Insect	Diptera	Sarcophagidae	NA- skipped
2020	Black	Terrestrial Insect	Hymenoptera	Apidae	Anthophora urbana

2020	Black	Terrestrial Insect	Hymenoptera	Formicidae	Camponotus modoc
2020	Black	Terrestrial Insect	Hymenoptera	Sphecidae	NA- skipped
2020	Black	Terrestrial Insect	Hymenoptera	Tenthredinidae	NA- skipped
2020	Black	Terrestrial Insect	Hymenoptera	Vespidae	Ancistrocerus
2020	Black	Terrestrial Insect	Hymenoptera	Vespidae	Vespula atropilosa
2020	Black	Terrestrial Insect	Lepidoptera	NA	NA
2020	Black	Terrestrial Insect	Odonata	Aeshnidae	Aeshna
2020	Black	Terrestrial Plant	Ericales	Ericaceae	Vaccinium
2020	Black	Terrestrial Plant	Lamiales	Phrymaceae	Erythranthe
2020	Black	Terrestrial Plant	Pinales	Pinaceae	Pinus
2020	Black	Terrestrial Plant	Poales	NA	NA
2020	Black	Terrestrial Plant	Poales	NA	NA
2020	Black	Terrestrial Plant	Rosales	Rosaceae	Spiraea
2020	Eleanor	Aquatic Insect	Amphipoda	Hyaellidae	Hyaella
2020	Eleanor	Aquatic Insect	Coleoptera	Dytiscidae	NA
2020	Eleanor	Aquatic Insect	Coleoptera	Hydrophilidae	Tropisternus lateralis
2020	Eleanor	Aquatic Insect	Diptera	Chironomidae	NA
2020	Eleanor	Aquatic Insect	Hemiptera	Gerridae	Aquarius remigis
2020	Eleanor	Aquatic Insect	Hemiptera	Notonectidae	NA
2020	Eleanor	Aquatic Insect	Odonata Anisoptera	Aeshnidae	Aeshna
2020	Eleanor	Aquatic Insect	Odonata Anisoptera	Aeshnidae	NA
2020	Eleanor	Aquatic Insect	Odonata Anisoptera	Corduliidae	Cordulia shurtleffii
2020	Eleanor	Aquatic Insect	Odonata Zygoptera	Coenagrionidae	Ischnura
2020	Eleanor	Aquatic Insect	Sarcoptiformes	NA	NA

2020	Eleanor	Aquatic Insect	Subclass Oligochaeta	NA	NA
2020	Eleanor	Aquatic Insect	Trichoptera	Limnephilidae	Limnephilus externus
2020	Eleanor	Aquatic Plant Emerged	Phylum Bryophyta	NA	NA
2020	Eleanor	Aquatic Plant Emerged	Poales	Cyperaceae	Carex
2020	Eleanor	Aquatic Plant Submerged	Alismatales	Alismataceae	Sagittaria
2020	Eleanor	Aquatic Plant Submerged	Phylum Bryophyta	NA	NA
2020	Eleanor	Aquatic Plant Submerged	Poales	Typhaceae	Sparganium
2020	Eleanor	Aquatic Submerged Algae	NA	NA	NA
2020	Eleanor	Fish	Salmoniformes	Salmonidae	Oncorhynchus mykiss
2020	Eleanor	Misc	NA	NA	NA
2020	Eleanor	Misc	Dacrymycetales	Dacrymycetaceae	Dacrymyces
2020	Eleanor	Terrestrial Insect	Araneae	Thomisidae	NA
2020	Eleanor	Terrestrial Insect	Coleoptera	Coccinellidae	Chilocorus stigma
2020	Eleanor	Terrestrial Insect	Coleoptera	Elateridae	NA
2020	Eleanor	Terrestrial Insect	Diptera	NA	NA
2020	Eleanor	Terrestrial Insect	Odonata	Coenagrionidae	Enallagma
2020	Eleanor	Terrestrial Plant	Ericales	Ericaceae	Arctostaphylos
2020	Eleanor	Terrestrial Plant	Ericales	Ericaceae	Phyllodoce breweri
2020	Eleanor	Terrestrial Plant	Ericales	Ericaceae	Vaccinium
2020	Eleanor	Terrestrial Plant	Pinales	Cupressaceae	NA
2020	Eleanor	Terrestrial Plant	Pinales	Pinaceae	Pinus
2020	Emerald	Aquatic Insect	Coleoptera	Dytiscidae	Leconectes striatellus
2020	Emerald	Aquatic Insect	Odonata Anisoptera	Aeshnidae	Aeshna
2020	Emerald	Aquatic Insect	Odonata Zygoptera	Coenagrionidae	Coenagrion

2020	Emerald	Aquatic Insect	Rhynchobdellida	Glossiphoniidae	Helobdella
2020	Emerald	Aquatic Insect	Trichoptera	Leptoceridae	Oecetis
2020	Emerald	Aquatic Insect	Trichoptera	Limnephilidae	Lenarchus
2020	Emerald	Aquatic Insect	Trichoptera	Limnephilidae	NA
2020	Emerald	Aquatic Plant Emerged	Poales	NA	NA
2020	Emerald	Aquatic Plant Submerged	NA	NA	NA
2020	Emerald	Fish	Salmoniformes	Salmonidae	Oncorhynchus mykiss
2020	Emerald	Misc	NA	NA	NA
2020	Emerald	Terrestrial Insect	Araneae	Thomisidae	NA
2020	Emerald	Terrestrial Insect	Archaeognatha	NA	NA
2020	Emerald	Terrestrial Insect	Diptera, Zoosubsection Calypterae	NA	NA
2020	Emerald	Terrestrial Insect	Hymenoptera	Formicidae	Camponotus modoc
2020	Emerald	Terrestrial Plant	NA	NA	NA
2020	Emerald	Terrestrial Plant	Gentianales	Apocynaceae	Apocynum
2020	Emerald	Terrestrial Plant	Lecanorales	Parmeliaceae	Letharia vulpina
2020	Emerald	Terrestrial Plant	Pinales	Cupressaceae	Juniperus grandis
2020	Emerald	Terrestrial Plant	Pinales	Pinaceae	Pinus
2020	Emerald	Terrestrial Plant	Poales	NA	NA
2020	Emerald	Terrestrial Plant	Rosales	Rhamnaceae	NA
2020	Gem	Aquatic Insect	Amphipoda	Hyalellidae	Hyalella
2020	Gem	Aquatic Insect	Coleoptera	Dytiscidae	Hygrotus
2020	Gem	Aquatic Insect	Coleoptera	Dytiscidae	Leconectes striatellus

2020	Gem	Aquatic Insect	Coleoptera	Hydrophilidae	Tropisternus lateralis
2020	Gem	Aquatic Insect	Ephemeroptera	Baetidae	NA
2020	Gem	Aquatic Insect	Megaloptera	Sialidae	Sialis californica
2020	Gem	Aquatic Insect	Odonata Anisoptera	Aeshnidae	Aeshna umbrosa
2020	Gem	Aquatic Insect	Odonata Anisoptera	Corduliidae	Cordulia shurtleffii
2020	Gem	Aquatic Insect	Odonata Zygoptera	Coenagrionidae	NA
2020	Gem	Aquatic Insect	Trichoptera	Limnephilidae	Limnephilus
2020	Gem	Aquatic Insect	Trichoptera	Limnephilidae	NA
2020	Gem	Aquatic Plant Emerged	NA	NA	NA
2020	Gem	Aquatic Plant Emerged	Poales	NA	NA
2020	Gem	Aquatic Plant Submerged	NA	NA	NA
2020	Gem	Aquatic Plant Submerged	Phylum Bryophyta	NA	NA
2020	Gem	Aquatic Plant Submerged	Poales	NA	NA
2020	Gem	Fish	Salmoniformes	Salmonidae	Oncorhynchus mykiss
2020	Gem	Misc	NA	NA	NA
2020	Gem	Terrestrial Insect	Coleoptera	Elateridae	NA
2020	Gem	Terrestrial Insect	Coleoptera	Tenebrionidae	Coelocnemis rugulosa
2020	Gem	Terrestrial Insect	Diptera	Asilidae	Tribe Stenopogonini
2020	Gem	Terrestrial Insect	Ephemeroptera	Baetidae	NA
2020	Gem	Terrestrial Insect	Ephemeroptera	Baetidae	NA
2020	Gem	Terrestrial Insect	Hemiptera	Aphididae	NA
2020	Gem	Terrestrial Insect	Hemiptera	Cicadellidae	Exitianus
2020	Gem	Terrestrial Insect	Hemiptera	Lygaeidae	Nysius

2020	Gem	Terrestrial Insect	Hemiptera	Rhopalidae	Brachycarenum tigrinus
2020	Gem	Terrestrial Insect	Hymenoptera	Formicidae	NA
2020	Gem	Terrestrial Insect	Hymenoptera	Formicidae	Camponotus modoc
2020	Gem	Terrestrial Insect	Odonata	Coenagrionidae	Enallagma
2020	Gem	Terrestrial Plant	NA	NA	NA
2020	Gem	Terrestrial Plant	Ericales	Ericaceae	Arctostaphylos nevadensis ssp. nevadensis
2020	Gem	Terrestrial Plant	Pinales	Pinaceae	Abies concolor ssp. lowiana
2020	Gem	Terrestrial Plant	Pinales	Pinaceae	Pinus
2020	Gem	Terrestrial Plant	Polypodiales	Dennstaedtiaceae	Pteridium aquilinum var. pubescens
2020	Jewel	Aquatic Insect	Amphipoda	Hyalellidae	Hyalella
2020	Jewel	Aquatic Insect	Hemiptera	Gerridae	Aquarius remigis
2020	Jewel	Aquatic Insect	Megaloptera	Sialidae	Sialis californica
2020	Jewel	Aquatic Insect	Odonata Anisoptera	Aeshnidae	NA
2020	Jewel	Aquatic Insect	Odonata Anisoptera	Corduliidae	NA
2020	Jewel	Aquatic Plant Emerged	Phylum Bryophyta	NA	NA
2020	Jewel	Aquatic Plant Emerged	Poales	NA	NA
2020	Jewel	Aquatic Plant Emerged	Poales	Cyperaceae	Carex
2020	Jewel	Aquatic Plant Submerged	NA	NA	NA
2020	Jewel	Aquatic Submerged Algae	NA	NA	NA
2020	Jewel	Fish	Cypriniformes	Leuciscidae	Rhinichthys osculus

2020	Jewel	Fish	Salmoniformes	Salmonidae	Oncorhynchus mykiss
2020	Jewel	Terrestrial Insect	Hymenoptera	Formicidae	Camponotus
2020	Jewel	Terrestrial Insect	Odonata	Coenagrionidae	Enallagma
2020	Jewel	Terrestrial Plant	Ericales	Ericaceae	Vaccinium
2020	Jewel	Terrestrial Plant	Liliales	Melanthiaceae	Veratrum californicum
2020	Jewel	Terrestrial Plant	Pinales	Cupressaceae	Juniperus
2020	Jewel	Terrestrial Plant	Pinales	Pinaceae	Pinus
2020	Jewel	Terrestrial Plant	Polypodiales	Dennstaedtiaceae	Pteridium aquilinum var. pubescens
2020	Jewel	Terrestrial Plant	Rosales	Rosaceae	Spiraea
2020	Shotoverin	Aquatic Insect	Amphipoda	Hyalellidae	Hyalella
2020	Shotoverin	Aquatic Insect	Diptera	Chironomidae	NA
2020	Shotoverin	Aquatic Insect	Megaloptera	Sialidae	Sialis californica
2020	Shotoverin	Aquatic Insect	Sphaeriida	Sphaeriidae	Euglesa
2020	Shotoverin	Aquatic Plant Emerged	NA	NA	NA
2020	Shotoverin	Aquatic Plant Emerged	Nymphaeales	Cabombaceae	Brasenia schreberi
2020	Shotoverin	Aquatic Plant Emerged	Phylum Bryophyta	NA	NA
2020	Shotoverin	Aquatic Plant Emerged	Poales	NA	NA
2020	Shotoverin	Aquatic Plant Emerged	Poales	Cyperaceae	Carex
2020	Shotoverin	Aquatic Plant Emerged	Poales	Typhaceae	Sparganium
2020	Shotoverin	Aquatic Plant Submerged	Poales	NA	NA
2020	Shotoverin	Fish	Siluriformes	Ictaluridae	Ameiurus nebulosus
2020	Shotoverin	Misc	NA	NA	NA

2020	Shotoverin	Terrestrial Insect	Araneae	NA	NA
2020	Shotoverin	Terrestrial Insect	Coleoptera	Carabidae	NA
2020	Shotoverin	Terrestrial Insect	Hymenoptera	Formicidae	Camponotus modoc
2020	Shotoverin	Terrestrial Insect	Hymenoptera	Tenthredinidae	NA
2020	Shotoverin	Terrestrial Insect	Odonata	Aeshnidae	Aeshna
2020	Shotoverin	Terrestrial Insect	Trichoptera	Limnephilidae	NA
2020	Shotoverin	Terrestrial Plant	Malpighiales	Salicaceae	Salix
2020	Shotoverin	Terrestrial Plant	Pinales	Pinaceae	Pinus contorta var. murrayana
2020	Shotoverin	Terrestrial Plant	Poales	NA	NA
2020	Shotoverin	Terrestrial Plant	Rosales	Rosaceae	Spiraea
2020	Triangle	Aquatic Insect	Coleoptera	Dytiscidae	NA
2020	Triangle	Aquatic Insect	Ephemeroptera	Caenidae	NA
2020	Triangle	Aquatic Insect	Odonata Anisoptera	Aeshnidae	Aeshna
2020	Triangle	Aquatic Insect	Odonata Anisoptera	Corduliidae	Cordulia shurtleffii
2020	Triangle	Aquatic Plant Emerged	Poales	Cyperaceae	Eleocharis
2020	Triangle	Aquatic Plant Submerged	NA	NA	NA
2020	Triangle	Aquatic Plant Submerged	Charales	Characeae	NA
2020	Triangle	Aquatic Plant Submerged	Hypnales	Fontinalaceae	NA
2020	Triangle	Aquatic Submerged Algae	NA	NA	NA
2020	Triangle	Fish	Cypriniformes	Leuciscidae	Rhinichthys osculus
2020	Triangle	Fish	Salmoniformes	Salmonidae	Oncorhynchus mykiss
2020	Triangle	Terrestrial Insect	NA	NA	NA
2020	Triangle	Terrestrial Insect	Coleoptera	Melyridae	NA
2020	Triangle	Terrestrial Insect	Coleoptera	Mordellidae	NA

2020	Triangle	Terrestrial Insect	Hymenoptera	Apidae	Anthophora
2020	Triangle	Terrestrial Plant	Ericales	Ericaceae	Arctostaphylos
2020	Triangle	Terrestrial Plant	Lamiales	Plantaginaceae	Penstemon
2020	Triangle	Terrestrial Plant	Pinales	Cupressaceae	Juniperus
2020	Triangle	Terrestrial Plant	Pinales	Pinaceae	Pinus contorta
2020	Triangle	Terrestrial Plant	Poales	Cyperaceae	Carex
2020	Triangle	Terrestrial Plant	Poales	Juncaceae	NA
2020	Turnaround	Aquatic Insect	Megaloptera	Sialidae	Sialis californica
2020	Turnaround	Aquatic Insect	Odonata Anisoptera	Aeshnidae	Aeshna
2020	Turnaround	Aquatic Insect	Odonata Anisoptera	Corduliidae	Somatochlora
2020	Turnaround	Aquatic Insect	Rhynchobdellida	Glossiphoniidae	Glossiphonia elegans
2020	Turnaround	Aquatic Insect	Trichoptera	Limnephilidae	Limnephilus
2020	Turnaround	Aquatic Plant Emerged	Phylum Bryophyta	NA	NA
2020	Turnaround	Aquatic Plant Emerged	Poales	NA	NA
2020	Turnaround	Aquatic Plant Submerged	Alismatales	Alismataceae	Sagittaria cuneata
2020	Turnaround	Aquatic Plant Submerged	Alismatales	Potamogetonaceae	Potamogeton
2020	Turnaround	Aquatic Plant Submerged	Caryophyllales	Polygonaceae	Persicaria amphibia var. stipulacea
2020	Turnaround	Aquatic Plant Submerged	Poales	Typhaceae	Sparganium
2020	Turnaround	Aquatic Submerged Algae	NA	NA	NA
2020	Turnaround	Fish	Cypriniformes	Leuciscidae	Rhinichthys osculus
2020	Turnaround	Fish	Cypriniformes	Leuciscidae	Siphateles bicolor
2020	Turnaround	Fish	Salmoniformes	Salmonidae	Oncorhynchus mykiss

2020	Turnaround	Misc	NA	NA	NA
2020	Turnaround	Terrestrial Insect	Araneae	Tetragnathidae	Tetragnatha
2020	Turnaround	Terrestrial Insect	Coleoptera	Buprestidae	NA
2020	Turnaround	Terrestrial Insect	Coleoptera	Chrysomelidae	Donacia hirticollis
2020	Turnaround	Terrestrial Insect	Coleoptera	Chrysomelidae	Galerucella nymphaeae
2020	Turnaround	Terrestrial Insect	Coleoptera	Tenebrionidae	NA
2020	Turnaround	Terrestrial Insect	Diptera	Syrphidae	Chrysotoxum
2020	Turnaround	Terrestrial Insect	Hymenoptera	Apidae	Anthophora urbana
2020	Turnaround	Terrestrial Insect	Hymenoptera	Formicidae	Camponotus modoc
2020	Turnaround	Terrestrial Insect	Hymenoptera	Sphecidae	Ammophila
2020	Turnaround	Terrestrial Insect	Odonata	Aeshnidae	Aeshna palmata
2020	Turnaround	Terrestrial Insect	Odonata	Coenagrionidae	Ischnura
2020	Turnaround	Terrestrial Insect	Raphidioptera	Raphidiidae	Agulla
2020	Turnaround	Terrestrial Plant	Ericales	Ericaceae	NA
2020	Turnaround	Terrestrial Plant	Ericales	Ericaceae	Arctostaphylos
2020	Turnaround	Terrestrial Plant	Malpighiales	Salicaceae	Salix
2020	Turnaround	Terrestrial Plant	NA	NA	NA
2020	Turnaround	Terrestrial Plant	Pinales	Pinaceae	Pinus
2020	Turnaround	Terrestrial Plant	Poales	NA	NA
2020	Turnaround	Terrestrial Plant	Poales	Poaceae	NA
2021	Big Bear	Aquatic Insect	Amphipoda	Hyaellidae	Hyaella
2021	Big Bear	Aquatic Insect	Coleoptera	Amphizoidae	NA - skipped
2021	Big Bear	Aquatic Insect	Coleoptera	Psephenidae	Eubrianax edwardsii

2021	Big Bear	Aquatic Insect	Diptera	Chironomidae	NA
2021	Big Bear	Aquatic Insect	Ephemeroptera	Leptophlebiidae	NA
2021	Big Bear	Aquatic Insect	Megaloptera	Sialidae	Sialis californica
2021	Big Bear	Aquatic Insect	Odonata Anisoptera	Aeshnidae	NA
2021	Big Bear	Aquatic Insect	Odonata Anisoptera	Corduliidae	NA
2021	Big Bear	Aquatic Insect	Odonata Zygoptera	Coenagrionidae	NA
2021	Big Bear	Aquatic Insect	Rhynchobdellida	Glossiphoniidae	Helobdella
2021	Big Bear	Aquatic Insect	Trichoptera	Calamoceratidae	Heteroplectron californicum
2021	Big Bear	Aquatic Insect	Trichoptera	Leptoceridae	NA
2021	Big Bear	Aquatic Insect	Trichoptera	Limnephilidae	NA
2021	Big Bear	Aquatic Plant Emerged	Phylum Bryophyta	NA	NA
2021	Big Bear	Aquatic Plant Emerged	Poales	Cyperaceae	Carex
2021	Big Bear	Aquatic Plant Submerged	NA	NA	NA
2021	Big Bear	Aquatic Plant Submerged	Phylum Bryophyta	NA	NA
2021	Big Bear	Aquatic Plant Submerged	Poales	NA	NA
2021	Big Bear	Aquatic Submerged Algae	NA	NA	NA
2021	Big Bear	Fish	Cypriniformes	Catostomidae	Catostomus occidentalis
2021	Big Bear	Fish	Cypriniformes	Leuciscidae	Rhinichthys osculus
2021	Big Bear	Fish	NA	NA	NA
2021	Big Bear	Misc	Squamata	Colubridae	Thamnophis couchii
2021	Big Bear	Terrestrial Insect	Coleoptera	Cantharidae	NA
2021	Big Bear	Terrestrial Insect	Coleoptera	Cerambycidae	Rhagium inquisitor
2021	Big Bear	Terrestrial Insect	Coleoptera	Coccinellidae	Anatis rathvoni

2021	Big Bear	Terrestrial Insect	Coleoptera	Coccinellidae	Hippodamia convergens
2021	Big Bear	Terrestrial Insect	Coleoptera	Tenebrionidae	NA
2021	Big Bear	Terrestrial Insect	Ephemeroptera	Baetidae	Callibaetis
2021	Big Bear	Terrestrial Insect	Hymenoptera	Apidae	NA
2021	Big Bear	Terrestrial Insect	Hymenoptera	Braconidae	NA
2021	Big Bear	Terrestrial Insect	Hymenoptera	Formicidae	Camponotus modoc
2021	Big Bear	Terrestrial Insect	Hymenoptera	Formicidae	NA
2021	Big Bear	Terrestrial Insect	Hymenoptera	Tenthredinidae	NA
2021	Big Bear	Terrestrial Insect	Lepidoptera	NA	NA
2021	Big Bear	Terrestrial Insect	Megaloptera	Sialidae	Complex Sialis californica
2021	Big Bear	Terrestrial Insect	Odonata	Coenagrionidae	Enallagma
2021	Big Bear	Terrestrial Insect	Odonata	Gomphidae	Octogomphus
2021	Big Bear	Terrestrial Insect	Trichoptera	NA	NA
2021	Big Bear	Terrestrial Plant	NA	NA	NA
2021	Big Bear	Terrestrial Plant	Ericales	Ericaceae	Rhododendron columbianum
2021	Big Bear	Terrestrial Plant	Pinales	Pinaceae	Abies concolor ssp. lowiana
2021	Big Bear	Terrestrial Plant	Pinales	Pinaceae	Pinus
2021	Big Bear	Terrestrial Plant	Polypodiales	Dennstaedtiaceae	Pteridium aquilinum
2021	Lower Salmon	Aquatic Insect	Amphipoda	Hyaellidae	Hyaella
2021	Lower Salmon	Aquatic Insect	Coleoptera	Dytiscidae	NA
2021	Lower Salmon	Aquatic Insect	Coleoptera	Staphylinidae	NA
2021	Lower Salmon	Aquatic Insect	Ephemeroptera	Caenidae	NA
2021	Lower Salmon	Aquatic Insect	Ephemeroptera	Leptophlebiidae	NA

2021	Lower Salmon	Aquatic Insect	Odonata Anisoptera	Aeshnidae	NA
2021	Lower Salmon	Aquatic Insect	Odonata Anisoptera	Corduliidae	NA
2021	Lower Salmon	Aquatic Insect	Odonata Zygoptera	Coenagrionidae	NA
2021	Lower Salmon	Aquatic Insect	Superorder Hygrophila	Physidae	NA
2021	Lower Salmon	Aquatic Insect	Trichoptera	Leptoceridae	NA
2021	Lower Salmon	Aquatic Insect	Trichoptera	Limnephilidae	NA
2021	Lower Salmon	Aquatic Plant Emerged	Nymphaeales	Nymphaeaceae	Nuphar
2021	Lower Salmon	Aquatic Plant Emerged	Phylum Bryophyta	NA	NA
2021	Lower Salmon	Aquatic Plant Emerged	Poales	NA	NA
2021	Lower Salmon	Aquatic Plant Emerged	Poales	Typhaceae	Sparganium
2021	Lower Salmon	Aquatic Plant Submerged	Poales	NA	NA
2021	Lower Salmon	Aquatic Submerged Algae	NA	NA	NA
2021	Lower Salmon	Fish	Cypriniformes	Leuciscidae	Rhinichthys osculus
2021	Lower Salmon	Fish	NA	NA	NA
2021	Lower Salmon	Fish	Salmoniformes	Salmonidae	Oncorhynchus mykiss
2021	Lower Salmon	Terrestrial Insect	NA	NA	NA
2021	Lower Salmon	Terrestrial Insect	Coleoptera	Cantharidae	NA
2021	Lower Salmon	Terrestrial Insect	Coleoptera	Cerambycidae	Tetropium
2021	Lower Salmon	Terrestrial Insect	Coleoptera	Coccinellidae	Anatis rathvoni
2021	Lower Salmon	Terrestrial Insect	Coleoptera	Elateridae	NA
2021	Lower Salmon	Terrestrial Insect	Coleoptera	Tenebrionidae	NA
2021	Lower Salmon	Terrestrial Insect	Diptera	NA	NA
2021	Lower Salmon	Terrestrial Insect	Ephemeroptera	Baetidae	Callibaetis
2021	Lower Salmon	Terrestrial Insect	Hemiptera	Cicadellidae	NA

2021	Lower Salmon	Terrestrial Insect	Hymenoptera	Formicidae	Camponotus modoc
2021	Lower Salmon	Terrestrial Insect	Hymenoptera	Tenthredinidae	NA
2021	Lower Salmon	Terrestrial Insect	Lepidoptera	NA	NA
2021	Lower Salmon	Terrestrial Insect	Megaloptera	Sialidae	Complex Sialis californica
2021	Lower Salmon	Terrestrial Insect	Odonata	Coenagrionidae	Enallagma
2021	Lower Salmon	Terrestrial Insect	Odonata	Gomphidae	Octogomphus
2021	Lower Salmon	Terrestrial Insect	Odonata	Libellulidae	Ladona
2021	Lower Salmon	Terrestrial Plant	NA	NA	NA
2021	Lower Salmon	Terrestrial Plant	Asterales	Asteraceae	Achillea
2021	Lower Salmon	Terrestrial Plant	Dipsacales	Caprifoliaceae	Lonicera
2021	Lower Salmon	Terrestrial Plant	Fabales	Fabaceae	Lupinus
2021	Lower Salmon	Terrestrial Plant	Liliales	Melanthiaceae	Veratrum californicum
2021	Lower Salmon	Terrestrial Plant	Malpighiales	Salicaceae	Salix
2021	Lower Salmon	Terrestrial Plant	Phylum Bryophyta	NA	NA
2021	Lower Salmon	Terrestrial Plant	Pinales	Pinaceae	Pinus
2021	Lower Salmon	Terrestrial Plant	Poales	Cyperaceae	Carex
2021	Lower Salmon	Terrestrial Plant	Rosales	Rosaceae	Spiraea
2021	Lower Sardine	Aquatic Insect	Amphipoda	Hyalellidae	Hyalella
2021	Lower Sardine	Aquatic Insect	Coleoptera	Dytiscidae	Acilius abbreviatus
2021	Lower Sardine	Aquatic Insect	Coleoptera	Psephenidae	Eubrianax edwardsii
2021	Lower Sardine	Aquatic Insect	Decapoda	Cambaridae	Procambarus clarkii
2021	Lower Sardine	Aquatic Insect	Diptera	Chironomidae	Chironomus
2021	Lower Sardine	Aquatic Insect	Diptera	Chironomidae	NA

2021	Lower Sardine	Aquatic Insect	Ephemeroptera	Batidae	NA
2021	Lower Sardine	Aquatic Insect	Ephemeroptera	Caenidae	Caenis
2021	Lower Sardine	Aquatic Insect	Ephemeroptera	Leptophlebiidae	Paraleptophlebia
2021	Lower Sardine	Aquatic Insect	Odonata Anisoptera	Aeshnidae	NA
2021	Lower Sardine	Aquatic Insect	Odonata Anisoptera	Corduliidae	Somatochlora
2021	Lower Sardine	Aquatic Insect	Odonata Anisoptera	Gomphidae	NA
2021	Lower Sardine	Aquatic Insect	Odonata Anisoptera	Libellulidae	NA
2021	Lower Sardine	Aquatic Insect	Odonata Zygoptera	Coenagrionidae	Zoniagrion
2021	Lower Sardine	Aquatic Insect	Rhynchohellida	Glossiphoniidae	Helobdella
2021	Lower Sardine	Aquatic Insect	Superorder Hygrophila	Physidae	Physa
2021	Lower Sardine	Aquatic Insect	Trichoptera	Leptoceridae	Oecetis
2021	Lower Sardine	Aquatic Insect	Trichoptera	Phryganeidae	Phryganea
2021	Lower Sardine	Aquatic Insect	Trombidiformes, Infraorder Hydrachnidia	NA	NA
2021	Lower Sardine	Aquatic Plant Emerged	Phylum Bryophyta	NA	NA
2021	Lower Sardine	Aquatic Plant Emerged	Poales	Cyperaceae	Eleocharis
2021	Lower Sardine	Aquatic Plant Emerged	Poales	Cyperaceae	Schoenoplectus
2021	Lower Sardine	Aquatic Plant Submerged	NA	NA	NA
2021	Lower Sardine	Aquatic Plant Submerged	Alismatales	Hydrocharitaceae	Elodea
2021	Lower Sardine	Aquatic Plant Submerged	Alismatales	Potamogetonaceae	Potamogeton
2021	Lower Sardine	Aquatic Plant Submerged	Isoetales	Isoetaceae	Isoetes
2021	Lower Sardine	Aquatic Plant Submerged	Spongillida	Spongillidae	NA
2021	Lower Sardine	Aquatic Submerged Algae	NA	NA	NA
2021	Lower Sardine	Fish	Cypriniformes	Leuciscidae	Notemigonus crysoleucas

2021	Lower Sardine	Fish	Cypriniformes	Leuciscidae	Rhinichthys osculus
2021	Lower Sardine	Fish	Cypriniformes	Leuciscidae	Richardsonius egregius
2021	Lower Sardine	Fish	Salmoniformes	Salmonidae	Oncorhynchus mykiss
2021	Lower Sardine	Misc	Anura	Ranidae	Lithobates catesbeianus
2021	Lower Sardine	Misc	NA	NA	NA
2021	Lower Sardine	Terrestrial Insect	Araneae	NA	NA
2021	Lower Sardine	Terrestrial Insect	Araneae	Tetragnathidae	Tetragnatha
2021	Lower Sardine	Terrestrial Insect	Coleoptera	Cerambycidae	Ortholeptura valida
2021	Lower Sardine	Terrestrial Insect	Coleoptera	Coccinellidae	Hippodamia convergens
2021	Lower Sardine	Terrestrial Insect	Hemiptera	Reduviidae	Zelus renardii
2021	Lower Sardine	Terrestrial Insect	Hymenoptera	Formicidae	Camponotus
2021	Lower Sardine	Terrestrial Insect	Hymenoptera	Vespidae	Dolichovespul a maculata
2021	Lower Sardine	Terrestrial Insect	Lepidoptera	NA	NA
2021	Lower Sardine	Terrestrial Plant	NA	NA	NA
2021	Lower Sardine	Terrestrial Plant	Asterales	Asteraceae	NA
2021	Lower Sardine	Terrestrial Plant	Asterales	Asteraceae	Cirsium
2021	Lower Sardine	Terrestrial Plant	Asterales	Asteraceae	Solidago
2021	Lower Sardine	Terrestrial Plant	Cornales	Cornaceae	Cornus
2021	Lower Sardine	Terrestrial Plant	Equisetales	Equisetaceae	Equisetum
2021	Lower Sardine	Terrestrial Plant	Ericales	Ericaceae	Arctostaphylos
2021	Lower Sardine	Terrestrial Plant	Ericales	Ericaceae	Rhododendron occidentale
2021	Lower Sardine	Terrestrial Plant	Fagales	Betulaceae	Alnus

2021	Lower Sardine	Terrestrial Plant	Lecanorales	Parmeliaceae	Letharia
2021	Lower Sardine	Terrestrial Plant	Malpighiales	Salicaceae	Populus
2021	Lower Sardine	Terrestrial Plant	Malpighiales	Salicaceae	Salix
2021	Lower Sardine	Terrestrial Plant	Pinales	Cupressaceae	Calocedrus
2021	Lower Sardine	Terrestrial Plant	Pinales	Pinaceae	Abies
2021	Lower Sardine	Terrestrial Plant	Pinales	Pinaceae	Pinus
2021	Lower Sardine	Terrestrial Plant	Pinales	Pinaceae	Tsuga
2021	Lower Sardine	Terrestrial Plant	Poales	NA	NA
2021	Lower Sardine	Terrestrial Plant	Poales	Cyperaceae	Carex
2021	Lower Sardine	Terrestrial Plant	Poales	Cyperaceae	Scirpus
2021	Lower Sardine	Terrestrial Plant	Polypodiales	Athyriaceae	Athyrium
2021	Lower Sardine	Terrestrial Plant	Rosales	Rosaceae	Spiraea
2021	Lower Sardine	Terrestrial Plant	Saxifragales	Grossulariaceae	Ribes
2021	Round	Aquatic Insect	Coleoptera	Dytiscidae	Leconectes striatellus
2021	Round	Aquatic Insect	Coleoptera	Dytiscidae	NA
2021	Round	Aquatic Insect	Coleoptera	Dytiscidae, Subfamily Hydroporinae	NA
2021	Round	Aquatic Insect	Coleoptera	Gyrinidae	NA
2021	Round	Aquatic Insect	Coleoptera	Psephenidae	Eubrianax edwardsii
2021	Round	Aquatic Insect	Diptera	Chironomidae	NA
2021	Round	Aquatic Insect	Ephemeroptera	Leptophlebiidae	NA
2021	Round	Aquatic Insect	Hemiptera	Corixidae	NA
2021	Round	Aquatic Insect	Megaloptera	Sialidae	Sialis californica
2021	Round	Aquatic Insect	Odonata Anisoptera	Aeshnidae	NA
2021	Round	Aquatic Insect	Odonata Anisoptera	Corduliidae	NA

2021	Round	Aquatic Insect	Odonata Zygoptera	Coenagrionidae	NA
2021	Round	Aquatic Insect	Trichoptera	Calamoceratidae	Heteroplectron californicum
2021	Round	Aquatic Insect	Trichoptera	Limnephilidae	NA
2021	Round	Aquatic Insect	Trichoptera	NA	NA
2021	Round	Aquatic Plant Emerged	NA	NA	NA
2021	Round	Aquatic Plant Submerged	NA	NA	NA
2021	Round	Fish	Salmoniformes	Salmonidae	Salvelinus fontinalis
2021	Round	Misc	NA	NA	NA
2021	Round	Misc	Plumatellida	NA	NA
2021	Round	Terrestrial Insect	Araneae	Araneidae	NA
2021	Round	Terrestrial Insect	Coleoptera	Buprestidae	Anambodera
2021	Round	Terrestrial Insect	Coleoptera	Buprestidae	Buprestis lyrata
2021	Round	Terrestrial Insect	Hemiptera	Saldidae	Saldula
2021	Round	Terrestrial Insect	Hymenoptera	Formicidae	Camponotus
2021	Round	Terrestrial Insect	Odonata	Coenagrionidae	Enallagma
2021	Round	Terrestrial Plant	Ericales	Ericaceae	Phyllodoce breweri
2021	Round	Terrestrial Plant	Ericales	Ericaceae	Rhododendron columbianum
2021	Round	Terrestrial Plant	Malpighiales	Salicaceae	Populus
2021	Round	Terrestrial Plant	Malpighiales	Salicaceae	Salix
2021	Round	Terrestrial Plant	Myrtales	Onagraceae	Chamaenerion angustifolium
2021	Round	Terrestrial Plant	Pinales	Pinaceae	Abies concolor
2021	Round	Terrestrial Plant	Pinales	Pinaceae	Pinus
2021	Round	Terrestrial Plant	Poales	NA	NA

2021	Round	Terrestrial Plant	Rosales	Rosaceae	Prunus emarginata
2021	Round	Terrestrial Plant	Rosales	Rosaceae	Sorbus
2021	Round	Terrestrial Plant	Rosales	Rosaceae	Spiraea
2021	Silver	Aquatic Insect	Amphipoda	Hyalellidae	Hyalella
2021	Silver	Aquatic Insect	Coleoptera	Dytiscidae	NA
2021	Silver	Aquatic Insect	Coleoptera	Psephenidae	Eubrianax edwardsii
2021	Silver	Aquatic Insect	Ephemeroptera	Leptophlebiidae	NA
2021	Silver	Aquatic Insect	Odonata Anisoptera	Aeshnidae	NA
2021	Silver	Aquatic Insect	Odonata Anisoptera	Corduliidae	NA
2021	Silver	Aquatic Insect	Odonata Zygoptera	Coenagrionidae	NA
2021	Silver	Aquatic Insect	Rhynchobdellida	Glossiphoniidae	Helobdella
2021	Silver	Aquatic Insect	Trichoptera	Calamoceratidae	Heteroplectron californicum
2021	Silver	Aquatic Insect	Trichoptera	Leptoceridae	NA
2021	Silver	Aquatic Insect	Trichoptera	Limnephilidae	NA
2021	Silver	Aquatic Plant Emerged	NA	NA	NA
2021	Silver	Aquatic Plant Emerged	Phylum Bryophyta	NA	NA
2021	Silver	Aquatic Plant Emerged	Poales	NA	NA
2021	Silver	Aquatic Plant Submerged	Poales	Typhaceae	Sparganium
2021	Silver	Fish	Cypriniformes	Leuciscidae	Rhinichthys osculus
2021	Silver	Fish	Salmoniformes	Salmonidae	Salvelinus fontinalis
2021	Silver	Misc	Spongillida	NA	NA
2021	Silver	Terrestrial Insect	Araneae	NA	NA
2021	Silver	Terrestrial Insect	Archaeognatha	NA	NA
2021	Silver	Terrestrial Insect	Ephemeroptera	Baetidae	Callibaetis

2021	Silver	Terrestrial Insect	Hymenoptera	Formicidae	Camponotus modoc Complex
2021	Silver	Terrestrial Insect	Hymenoptera	Formicidae	Polyergus rufescens
2021	Silver	Terrestrial Insect	Hymenoptera	Formicidae	Lasius
2021	Silver	Terrestrial Insect	Odonata	Coenagrionidae	Enallagma
2021	Silver	Terrestrial Plant	Asterales	Asteraceae	NA
2021	Silver	Terrestrial Plant	Ericales	Ericaceae	Leucothoe
2021	Silver	Terrestrial Plant	Ericales	Ericaceae	Rhododendron
2021	Silver	Terrestrial Plant	Fabales	Fabaceae	Lupinus
2021	Silver	Terrestrial Plant	Fagales	Fagaceae	NA
2021	Silver	Terrestrial Plant	Lecanorales	Parmeliaceae	Letharia
2021	Silver	Terrestrial Plant	Malpighiales	Salicaceae	Populus
2021	Silver	Terrestrial Plant	Pinales	Pinaceae	Abies magnifica var. magnifica
2021	Silver	Terrestrial Plant	Pinales	Pinaceae	Pinus
2021	Silver	Terrestrial Plant	Poales	NA	NA
2021	Silver	Terrestrial Plant	Polypodiales	Dennstaedtiaceae	Pteridium
2021	Silver	Terrestrial Plant	Rosales	Rosaceae	Sorbus
2021	Silver	Terrestrial Plant	Rosales	Rosaceae	Spiraea
2021	Snag	Aquatic Insect	Coleoptera	Dytiscidae	Hydroporus
2021	Snag	Aquatic Insect	Coleoptera	Dytiscidae	NA
2021	Snag	Aquatic Insect	Coleoptera	Gyrinidae	Gyrinus
2021	Snag	Aquatic Insect	Diptera	Chironomidae	NA
2021	Snag	Aquatic Insect	Ephemeroptera	Caenidae	NA
2021	Snag	Aquatic Insect	Hemiptera	Gerridae	Aquarius remigis

2021	Snag	Aquatic Insect	Odonata Anisoptera	Aeshnidae	NA
2021	Snag	Aquatic Insect	Rhynchohellida	Glossiphoniidae	Helobdella
2021	Snag	Aquatic Plant Emerged	NA	NA	NA
2021	Snag	Aquatic Plant Emerged	Alismatales	Potamogetonaceae	NA
2021	Snag	Fish	Cypriniformes	Leuciscidae	Notemigonus crysoleucas
2021	Snag	Fish	Siluriformes	Ictaluridae	Ameiurus
2021	Snag	Misc	Anura	Hylidae	Pseudacris regilla
2021	Snag	Terrestrial Insect	Coleoptera	NA	NA
2021	Snag	Terrestrial Insect	Diptera	Bombyliidae	Anthrax irroratus
2021	Snag	Terrestrial Insect	Hemiptera	Aphididae	NA
2021	Snag	Terrestrial Insect	Hemiptera	Saldidae	Saldula
2021	Snag	Terrestrial Insect	Hymenoptera	Apidae	Xylocopa
2021	Snag	Terrestrial Insect	Hymenoptera	Formicidae	Camponotus modoc
2021	Snag	Terrestrial Insect	Lepidoptera	NA	NA
2021	Snag	Terrestrial Plant	NA	NA	NA
2021	Snag	Terrestrial Plant	Asterales	Asteraceae	NA
2021	Snag	Terrestrial Plant	Lamiales	Phrymaceae	Erythranthe
2021	Snag	Terrestrial Plant	Lecanorales	Parmeliaceae	Letharia
2021	Snag	Terrestrial Plant	Malpighiales	Salicaceae	Salix
2021	Snag	Terrestrial Plant	NA	NA	NA
2021	Snag	Terrestrial Plant	Pinales	Pinaceae	Abies concolor ssp. lowiana
2021	Snag	Terrestrial Plant	Pinales	Pinaceae	Abies magnifica var. magnifica

2021	Snag	Terrestrial Plant	Pinales	Pinaceae	Pinus
2021	Snag	Terrestrial Plant	Poales	NA	NA
2021	Snag	Terrestrial Plant	Poales	Cyperaceae	NA
2021	Snag	Terrestrial Plant	Polypodiales	Dennstaedtiaceae	Pteridium
2021	Snag	Terrestrial Plant	Rosales	Rosaceae	Spiraea
2021	Upper Salmon	Aquatic Insect	NA	NA	NA
2021	Upper Salmon	Aquatic Insect	Amphipoda	Hyaellidae	Hyaella
2021	Upper Salmon	Aquatic Insect	Coleoptera	Psephenidae	Eubrianax edwardsii
2021	Upper Salmon	Aquatic Insect	Diptera	Chironomidae	NA
2021	Upper Salmon	Aquatic Insect	Ephemeroptera	Baetidae	NA
2021	Upper Salmon	Aquatic Insect	Ephemeroptera	NA	NA
2021	Upper Salmon	Aquatic Insect	Megaloptera	Sialidae	Sialis californica
2021	Upper Salmon	Aquatic Insect	Odonata Anisoptera	Aeshnidae	Aeshna
2021	Upper Salmon	Aquatic Insect	Odonata Anisoptera	Corduliidae	Cordulia shurtleffii
2021	Upper Salmon	Aquatic Insect	Odonata Zygoptera	Coenagrionidae	NA
2021	Upper Salmon	Aquatic Insect	Rhynchobdellida	Glossiphoniidae	Helobdella
2021	Upper Salmon	Aquatic Insect	Trichoptera	Calamoceratidae	Heteroplectron californicum
2021	Upper Salmon	Aquatic Insect	Trichoptera	Leptoceridae	Oecetis
2021	Upper Salmon	Aquatic Insect	Trichoptera	Limnephilidae	Halesochila taylori
2021	Upper Salmon	Aquatic Insect	Trichoptera	Limnephilidae	Limnephilus
2021	Upper Salmon	Aquatic Insect	Trichoptera	Phryganeidae	Phryganea
2021	Upper Salmon	Aquatic Plant Emerged	Phylum Bryophyta	NA	NA
2021	Upper Salmon	Aquatic Plant Emerged	Poales	NA	NA
2021	Upper Salmon	Aquatic Plant Submerged	NA	NA	NA

2021	Upper Salmon	Aquatic Plant Submerged	Phylum Bryophyta	NA	NA
2021	Upper Salmon	Aquatic Plant Submerged	Spongillida	Spongillidae	Spongilla
2021	Upper Salmon	Aquatic Submerged Algae	NA	NA	NA
2021	Upper Salmon	Fish	Cypriniformes	Leuciscidae	Rhinichthys osculus
2021	Upper Salmon	Fish	NA	NA	NA
2021	Upper Salmon	Fish	Salmoniformes	Salmonidae	Oncorhynchus mykiss
2021	Upper Salmon	Fish	Salmoniformes	Salmonidae	Salvelinus fontinalis
2021	Upper Salmon	Fish	Salmoniformes	Salmonidae	Oncorhynchus mykiss
2021	Upper Salmon	Fish	Salmoniformes	Salmonidae	Salvelinus fontinalis
2021	Upper Salmon	Fish	Salmoniformes	Salmonidae	Salvelinus fontinalis
2021	Upper Salmon	Fish	Salmoniformes	Salmonidae	Salvelinus fontinalis
2021	Upper Salmon	Misc	Spongillida	NA	NA
2021	Upper Salmon	Misc	Squamata	Colubridae	Thamnophis couchii
2021	Upper Salmon	Terrestrial Insect	Araneae	Salticidae	Pelegrina
2021	Upper Salmon	Terrestrial Insect	Araneae	Tetragnathidae	Tetragnatha
2021	Upper Salmon	Terrestrial Insect	Coleoptera	Chrysomelidae	Donacia hirticollis
2021	Upper Salmon	Terrestrial Insect	Coleoptera	Coccinellidae	Cycloneda polita
2021	Upper Salmon	Terrestrial Insect	Coleoptera	Curculionidae	Curculio
2021	Upper Salmon	Terrestrial Insect	Coleoptera	Dytiscidae, Tribe Hydroporini	NA
2021	Upper Salmon	Terrestrial Insect	Coleoptera	Haliplidae	Haliplus

2021	Upper Salmon	Terrestrial Insect	Diptera, Zoosubsection Calyptratae	NA	NA
2021	Upper Salmon	Terrestrial Insect	Hemiptera	Cicadellidae	Momoria
2021	Upper Salmon	Terrestrial Insect	Hymenoptera	Formicidae	Camponotus modoc
2021	Upper Salmon	Terrestrial Insect	Lepidoptera	Saturniidae	Hemileuca eglanterina
2021	Upper Salmon	Terrestrial Insect	Odonata	Coenagrionidae	Enallagma
2021	Upper Salmon	Terrestrial Plant	NA	NA	NA
2021	Upper Salmon	Terrestrial Plant	Apiales	Apiaceae	Angelica
2021	Upper Salmon	Terrestrial Plant	Cornales	Cornaceae	Cornus
2021	Upper Salmon	Terrestrial Plant	Ericales	Ericaceae	Leucothoe
2021	Upper Salmon	Terrestrial Plant	Fagales	Betulaceae	Alnus
2021	Upper Salmon	Terrestrial Plant	Garryales	Garryaceae	Garrya
2021	Upper Salmon	Terrestrial Plant	Lamiales	Orobanchaceae	Castilleja
2021	Upper Salmon	Terrestrial Plant	Lecanorales	Parmeliaceae	Letharia
2021	Upper Salmon	Terrestrial Plant	Malpighiales	Hypericaceae	Hypericum
2021	Upper Salmon	Terrestrial Plant	Malpighiales	Salicaceae	Salix
2021	Upper Salmon	Terrestrial Plant	Pinales	Pinaceae	Abies concolor ssp. lowiana
2021	Upper Salmon	Terrestrial Plant	Pinales	Pinaceae	Abies magnifica var. magnifica
2021	Upper Salmon	Terrestrial Plant	Pinales	Pinaceae	Pinus
2021	Upper Salmon	Terrestrial Plant	Poales	NA	NA
2021	Upper Salmon	Terrestrial Plant	Polypodiales	Dennstaedtiaceae	Pteridium aquilinum
2021	Upper Salmon	Terrestrial Plant	Rosales	Rosaceae	Sorbus
2021	Upper Salmon	Terrestrial Plant	Rosales	Rosaceae	Spiraea

2021	Upper Sardine	Aquatic Insect	Coleoptera	Dytiscidae, Subfamily Hydroporinae	NA
2021	Upper Sardine	Aquatic Insect	Diptera	Chironomidae	NA
2021	Upper Sardine	Aquatic Insect	Ephemeroptera	Heptageniidae	Epeorus
2021	Upper Sardine	Aquatic Insect	Ephemeroptera	Heptageniidae	Heptagenia
2021	Upper Sardine	Aquatic Insect	Megaloptera	Sialidae	Sialis californica
2021	Upper Sardine	Aquatic Insect	Odonata Anisoptera	Aeshnidae	Aeshna
2021	Upper Sardine	Aquatic Insect	Plecoptera	NA	NA
2021	Upper Sardine	Aquatic Insect	Rhynchobdellida	Glossiphoniidae	Helobdella
2021	Upper Sardine	Aquatic Insect	Trichoptera	Limnephilidae	Lenarchus
2021	Upper Sardine	Aquatic Insect	Trichoptera	Limnephilidae	Limnephilus
2021	Upper Sardine	Aquatic Insect	Trichoptera	Polycentropodidae	Polycentropus
2021	Upper Sardine	Aquatic Plant Emerged	NA	NA	NA
2021	Upper Sardine	Aquatic Plant Emerged	Phylum Bryophyta	NA	NA
2021	Upper Sardine	Aquatic Plant Submerged	Charales	Characeae	Nitella
2021	Upper Sardine	Aquatic Plant Submerged	Phylum Bryophyta	NA	NA
2021	Upper Sardine	Aquatic Plant Submerged	Poales	NA	NA
2021	Upper Sardine	Aquatic Plant Submerged	Ranunculales	Ranunculaceae	Ranunculus
2021	Upper Sardine	Aquatic Submerged Algae	NA	NA	NA
2021	Upper Sardine	Fish	Cypriniformes	Leuciscidae	Rhinichthys osculus
2021	Upper Sardine	Fish	Salmoniformes	Salmonidae	Salvelinus fontinalis
2021	Upper Sardine	Misc	Squamata	Colubridae	Thamnophis couchii
2021	Upper Sardine	Terrestrial Insect	NA	NA	NA
2021	Upper Sardine	Terrestrial Insect	Araneae	NA	NA
2021	Upper Sardine	Terrestrial Insect	Coleoptera	NA	NA

2021	Upper Sardine	Terrestrial Insect	Coleoptera	Coccinellidae	<i>Adalia bipunctata</i>
2021	Upper Sardine	Terrestrial Insect	Coleoptera	Coccinellidae	<i>Anatis rathvoni</i>
2021	Upper Sardine	Terrestrial Insect	Coleoptera	Coccinellidae	<i>Hippodamia convergens</i>
2021	Upper Sardine	Terrestrial Insect	Coleoptera	Elateridae	Stropenron
2021	Upper Sardine	Terrestrial Insect	Coleoptera	Haliplidae	Haliplus
2021	Upper Sardine	Terrestrial Insect	Coleoptera	Meloidae	NA
2021	Upper Sardine	Terrestrial Insect	Coleoptera	Melyridae	Listrus
2021	Upper Sardine	Terrestrial Insect	Coleoptera	Oedemeridae	Ditylus
2021	Upper Sardine	Terrestrial Insect	Coleoptera	Tenebrionidae	NA
2021	Upper Sardine	Terrestrial Insect	Hymenoptera	Andrenidae	Andrena
2021	Upper Sardine	Terrestrial Insect	Hymenoptera	Formicidae	Formica
2021	Upper Sardine	Terrestrial Insect	Hymenoptera	Sphecidae	Podalonia
2021	Upper Sardine	Terrestrial Insect	Hymenoptera	Tenthredinidae	Complex <i>Rhogogaster viridis</i>
2021	Upper Sardine	Terrestrial Insect	Odonata	Gomphidae	NA
2021	Upper Sardine	Terrestrial Insect	Odonata	Libellulidae	<i>Ladona julia</i>
2021	Upper Sardine	Terrestrial Insect	Plecoptera	Chloroperlidae (adult key)	Suwallia
2021	Upper Sardine	Terrestrial Plant	NA	NA	NA
2021	Upper Sardine	Terrestrial Plant	Asterales	Asteraceae	Helenium
2021	Upper Sardine	Terrestrial Plant	Boraginales	Boraginaceae	Amsinckia
2021	Upper Sardine	Terrestrial Plant	Brassicales	Brassicaceae	<i>Streptanthus tortuosus</i>
2021	Upper Sardine	Terrestrial Plant	Malpighiales	Salicaceae	Populus
2021	Upper Sardine	Terrestrial Plant	Malpighiales	Salicaceae	Salix
2021	Upper Sardine	Terrestrial Plant	Pinales	Pinaceae	Pinus
2021	Upper Sardine	Terrestrial Plant	Poales	NA	NA

2021	Upper Sardine	Terrestrial Plant	Rosales	Rhamnaceae	Frangula californica
2021	Upper Sardine	Terrestrial Plant	Rosales	Rosaceae	Spiraea splendens
2021	Upper Sardine	Terrestrial Plant	Sapindales	Sapindaceae	Acer
2021	Upper Sardine	Terrestrial Plant	Saxifragales	Grossulariaceae	Ribes

Table S3.2

Summary statistics for linear mixed effect models used in study.

Metric	Pseudo R ²	Parent Intercept	Parent Slope	Model Slope (Volume Effect)			(Intercept) p-value
				df	t-value	p-value	
Metric (Dependent) ~ Volume (Independent)							
Trophic Area (TA)	0.28	1.40	0.07	21.0	2.41	0.03 *	< 0.001 *
δ ¹⁵ N Range (dY)	0.32	0.84	0.02	3.4	0.78	0.49	0.005 *
δ ¹³ C Range (dX)	0.52	0.67	0.08	2.62	2.18	0.13	0.06
Centroid Distance (CD)	0.58	0.28	0.06	16.2	3.30	0.004 *	0.03 *
Mean Nearest Neighbor Distance (MNND)	0.44	0.10	0.04	9.4	1.34	0.21	0.56
Standard Deviation of Nearest Neighbor Distance (SDNND)	0.36	-0.28	0.08	26.7	1.72	0.09	0.24
Food Chain Length (FCL)	0.10	0.005	0.06	26.0	1.77	0.09	0.98
Productivity (via Chl- <i>a</i> µg/L concentration)	0.27	1.07	-0.21	5.85	-0.86	0.42	0.47
Metric (Dependent) ~ Productivity (Independent)							
Trophic Area (TA)	0.07	1.78	0.05	32.00	1.58	0.12	<0.001 *
δ ¹⁵ N Range (dY)	0.07	0.94	0.01	23.33	0.26	0.79	<0.001 *
δ ¹³ C Range (dX)	0.25	1.11	0.01	13.68	0.21	0.84	<0.001 *
Centroid Distance (CD)	0.26	0.58	0.01	25.19	0.54	0.60	<0.001 *

Mean Nearest Neighbor Distance (MNND)	0.38	0.30	0.04	5.94	1.59	0.16	0.004
Standard Deviation of Nearest Neighbor Distance (SDNND)	0.07	0.11	0.04	15.94	0.90	0.38	0.07
Food Chain Length (FCL)	0.14	0.32	-0.05	15.40	-1.92	0.07	0.0003 *

Table S3.3

Summary statistics for generalized additive models (GAMs) examining consumer sourcing change along an ecosystem size gradient (for Fig. 4). Models used the structure: *Diet Proportion of Source* ~ $s(\text{Volume_m3_Log10}, \text{bs}="tp") + s(\text{Region}, \text{bs}="re")$, *family=quasibinomial(link = "logit"), method="REML"*). The six models were performed separately.

Source	Deviance Explained (%)	Adjusted R-sq.	n	p-value (Volume)	p-value (Region)
Aquatic Insect	20.8%	0.12	20	0.31	0.44
Periphyton	3.12%	-0.05	14	0.55	0.55
Aquatic Plant	47.4%	0.39	20	0.20	0.006 *
Terrestrial Insect	54.4%	0.42	20	0.16	0.07
Particulate Organic Matter	46.2%	0.35	20	0.21	0.04 *
Zooplankton	40.4%	0.29	20	0.25	0.11