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The ecology and evolution of top-down and bottom-up control in mountain lakes

A dissertation submitted in partial satisfaction of the requirements for the degree
Doctor of Philosophy

in

Biology

by

Celia Claire Symons

Committee in charge:

- Professor Jonathan Shurin, Chair
- Professor Ronald Burton
- Professor Carolyn Kurle
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2017

The Dissertation of Celia Claire Symons is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

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ABSTRACT OF THE DISSERTATION

The ecology and evolution of top-down and bottom-up control in mountain lakes

by

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Doctor of Philosophy in Biology

University of California, San Diego, 2017

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Determining factors that control how biomass is distributed among plants, animals, microbes and non-living components of ecosystems is a major goal of ecology. Theoretical and empirical work have demonstrated that ecosystem structure and function may vary with the environment, but studies often overlook the role of adaptation and shifts in species composition that will occur over longer timescales relevant to climate change. For my doctoral research I used a ‘natural experiment’ in

Sierra Nevada mountain lakes to ask questions about the strength of top-down and bottom-up forcing in a natural system where communities have assembled and adapted to differences in the environment over periods from years to millennia.

In Chapter 1 I compare fish and fishless lakes along an elevational gradient, and show that an interaction between fish presence and temperature alters food web structure, ecosystem function, species and trait composition. Top-down forcing from fish on plankton biomass was stronger in warm lakes, suggesting that a warmer climate will magnify the effect of introduced predators on biomass distribution. Fish and warmer temperatures select for the same species and traits of zooplankton in lakes, suggesting that lakes containing invasive predators may be less sensitive to warming. In Chapter 2 I test this hypothesis using a large-scale community transplant experiment, where I transplanted plankton communities that assembled and evolved at different elevations and predator regimes to new elevations and the addition or removal of fish. I found that past exposure to fish caused an evolutionary response in keystone members of the zooplankton community that increased their fitness in environments without fish. This suggests that past selection can change how communities will respond to further environmental change. In Chapter 3, I show that bottom-up processes influence fish growth, with higher growth rates occurring in warmer, clearer lakes. My thesis helps to elucidate the effects of temperature and predators on physiology, evolution, species ranges and community interactions, which is necessary to forecast the response of ecosystems to climate change. My thesis integrates across these levels of organization to understand the origin of ecosystem resilience in a changing climate.

INTRODUCTION

Determining the factors that control primary productivity and regulate its distribution among ecosystem components (including plants, animals, microbes, detritus and inorganic material) is a long-standing goal of ecology. The availability of resources can limit productivity through bottom-up forcing. For example, large-scale ecosystem productivity is frequently related to the supply of resources such as nitrogen and phosphorus in terrestrial, marine and freshwater ecosystems (Hecky and Kilham 1988, Elser et al. 1990, Vitousek and Howarth 1991, Stevens et al. 2015). In addition, the intensity of top-down consumption can alter the production and standing biomass of lower trophic levels across broad scales. Hairston *et al.*'s (1960) 'Green World' hypothesis posited that predators limit herbivores, allowing plants to grow abundant. Top-down forcing from consumers can result in a trophic cascade, or alternating top-down vs. bottom-up control of biomass of adjacent trophic levels (Carpenter et al. 1985, Terborgh and Estes 2010). As humans alter the global availability of nutrients (Falkowski et al. 2000) and introduce and extirpate species, particularly large-bodied top predators (Estes et al. 2011), understanding the role of consumer and resource control on ecosystems is of increasing importance.

Despite historical disagreements in the field of Ecology, both top-down and bottom-up control have been established as important structuring processes in ecosystems and food webs, and contemporary ecologists focus instead on the relative strength of bottom-up and top-down forces in food webs (e.g., Elton 1927, Hairston et al. 1960, Polis and Strong 1996, Gruner et al. 2008). The strength of resource and consumer control can vary greatly among ecosystems (Borer et al. 2005). For example, the addition of nitrogen and phosphorus generally increase primary productivity through bottom-up control, though the strength of the effect varies among habitat types (Elser et al. 2007). Similarly, the strength of consumer control can vary among ecosystems (Shurin et al. 2002). For example, the addition or extirpation of fish in lakes can cause a range of outcomes, from a strong change in algal abundance (Carpenter et al. 1987, Pace et al. 1999), to weaker or undetectable effects (e.g., Elser et al. 1995, Kim and DeVries 2000). The strength of both bottom-up and top-down control can be altered by biotic factors that affect predator-prey interactions. Bottom-up control can be altered by factors such as anti-herbivory traits and nutrient ratios (Cruz-Rivera and Hay 2000, Hessen et al. 2002, Hillebrand et al. 2009, Anderson et al. 2010), while the strength of top-down control can depend on the availability of prey refugia (Beukers and Jones 1998), body-size differences between predators and prey (Shurin and Seabloom 2005) and anti-predator adaptations (Sih et al. 2010, Ingram et al. 2012).

Abiotic environmental factors can also change the strength of resource and consumer control. Global warming has focused attention on the influence of temperature on the balance between top-down and bottom-up forcing. Different organisms and physiological processes vary in their thermal sensitivity (Dewar et al. 1999, Allen et al. 2005, Lopez-Urrutia et al. 2006, Dell et al. 2014, Uszko et al. 2017). For example, metabolism increases with temperature in both consumers and producers; however, empirical data show that photosynthesis does not increase as quickly as consumer metabolism (Dewar et al. 1999). Mathematical models indicate that the different temperature sensitivities of these processes influences the strength of top-down control (Vasseur and McCann 2005, O'Connor et al. 2011, Dell et al. 2014), though the predictions of the models are highly dependent on assumptions (Uszko et al. 2017). Experimental work has provided evidence that top-down control may increase with temperature (e.g., Hoekman 2011, Shurin et al. 2012). For example, an aquatic mesocosm experiment showed that increasing temperatures decreased phytoplankton and periphyton biomass while consumer biomass was relatively unchanged (Shurin et al. 2012). However, it remains unclear how bottom-up and top-down forces vary along broad environmental gradients in nature, such as temperature or nutrient supply.

This thesis describes work aimed at understanding the role of important abiotic and biotic factors, such as temperature, dissolved organic carbon (DOC) and community composition, in determining the relative strength of top-down and bottom-up control in California mountain lake ecosystems. Past studies measured the metabolic response of communities to changes in the environment in the absence of major ecological or evolutionary shifts. However, climate change occurs over long time-scales, where species composition and traits may shift in response to new environmental conditions and ultimately determine lake ecosystem structure and function. To answer important questions about the longer-term impact of higher temperatures, DOC and the introduction of predators, I used a unique large ‘natural laboratory’ of lakes in the Sierra Nevada where lakes are arrayed along a temperature and DOC gradient driven by elevation, and have a varied history of fish stocking. First, I ask how the strength of top-down control varies along broad elevational (temperature, DOC) gradients. Second, I ask how shifts in zooplankton species and trait composition alter community responses to changes in the environment and introduction of predators. Finally, I ask how bottom-up control on fish growth varies along the gradients in temperature and DOC. In each case, theory and empirical work provide conflicting evidence about the cumulative effects of consumers, prey and the environment. Theory and experiments in controlled environments such as mesocosms present a range of possible outcomes for the effects of warming and dissolved organic carbon (DOC) on top-down and bottom-up processes, which have yet to be evaluated in natural ecosystems. The use of this natural experiment can elucidate responses to changes in the environment over long time periods.

Recent changes to lake ecosystems – temperature, resources and predators

Increases in temperature over the last century have already greatly affected aquatic ecosystems and it is predicted that global temperatures, temperature variability, and frequency of extreme weather events will continue to increase (IPCC 2014). Alpine and polar aquatic ecosystems are particularly sensitive to climate warming (Hauer et al. 1997), as reduced snowpack and ice cover results in decreased albedo and higher heat absorption, magnifying the effect of higher air temperatures (Bradley et al. 2004). As a result, organisms inhabiting these environments are more susceptible to warming. In lakes, many cold-water zooplankton that are large-bodied (cladoceran and copepods) are expected to decline as temperatures warm (Moore et al. 1996). Warmer temperatures favor small zooplankton because warming increases the cost of development and respiration more than ingestion (Moore et al. 1996). A reduction in mean body size of zooplankton can have large effects on aquatic ecosystems (reviewed in Moore and Folt 1993). For example, a decrease in the mean size of zooplankton can influence the biomass of phytoplankton, resulting in lower water clarity (Mazumder et al. 1990) and lower fish abundance (Moore and Folt 1993). Therefore, indirect effects of climate change through physical processes and ecological interactions are likely to be critical determinants of the future state of aquatic ecosystems and may be as important as the direct effects of changes in the physical environment (Blois et al. 2013, Alexander et al. 2015).

One indirect effect of warming is the "browning" of lakes, as inputs of DOC of terrestrial origin increases (Larsen et al. 2011). In particular, allochthonous DOC inputs to inland waters in Europe and North America have increased since the 1990s (Evans et al. 2006), driven by an increase in soil decomposition at higher temperatures (Schmidt et al. 2002) and increases in vegetation growth in alpine watersheds due to tree-line advance (Walther et al. 2005). Terrestrially-derived allochthonous DOC contains recalcitrant, colored compounds, which reduce water transparency, attenuate light, increase bacterial production, and suppress phytoplankton production (reviewed in Williamson et al. 1999). Conflicting hypotheses have been proposed to relate bottom-up forcing from DOC to fish production in lakes (Karlsson et al. 2009, Jones et al. 2012, Finstad et al. 2014, Benoît et al. 2016)**.** DOC may enhance fish production by blocking harmful UV rays and by stimulating microbial production that is transferred through food webs (Hessen et al. 2009, Karlsson et al. 2009). Alternatively, DOC may reduce fish production if it provides poor quality food, and decreases aquatic primary production through shading (Brett et al. 2017). Examining the role of DOC in nature will help to determine when DOC will function to as a subsidy or control on production in lakes. Additionally, increases in temperature and

DOC are occurring simultaneously, yet we have little understanding of their synergistic effects on lake ecosystems.

In addition to changes in environmental condition, many species of fish have been introduced to lakes outside their natural ranges intentionally for food and sport, or unintentionally from aquaria and bait buckets (Strayer 2010). Relevant to this thesis, fishes have been introduced into many naturally fishless high elevation lakes around the world, reducing the diversity and abundance of native fauna (Schindler and Parker 2002, Sarnelle and Knapp 2005). Many impacts of introduced predators result from large consumptive effects on naïve prey (reviewed in Sih et al. 2010). Most fish are visual predators and selectively prey on large zooplankton (e.g., keystone *Daphnia* spp.), thereby reducing zooplankton abundance and mean body size (Brooks and Dodson 1965). The effects of fish predation propagate through cascading trophic interactions (Carpenter et al. 1985). For example, in a 3-level food chain, planktivorous fish suppress herbivorous zooplankton, resulting in increased phytoplankton biomass (Carpenter et al. 1985). Indeed, lake trophic cascades have been shown in whole-lake experiments, cross-lake comparisons and mesocosm experiments (Estes et al. 2011), though there is large variation in the magnitude of predator effects (Terborgh and Estes 2010). Thus, the introduction of fish to lakes has cascading effects on diversity, species composition and biomass.

Multiple stressors and timescales of change

The possibility for adaptive phenotypic changes to occur on ecological time-scales has been highlighted by studies of species responses to anthropogenic stressors (Hairston et al. 1999, Latta et al. 2010). These studies demonstrate that genetically based phenotypic changes can influence ecological processes such as consumer-resource dynamics (Hairston et al. 1999, Yoshida et al. 2003) and rescue species from extinction (Carlson et al. 2014). Although population differentiation can influence ecological processes, many studies are conducted over time scales too short for ecological or evolutionary shifts, ignoring the role of local adaptation in community resilience (but see Zuppinger-Dingley et al. 2014 for example). For example, experiments examining community response to temperature typically expose a community to different temperatures (e.g., Strecker et al. 2004); however, shifts of species and traits over longer time periods may moderate the effect of environmental change on populations or communities. Therefore, a combination of experiments and studies over natural temperature gradients where communities have assembled and evolved over longer time periods will give a clearer indication of the long-term effects of changes in climate.

Global environmental change may interact to reduce or amplify the impact of other stressors on communities depending on the co-tolerances of species to the stressors in question (Vinebrooke et al. 2004, Christensen et al. 2006). For example, higher temperatures favor small-bodied zooplankton, thus warmer lakes may be more resistant to changes in composition and biomass when fish are introduced. However, the indirect effects of the environment on species interactions can be as important as the direct effect of climate change on species (Blois et al. 2013, Alexander et al. 2016). It remains unclear how many of the stressors facing mountain lakes will interact to influence community structure and function in nature where there is turnover in species composition and adaptation to new environments over time (Alexander et al. 2016).

In addition, the type of disturbance (e.g., press, pulse, fluctuating) will influence population and community responses. For example, the addition of invasive fish to a lake is akin to a press disturbance where the lake community experiences fish presence from the point of introduction onward. Conversely, although mean temperatures are increasing, temperature varies spatially and temporally within lakes – with depth, interannually, seasonally – which may change the strength or type of selection to temperature change (Murren et al. 2015). We might expect to see more local adaptation, or fixed differences among populations in response to the addition of fish, whereas populations may adapt to new temperature regimes with increased plasticity due to natural temperature fluctuations. The mechanisms by which populations adapt to changes in the environment have not been examined over broad environmental gradients in nature.

Study site

Alpine lakes in the Sierra Nevada provide an ideal system to ask questions about the independent and interactive effects of temperature, DOC and introduced predators. The altitudinal gradient provides a natural gradient in temperature and DOC, and the history of fish stocking means that some lakes are fishless, while others contain self-sustaining populations of trout. Generally, lakes in the Sierra are small (0.5-10 ha surface area), shallow (<15 m in maximum depth) and are located throughout subalpine and alpine zones (Knapp et al. 2001). They are oligotrophic, species-poor and ice-free for only 4 months per year (Melack et al. 1985). Due to similar glacial origin and bedrock, these lakes show little variation in physical and chemical characteristics (Melack et al. 1985, Sadro et al. 2011, Piovia-Scott et al. 2016).

Prior to fish stocking, 99% of the lakes of the Sierra Nevada were fishless due to barriers to upstream movement of fish (Knapp 1996). Fish stocking began in the mid-1800s, and over the next century 80-95% of the lakes were stocked to create recreational fishing opportunities (Knapp 1996, Knapp and Matthews 2000). The three most commonly stocked fish were rainbow trout (*Oncorhynchus mykiss*), golden trout (*O. m. auguabonita*), and brook trout (*Salvelinus fontinalis*) (Knapp 1996). This decreased zooplankton species richness, and shifted community composition to small crustacean species, extirpating formerly abundant species of large crustacean zooplankton (Knapp and Matthews 2000, Knapp et al. 2001). The species of zooplankton that were not extirpated by fish introduction rapidly evolved new life history traits associated with fish predation: smaller offspring, smaller size at maturity and shorter time to maturity (Fisk et al. 2007). Lakes with introduced fish have higher phytoplankton biomass than their fishless counterparts, which is mainly driven by reduced zooplankton herbivory (Sarnelle and Knapp 2005). Because some lakes contain introduced populations of trout while others remain fishless, this is an ideal system to ask questions about the role of predators in lakes. Additionally, the elevation gradient provides broad environmental gradients, particularly in temperature and terrestrial DOC loading, to examine how the environment shapes top-down and bottom-up forcing in nature.

Chapter summaries

In Chapter 1, I ask if climate determines predators' impact on lake ecosystems. I address this knowledge gap by comparing lakes with and without stocked trout along an elevational temperature and DOC gradient. I show that a warmer climate destabilizes mountain lake ecosystems by increasing the cascading effects of predators on lower trophic level biomass. Shifts in species composition dampened the impact of fish on invertebrate and algal biomass in cold, low DOC lakes more than warm, high DOC lakes. Warming experiments have shown that consumer-resource interactions increase in strength with temperature due to differential physiological responses of producers and consumers. My results from a natural system where communities vary in species and size composition along an elevational gradient show that temperature can mediate the strength of trophic cascades.

In Chapter 2, I ask if phenotypic selection within and among species can shape responses to top-down (fish) and bottom-up (temperature) forcing. I used an innovative and large-scale community transplant experiment (analogous to a common garden experiment) across elevation to determine how communities that varied in their ecological and evolutionary history respond to changes in elevation-related environmental variables and addition of predators. My experiment revealed that past selection by fish on plankton species composition and phenotypic traits influence resilience to predator extirpation. Zooplankton communities with an evolutionary history of exposure to fish predation reached higher trophic level biomass in the absence of fish than those from fishless lakes. This non-transitive response of fish addition and removal was likely driven by selection on life-history traits that persisted over many generations. Interestingly, the effect of experimental elevation was unrelated to the origin of the community, suggesting that phenotypic plasticity dominates the response of zooplankton to temperature, while genetic adaptation is more important for predation.

In Chapter 3, I ask how bottom-up forcing from temperature and DOC affects fish growth rates. I sampled fish populations along broad environmental gradients to determine correlates of fish growth rates and body condition. I found that fish grew faster in warmer lakes, and slower in high DOC lakes. Additionally, I examined the role of chemical characteristics of the DOC pool (the contributions of terrestrial or algal based DOC) and found that high DOC quality was associated with better fish body condition. Lakes are experiencing ongoing warming and browning, and this chapter provides insight into the impact these changes will have on the growth rates of fish in oligotrophic, low DOC mountain lakes that are predicted to be the most influenced by small changes in DOC concentration. The antagonistic interaction between temperature and DOC suggests that as lakes warm and brown there will be a weaker impact on fish growth if these two stressors occur simultaneously than if either occurred independently.

Conclusion

The impacts of environmental change on populations, communities and ecosystems play out over long periods through community assembly and trait evolution. However, most climate change experiments are too short to observe the effects of these processes on population persistence and ecosystem functioning. By integrating information from lake surveys and a mesocosm experiment using communities from different selective histories, I was able to disentangle the effects of temperature, DOC and predators on the structure of lake populations, communities and ecosystems over times scales that are relevant to future climate change. By examining the impact of temperature and predators on natural lake ecosystems I determined their long-term effects on food web structure and community composition (Chapter 1). By measuring the response of communities with different selective histories to the combined impacts of predators and elevation I determined how ecological and evolutionary change influence the resilience of lakes communities to future environmental change (Chapter 2). Finally, by examining the growth of fish along temperature and DOC gradients, I determined how this important ecosystem service may respond to different environmental changes in the future (Chapter 3). These studies provide insight into how climate change will influence California mountain lakes and supplement theory and experiments that have not considered the implications of long-term shifts in traits and species, and the impact of these on ongoing and future climate change.

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CHAPTER 1

Climate constrains lake community and ecosystem responses to introduced predators

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Climate constrains lake community and ecosystem responses to introduced predators

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Human activities have resulted in rising temperatures and the introduction or extirpation of top predators worldwide. Both processes generate cascading impacts throughout food webs and can jeopardize important ecosystem services. We examined the impact of fish stocking on communities and ecosystems in California mountain lakes across an elevation (temperature and dissolved organic carbon) gradient to determine how trophic cascades and ecosystem function vary with climate. Here, we show that the impact of fish on the pelagic consumer-to-producer biomass ratio strengthened at low elevation, while invertebrate community composition and benthic ecosystem rates (periphyton production and litter decomposition) were most influenced by predators at high elevation. A warming climate may therefore alter the stability of lake ecosystems by shifting the strength of top-down control by introduced predators over food web structure and function.

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1. Introduction

Predators can have a large impact on community structure, biomass and ecosystem productivity in terrestrial, marine and freshwater ecosystems through trophic cascades [1,2]. However, the magnitude of predator effects (i.e. trophic cascade strength) [2] varies tremendously within and among systems. While there are iconic examples of trophic cascades across many types of ecosystems [2], similar studies have shown weak or non-existent effects under different conditions [3]. Climate and its indirect effects on species interactions may be one of the many factors explaining variation in predator effects. Trophic cascade strength may be influenced by temperature and associated terrestrial subsidies to aquatic environments [4]. Temperature may influence trophic cascade strength because organisms within a community vary in their thermal sensitivity [5]. Similarly, terrestrial subsidies to aquatic environments may influence trophic cascade strength by disproportionately benefitting top predators [6]. Therefore, indirect effects of climate, as a result of changing species interactions, may be as important as the direct physiological effects of climate on populations [7,8]. However, there is a lack of data from natural systems to predict the effect of climate on trophic interactions and resulting changes to future ecosystem states.

Two major changes occurring in aquatic systems as a consequence of climate change are warming and 'browning', or increasing inputs of dissolved organic carbon (DOC) of terrestrial origin. Indications of warming are apparent in rising water temperatures, reduced duration of ice cover and shallower mixed-layer depths [9]. Allochthonous DOC inputs to inland waters in Europe and North America have increased concurrently with warming since the 1990s [10], due to decreasing atmospheric acid deposition [11], an increase in soil decomposition [12] or increases in vegetation growth in alpine watersheds due to tree-line advance [13]. Thus, increases in temperature and DOC are occurring simultaneously, yet we have little understanding of their independent or synergistic effects on lake ecosystems.

Experiments and theory show that trophic cascades may become stronger at warmer temperatures and higher DOC concentrations [4,6,14–16]. Predictable scaling of physiological processes such as photosynthesis and metabolism with

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temperature allow for mechanistic modelling of food web interactions and dynamics under global warming [4,15]. Food web models predict that the ratio of herbivores to producer biomass should increase with temperature, suggesting that higher temperature increases top-down control [16]. Experiments manipulating temperature also generally show stronger top-down control at high temperatures [14,16]. For example, Shurin *et al*. [16] showed that warming by 3°C magnified the cascading impact of fish predators on phytoplankton in shallow experimental freshwater ecosystems. Studies to date have largely focused on responses to warming due to differential physiological responses of organisms to their environment [5]. Less is known about the impact of brownification on top-down control [6]. DOC may have similar effects to temperature by subsidizing higher trophic levels, leading to increased predation and stronger cascading effects on lower trophic levels [6,17]. However, the independent and interactive effects of temperature and allochthonous detritus on the strength of trophic cascades in natural lakes remain unknown.

Climate and predators may interactively affect food web structure in lakes because they each exert large effects on a common set of prey traits [18–20]. For instance, fish preferentially prey on large zooplankton (e.g. keystone *Daphnia* spp.), reducing zooplankton mean body size [18]. Warmer water also selects for smaller body size of aquatic organisms across trophic levels [20,21]. As both the presence of fish and higher temperatures favour smaller zooplankton body size, we expect the two to exert interactive effects on lake food webs and ecosystems.

In addition, fish and warming influence rates of production and decomposition in benthic ecosystems [16,22]. Benthic food webs have greater overlap in body size between trophic levels than in pelagic environments [23]. Trophic interaction strength is increased by larger predator–prey size ratios [24]. As predator–prey size ratios are often greater in pelagic than benthic habitats [23], the effect of predators on lower trophic levels may also be stronger. However, the interactive effects of predators and climate on benthic productivity and decomposition in natural lakes are unknown.

Alpine lakes in the Sierra Nevada mountains are an ideal system to ask questions about the independent and interactive effects of climate and changing trophic structure. Altitudinal variation provides a natural gradient in temperature and DOC, and while all lakes are naturally fishless, some contain introduced populations of trout. We tested the hypothesis that trophic cascades are stronger at lower elevations in mountain lake ecosystems where communities have assembled and species have adapted to different climates and predation regimes over periods from decades to millenia. Here, we show that turnover in species composition and traits can buffer against changes in biomass ratios induced by introduced trout in high-elevation, but not low-elevation lakes.

2. Material and methods

(a) Sampling design

The study concentrated on 29 lakes that varied in elevation, of which 15 contained trout populations and 14 were fishless. The presence of fish was determined by a survey published in 2001 [25] and sustained fish presence was confirmed by visual inspection at the time of sampling at each lake by observing fish through the water or jumping at the surface. Brook trout (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*) are the only species found in these lakes and fish biomass is greater in high elevation lakes (R. Knapp 2013, personal communication). In July and August 2013, we collected samples of macroinvertebrates, zooplankton, chlorophyll-*a* (chl-*a*), water chemistry and ecosystem rate measurements (benthic production and litter decomposition) from each lake. All lakes were sampled twice, 31 days apart, except for four fishless lakes that were only sampled once due to a forest fire (the Rim Fire), and three fishless lakes were sampled 28 days apart due to the likelihood that fire would move into the area.

(b) Sampling procedure

During the first visit to each lake a HOBO pendant temperature logger (Onset Computer Corporation, Bourne, MA, USA) was installed at an approximately 45 cm depth at the edge of the lake. The logger recorded temperature at hourly intervals between the two sampling dates. Zooplankton samples were collected from the deepest point of the lake by pulling a 63 µm mesh conical net with a 30 cm diameter through the water column, starting 2 m above the lake bottom. Macroinvertebrate samples were collected using a 20 cm wide sweep net with 0.5 mm mesh. Twenty 1 m sweeps were taken from the shoreline and care was taken to include sweeps from each type of littoral substrate. Zooplankton and macroinvertebrates were preserved in 70% ethanol.

Macroinvertebrate samples were enumerated and identified in their entirety, usually to the taxonomic level of family. Zooplankton samples were identified and enumerated using a Leica microscope, using a protocol designed by Girard & Reid [26]. Successive subsamples representing between 0.5 and 4% of standardized 100 ml sample volume were processed until a minimum of 250 individuals were enumerated, such that the maximum contribution of each individual taxon to the total count was less than 50 for adults and less than 30 for copepidids and nauplii, even if more of these individuals were enumerated. After 250 individuals were enumerated, the remaining sample was scanned to detect rare species. Adult crustacean zooplankton were identified to the species level, copepodites were identified to order and rotifers were identified to genus. For both macroinvertebrate and zooplankton samples, 15 individuals of each taxon from each lake were measured and converted to biomass using published length–weight regressions. Community biomass was calculated using a weighted average of the lake-specific biomass of each taxa.

Surface water samples were collected at the deepest point of each lake using a 1 m integrated tube sampler and filtered through 63 µm mesh to remove zooplankton. For chl-*a* analysis, a known volume of water was filtered through a glass fibre filter (Whatman GF/F, pore size 0.45 µm), which was kept cool until returning to the laboratory and then frozen until extraction. Chl-*a* concentration was then determined using a Turner Trilogy fluorometer (Turner, USA) following a 24 h cold (approx. 4°C) methanol extraction.

At the deepest point in each lake we took *in situ* measurements of temperature, conductivity, dissolved oxygen (DO) and pH at each metre of depth using a field probe (YSI Incorporated, Yellow Springs, Ohio, USA). Surface water samples for total Kjeldahl nitrogen (TKN), total phosphorus (TP), DOC and alkalinity were collected from the deepest point of each lake using a 1 m integrated tube sampler, filtered through 63 µm mesh to remove zooplankton and stored in a cool place until returning to the laboratory. TKN and TP samples were preserved in 20 ml triple-rinsed high-density polyethylene (HDPE) scintillation vials with H_2SO_4 to a pH below 2 and kept cool. Samples were processed at the University of California, Davis analytical laboratory (http://anlab.ucdavis.edu/) within 30 days of being collected. DOC samples were filtered through pre-combusted glass fibre filters (Whatman GF/F filters, 0.45 µm pore size) and preserved with HCl in triple-rinsed 40 ml glass vials. DOC was measured using a total organic carbon analyser (TOC-V CSN, Shimadzu Scientific Instruments, Japan). Alkalinity was measured using a total alkalinity test kit (Thermo Scientific Orion total alkalinity test kit).

(c) Ecosystem function measurements

Benthic production was determined by measuring the growth of periphyton on ceramic tiles placed at a depth of 30 cm, similar to the one described in [22]. On the first visit to each lake, five 10.6 cm^2 unglazed tiles were placed along the shore. On the second visit, tiles were collected and periphyton was scrubbed off and filtered through a glass fibre filter to be analysed in the same way as chl-*a* samples. Benthic production was not measured for four lakes that were only visited once due to fire, as well as one that was fishless and three containing fish where the tiles disappeared. Benthic production was calculated as microgram of chl-*a* per centimetre of tile produced over the incubation period.

Decomposition rates were measured by installing leaf litter bags into each lake and measuring mass loss over time. Willow (genus *Salix*) litter was collected from a single stand of trees and dried for 24 h at 40°C. We weighed 5 g of dried litter and enclosed it in a 1 mm mesh bag. These bags were anchored to the lake bottom at a depth of approximately 45 cm. Bags were collected during the second visit to the lake. Upon returning to the laboratory, all invertebrates present in the litter were separated and preserved in 70% ethanol for enumeration. Wet litter was dried for 24 h at 40°C and weighed to determine mass lost during incubation. Decomposition rate was calculated as the mass lost per day. In addition to the four lakes that were only visited once, decomposition rate was not measured for two lakes, one fishless and one containing fish, due to missing litter bags. Invertebrates in the litter bags were identified, enumerated and biomass was calculated according to the methods described for macroinvertebrates.

(d) Calculations and statistical analysis

For all analyses, elevation was used as the predictor when we were interested in the response along both the temperature and DOC gradient, and DOC and temperature were analysed in structural equation models (SEMs) in order to distinguish their independent effects. The mean temperature for each lake was calculated as the mean recorded by the temperature logger between the two sampling occasions. For lakes that were only visited once and for three lakes where the temperature logger was lost, the mean temperature was taken to be the mean temperature recorded during sampling dates. Linear mixed-effects models (LMEs) were used to determine additive and interactive effects of fish and elevation on temperature, DOC, pH, conductivity, DO, TKN and TP (electronic supplementary material, appendix S1). Lake was included as a random effect to account for temporal pseudoreplication. Data were log-transformed when it improved normality by observing plots of fitted versus residual values, histogram of the residual values, normal quantile plots and leverage plots. The function lme from the package 'nlme' was used.

To investigate the effect of elevation and fish on community composition, we compared zooplankton species turnover along elevation gradients in lakes with and without fish following [27]. First, rare species (those that both occurred in less than 5% of lakes and represented less than 0.02% of total individuals across all lakes) were removed from this analysis as they can have a disproportionate influence on ordination results. Remaining species abundances were Hellinger-transformed to reduce the influence of zeros common in community data. We used a Mantel test to test the significance of the relationship between Bray–Curtis community dissimilarity and the difference in elevation between pairs of lakes separately for fish and fishless lakes. The slope of this line is defined as the species turnover along the elevation gradient [27]; therefore, an analysis of covariance (ANCOVA) was used to determine if there was a difference in species turnover between lakes with and without fish. To determine whether the effect of fish on community composition varied with elevation, the Bray–Curtis dissimilarity of zooplankton communities from all pairwise comparisons of lakes where one contained fish and one was fishless was regressed against the mean elevation of the two lakes.

Both water temperature and input of terrestrial detritus can change with elevation. To understand how zooplankton body size varied with elevation and predation gradients, we fitted a multigroup SEM [28] to examine the indirect effect of elevation on average zooplankton body size through both temperature and DOC (figure 2*c*). We used log-transformed data to ensure relationships were linear and normalize variance. We compared linear models to ones including both first- and second-order terms using AICc, and all relationships were best modelled using a linear function. We fitted our SEM by fixing the variance of each exogenous variable to 1, to reduce the number of parameters estimated due to low sample size and our goal of estimating path parameters [28]. We used fish status as a grouping variable and compared models using log-likelihood tests where each path coefficient was either the same or allowed to vary between the fish and fishless group. We fitted the model using the function *sem*() in the lavaan package in R [29]. Because DOC was the only significant predictor of zooplankton body size in the SEM (figure 3), we used LME models as above to determine the additive and interactive effects of fish presence and DOC average zooplankton body size.

To assess how food web structure varied along the elevation gradient we fitted a SEM as above to log-transformed ratio of zooplankton biomass to chl-*a* (the pelagic consumer : producer biomass ratio). Because temperature was the only significant predictor of food web structure, we used LME models as above to determine the additive and interactive effects of fish presence and mean temperature on zooplankton biomass, chl-*a* and the ratio of zooplankton biomass to chl-*a*.

To determine how litter decomposition and benthic productivity varied along the elevation gradient, we again first used SEM to identify temperature as the only significant variable influencing these variables and then a LME model to determine the independent and interactive effects of temperature and fish on benthic ecosystem rates.

All analyses were completed in R [30].

3. Results

Lakes with and without fish were similar in many physical and chemical characteristics due to common glacial origin and bedrock (electronic supplementary material, appendix S1) [31]. Generally, the lakes sampled were small (0.5–10 ha surface area), shallow (less than 15 m in maximum depth) and oligotrophic (chl-$a < 3.4\ \mu g\ l^{-1}$). Both DOC and temperature were correlated with elevation ($p < 0.001$; DOC: $r = -0.63$, temperature: $r = -0.81$). Although there was a significant positive relationship between DOC and temperature, temperature only explained about half of the variation in DOC (figure 1), therefore the two were not perfectly co-linear, allowing us to statistically distinguish their associations with ecological structure and function.

(a) Species composition

We found that zooplankton species composition varied strongly with elevation in fishless lakes, but not those with fish populations (figure 2*a*). That is, warm and cold fishless lakes contained very different communities of zooplankton,

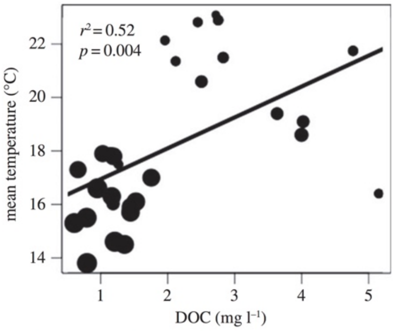

Figure 1. The relationship between DOC and mean water temperature. The size of the points corresponds to elevation, with size increasing from low to high elevation.

while similar species were found at all elevations in lakes containing fish. In addition, fish-containing and fishless lakes had entirely distinct zooplankton communities in high-elevation lakes, but converged in composition at lower elevation (figure 2*b*; electronic supplementary material, figure S3). This result is consistent even when we only compared lakes at similar elevations instead of all pairwise comparisons of fish-containing and fishless lakes (electronic supplementary material, figure S4). Body size was a key predictor of species responses (figure 2*c*). Average individual zooplankton size was not influenced by DOC in fishless lakes (lm, $p = 0.12$), but increased with DOC in lakes with fish (lm, $p = 0.02$; figure 2*c*).

(b) Pelagic food web structure

Our SEM shows that elevation acted though temperature and not through DOC to influence the biomass ratio of zooplankton : chl-*a*. Neither DOC nor temperature influenced consumer : producer biomass ratios in the presence of fish (figure 3*a*); however, in fishless lakes, temperature had a strong positive influence on biomass ratios (figure 3*b*). By contrast, average zooplankton body size increased with DOC in lakes containing fish (figure 3*c*), but not in fishless lakes (figure 3*d*).

Both chl-*a* concentration (a proxy for phytoplankton biomass) and zooplankton biomass increased with temperature regardless of fish presence (figure 4*a*,*b*). However, zooplankton biomass showed a steeper increase with temperature than chl-*a*, and biomass pyramids (the ratio of zooplankton biomass to chl-*a*) were interactively affected by temperature and fish (figure 4*c*). Cold lakes had similar biomass ratios regardless of fish presence; however, warm lakes sustained a higher biomass of zooplankton per unit chl-*a* when fish were absent than in their presence.

(c) Benthic ecosystem rates

Both benthic primary production and the decomposition of organic matter responded to elevation differently between lakes with versus without fish. Decomposition decreased with increasing temperature in fishless lakes, whereas lakes containing fish had slow decomposition at all temperatures (figure 5*a*). Decomposition was positively correlated with the number of invertebrate detritivores ($r = 0.54$, $p < 0.001$), which was lowest in the presence of fish and at high temperatures ($r = 0.54$, $p < 0.001$). The growth of periphyton was positively affected by fish and high temperature (figure 5*b*). Fish increased benthic production and reduced decomposition most at lower temperatures. Thus, predators had larger effects on benthic ecosystem processes in colder lakes where they tended to exert stronger control on the numbers of benthic invertebrates that consume algae and terrestrial detritus.

4. Discussion

Our lake survey indicates that environmental temperature alters the expression of trophic cascades in mountain lake ecosystems varying in elevation. We found the most pronounced pelagic trophic cascades in warmer, low-elevation lakes where fish exerted stronger effects on the biomass of pelagic consumers relative to producers. At high elevation, trophic cascade strength was probably dampened by both lower temperature and the large shift in species composition and body size between lakes with and without fish. These results suggest that species turnover among zooplankton between fish and fishless lakes reduces the strength of trophic cascades in cold lakes, but not in warm lakes. Warming and associated increases in DOC concentration may therefore reduce the resilience of food webs to introduced predators by eliminating the large zooplankton species that persist in cold, low-DOC fishless lakes.

Similar zooplankton species were found in lakes with fish at all elevations, consistent with previous findings that both fish and higher temperatures independently select for a similar set of species [32]. In past studies, the mechanism invoked to explain this pattern is that high temperature and fish both select for small-bodied species. However, in our survey we found that zooplankton body size was more closely related to DOC concentration than to temperature (figure 3). This may be because larger-bodied zooplankton are protected from visual fish predation at high DOC [33]. Another possibility is that DOC attenuates ultraviolet radiation (UVR) in the water column, protecting zooplankton from potential UVR damage (reviewed in [34]). Interestingly, our data are consistent with the conceptual model and data presented in [35], which shows that UVR tolerance is related to zooplankton body size via the behavioural response to visual predators such as fish. This model assumes that in lakes with fish, large-bodied zooplankton are found in the hypolimnion and smaller-bodied zooplankton are more often in the epilimnion during the day. This leads to selection for higher UV tolerance in small-bodied species in lakes with fish and is consistent with the pattern we found of increasing body size with DOC (figure 2). In fishless lakes, all sizes of zooplankton are found in the surface waters where UVR is high and the UVR shading effect of DOC should be similar for large and small zooplankton. Our results are consistent with this expectation (figure 2). It is likely that UVR imposes selection on zooplankton in this system because species found in low-DOC fishless lakes (*Hesperodiaptomus shoshone* and *Daphnia melanica*) are heavily pigmented, indicating adaptations to protect against photo-damage [34]. Previous research in California's Sierra Nevada alpine lakes has shown that zooplankton species less than 1 mm in size are more often found sympatric with fish [36]. Our study further reveals an interactive effect of DOC and fish on zooplankton,

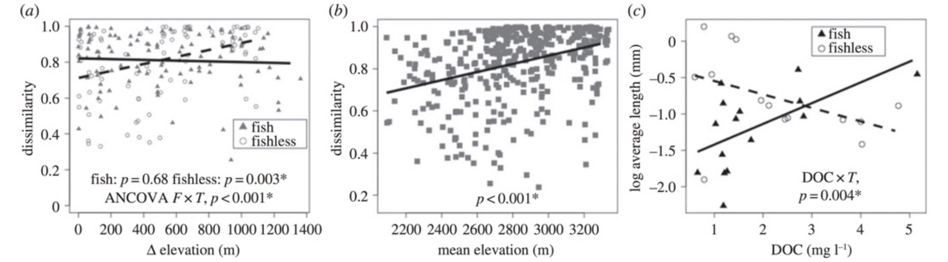

Figure 2. The effect of elevation and fish on zooplankton species turnover and size structure. (*a*) The Bray–Curtis dissimilarity of zooplankton communities in all pairwise comparisons of lakes containing fish (grey triangles, solid line) and all pairwise comparisons of fishless lakes (white circles, dashed line) as a function of the difference in mean temperature between the two lakes. The slopes represent species turnover along a temperature gradient. *p*-values were calculated using Mantel tests. (*b*) The Bray–Curtis dissimilarity of all pairwise comparisons of zooplankton communities in fish–fishless pairs of lakes as a function of the mean elevation of the lakes. (*c*) The mean body length of zooplankton as a function of DOC and fish.

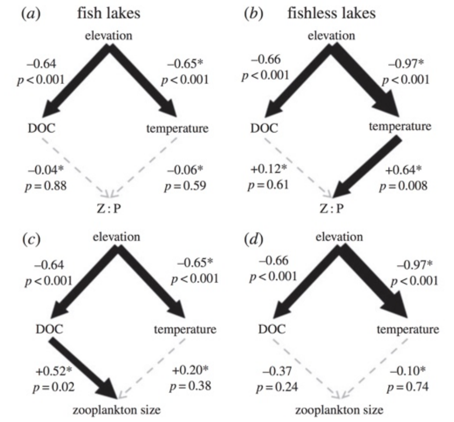

Figure 3. The results of the SEM for lakes (*a*,*c*) with and (*b*,*d*) without fish. (*a*,*b*) Results of the SEM for the ratio of zooplankton biomass to chl-*a*, and (*c*,*d*) for average zooplankton body size. The widths of the arrows are scaled to the standardized coefficients which are also reported with the corresponding *p*-values next to each arrow. Significant relationships are shown in black, while non-significant relationships are shown in grey. Asterisks represent path coefficients that are significantly different between fish and fishless lakes.

such that body size increases with DOC only in lakes with fish. Thus, fish effects on zooplankton size structure are strongest in high-elevation lakes, possibly due to higher UVR tolerance of small-bodied zooplankton, induced by a behavioural response to fish among larger zooplankton.

Although predators' influence on prey community composition and size structure was strongest in high-elevation lakes, their effect on the distribution of biomass among planktonic producers and consumers was greatest in warm, low-elevation lakes. The amount of consumer (zooplankton) biomass sustained per unit producer (chl-*a*) biomass increased with temperature, but only in the absence of fish (figures 3 and 6). Thus, the cascading effect of predators on the distribution of biomass among lower trophic levels was strongest at high temperature. Warming experiments have shown that consumer–resource interactions increase in strength with temperature due to differential physiological responses of producers and consumers [4,6,14–16], as predicted by metabolic theory [37]. Our results from a natural system where communities vary in species and size composition along an elevational gradient show the generality of temperature in mediating the strength of trophic cascades.

Producers and consumers may also be differently sensitive to UVR, which varies with elevation (reviewed in [38]). Studies of UVR effects on zooplankton and phytoplankton have produced mixed results. Some show UVR inhibits phytoplankton photosynthesis in high-elevation alpine lakes [39], while others indicate no change [40]. Some studies have found that grazers are more sensitive to damage from UVR than producers, suggesting that top-down control is weakened in high-elevation sites with high UVR [41,42]. For our study, this suggests that ZB : PB ratios would increase in high-elevation, low-DOC lakes; however, we only found this pattern in fishless lakes (figure 2). In addition, temperature was a stronger predictor of pelagic biomass ratios than DOC (figure 3), indicating that thermal constraints on food webs may be more important than UVR. Overall, our results are consistent with theory and experiments that have shown stronger top-down control with increasing temperature.

There are probably two mechanisms by which trophic cascade strength is dampened at high elevation. First, metabolic theory predicts that heterotrophs will be more sensitive to rising temperatures than autotrophs, resulting in higher rates of photosynthesis relative to heterotrophic respiration in cold waters [4,5,15]. Second, turnover in species composition and size structure can change the strength of trophic interactions [19,24]. Cold, low-DOC, fishless lakes had the most distinct community composition and largest average zooplankton body size (figure 6). Many large-bodied species (e.g. *H. shoshone* and *D. melanica*) do not co-occur with fish [25]. When fish are introduced to these lakes, trophic cascades may be initially strong as fish extirpate large-bodied grazers. However, over time new smaller zooplankton species invade, potentially reducing the strength of trophic cascades [25]. Our data indicate that the buffering capacity of species turnover is weaker in warm lakes than colder lakes, probably because zooplankton communities in warm fishless lakes already contain the smallest species in

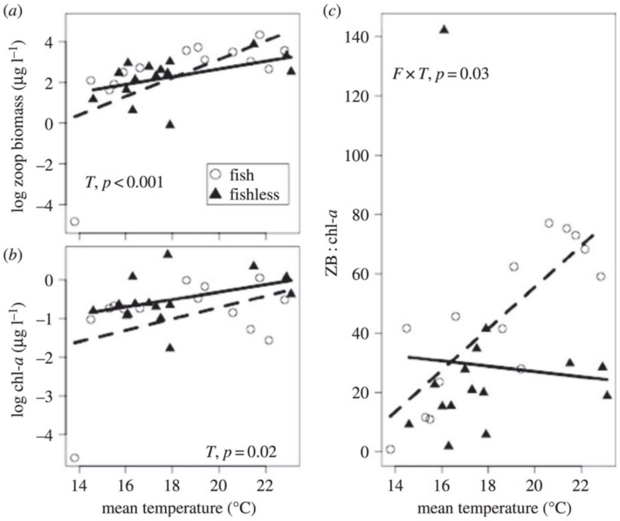

Figure 4. The effect of temperature on the log-transformed average pelagic biomass of (*a*) zooplankton, (*b*) phytoplankton (chl-*a* concentration) and (*c*) the ratio of zooplankton to chl-*a* (ZB : PB) for lakes along a temperature gradient. Lakes containing fish are represented by triangles and a solid line; fishless lakes are represented by circles and a dashed line.

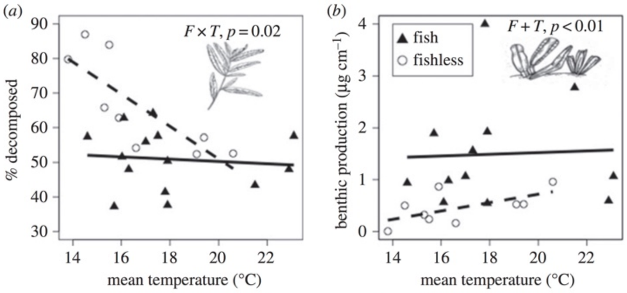

Figure 5. The effect of temperature on ecosystem rates, including (*a*) the percentage of leaves decomposed over a 31-day incubation period and (*b*) benthic production per incubation period (31 days) for lakes along a temperature gradient. Lakes containing fish are represented by triangles and a solid line; fishless lakes are represented by circles and a dashed line.

the regional pool (figure 6). Thus, warmer temperatures reduce the capacity of species replacement to buffer the effects of fish on pelagic food web structure.

Trophic interactions and climate can also determine the flux of materials through ecosystems and transformation between the organic and inorganic state [22,43]. We found that both benthic biomass production and decomposition of organic matter in the study lakes responded to temperature differently in lakes with versus without fish. Fish increased benthic production and reduced decomposition similar to previous experiments [16,22] and their effect was strongest at lower temperatures (figure 5). Fish can have cascading effects on periphyton growth through predation on zoobenthos [44]. This effect may have been stronger in cold lakes due to low abundance of macrophytes, which can provide refugia for invertebrates from fish predation [45]. Surprisingly, leaf detritus decomposed fastest in cold lakes. Microbial and invertebrate metabolisms are expected to increase with temperature, leading to faster degradation of organic matter [46,47]. However, benthic invertebrates were most abundant in cold lakes without fish, suggesting that detrital processing may be limited by their activity more than the temperature sensitivity of microbes. Thus, predators had larger effects on benthic ecosystem processes in colder lakes, where they tended to reduce the numbers of invertebrates that consume algae and terrestrial detritus.

The cascading effect of top predators on lake ecosystems has become one of the dominant paradigms of ecology [48].

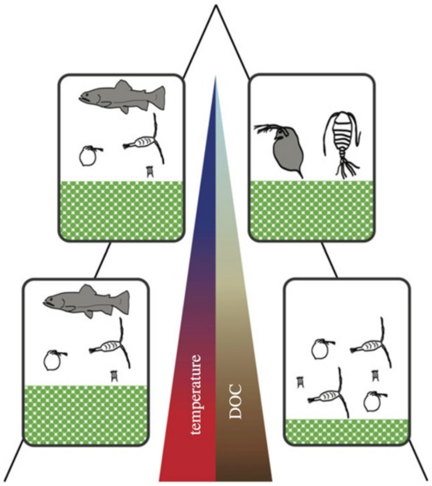

Figure 6. A schematic of communities and relative biomass of zooplankton and chl-*a* along the elevational temperature gradient. Boxes on the left show communities sympatric with fish. The biomass ratio of zooplankton and chl-*a* is represented by the ratio of green to white space in each box. We found higher zooplankton species turnover in the fishless lakes along the elevation gradient (figure 2*a*) and a stronger fish effect of species composition at low elevation (figure 2*b*). Fish reduce the biomass of consumers relative to producers in warm lakes but not in cold lakes.

Despite clear evidence that top-down forces shape communities and ecosystems, tremendous variation in space and time has been observed in the strength of predator effects [49]. Our results show that the impacts of trophic cascades on lake communities and ecosystem processes vary along a natural gradient in climate associated with temperature and input of detrital resources. As the spread of invasive predators and climate change continue to unfold over the next century, their effects on the world's ecosystems will be determined by their combined selective pressure on species' traits. To predict the future state of ecosystems and the irreplaceable services they provide to societies, we must understand how predation and climate interact to shape ecosystems. Our results demonstrate that the capacity of species replacements to buffer the effects of trophic cascades on pelagic food web structure are strongest in cold lakes. Conversely, benthic production and decomposition were most influenced by predator introductions in cold lakes. Warming may therefore alter effects of predator losses or introductions on future ecosystems.

Data accessibility. All data available from http://dx.doi.org/10.5061/dryad.nj3q5.

Authors' contributions. C.C.S. was involved in designing the study, collecting data, analysing data and writing the paper. J.B.S. was involved in developing the research questions, designing the study, collecting data and writing the manuscript.

Competing interests. We have no competing interests.

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Appendix 1A

The relationship between elevation and other variables of interest

Comparisons along elevation gradients are a common approach for testing hypotheses about the effect of temperature on biological systems among locations that have access to the same regional species pool. We tested for correlations between fish presence, and temperature with physical variables (area and depth) and water chemistry (conductivity, pH, alkalinity, total phosphorus [TP], total Kjeldahl nitrogen [TKN], and dissolved organic carbon [DOC]) (Table 1A.1). We were not able to measure total phosphorus, which was always below the detection limit of our analytical methods (http://anlab.ucdavis.edu/).

Most physical and chemical variables did not show patterns of association with the presence of stocked fish populations (Table 1A.1). However, lakes with fish had higher conductivity (Figure 1A.1), although this relationship is not significant when the outlier with the highest conductivity was removed. Lakes with fish also had higher pH (Figure 1A.1). A likely explanation is that these lakes had higher productivity due to fish predation on zooplankton, as shown in Yosemite lakes by Sarnelle and Knapp (2005) resulting in increased pH. It is therefore unlikely that the effects of fish on community or ecosystem structure detected in our analyses were related to spurious correlations with physical or chemical variables.

Other than temperature, the only variable correlated with elevation was dissolved organic carbon (DOC) (Figure 1A.1). DOC was low at high elevation, particularly above tree line, where input of terrestrial vegetation was low. DOC affects communities of both consumers and producers by attenuating UV radiation and fueling microbial production that can sustain zooplankton (Hessen and Anderson 1990). In addition, DOC is likely to increase along with higher temperatures due to accelerated decomposition in warmer soils.

To determine if elevation was acting on response variables more strongly through temperature or DOC we use structural equation models (SEMs). We did this separately for both lakes that contained fish and lakes that are fishless. We used log-transformed data, to ensure all relationships were linear. We compared linear models to models including a squared term using AICc, and all relationships were best modeled using a linear function. We fit our SEM by fixing the variance of each exogenous variable to 1, which means we were not estimating variance for each variable, and instead accepting the variance of the measured variable. We chose this due to low sample size and our goal of estimating path parameters. We used fish status as a grouping variable, and compared models using log-likelihood tests where each path coefficient was either same, or allowed to vary between the fish and fishless group. We fit the model using the function *sem()* in the lavaan package in R (Rosseel 2012). For both benthic production and litter decomposition we found that temperature was the only significant predictor (Figure 1A.2), therefore we used temperature as the predictor variable for further analysis.

The effect of fish and elevation on zooplankton species composition

To show the way that fish and elevation influenced zooplankton species composition, we completed a permutational multivariate analysis of variance using Bray-Curtis community dissimilarity. We found that both fish and elevation had a significant effect on zooplankton community composition, and the interaction between fish and elevation was marginally significant (Figure 1A.3). To plot these results, we completed a redundancy analysis (RDA; Figure 1A.3).

Finally, we wanted to determine if the effect of fish on community composition varied with elevation. The Bray-Curtis dissimilarity of zooplankton communities from all pairwise comparisons of lakes where one contained fish and one was fishless was regressed against the mean elevation of the two lakes. We found that fish and fishless lakes had entirely distinct zooplankton communities in high elevation lakes, but converged in composition at lower elevation (Figure 1A.3). However, we wanted to determine if this result was partially due to the pseudoreplication of using all pairwise comparisons. To check this, we used pairs of lakes that were within a certain elevational range (100m, 200m, 300m, 400m and 500m) to reduce the number of comparisons. We found that our original result was consistent for all cutoffs (Figure 1A.4).

Table 1A.1: *p*-values of ANOVAs testing the effects of elevation and fish presence on physical and chemical lake variables

	Elevation	Fish	E*F
Temperature (C)	<0.001*	0.28	0.03*
Area (ha)	0.63	0.14	0.89
Depth (m)	0.33	0.37	0.94
Conductivity (μS cm^{-1})	0.81	0.01*	0.82
pH	0.09	<0.01*	0.11
TKN (mg L^{-1})	0.89	0.82	0.60
DOC (mg L^{-1})	<0.01*	0.19	0.59
Alkalinity (ppm)	0.16	0.06	0.11

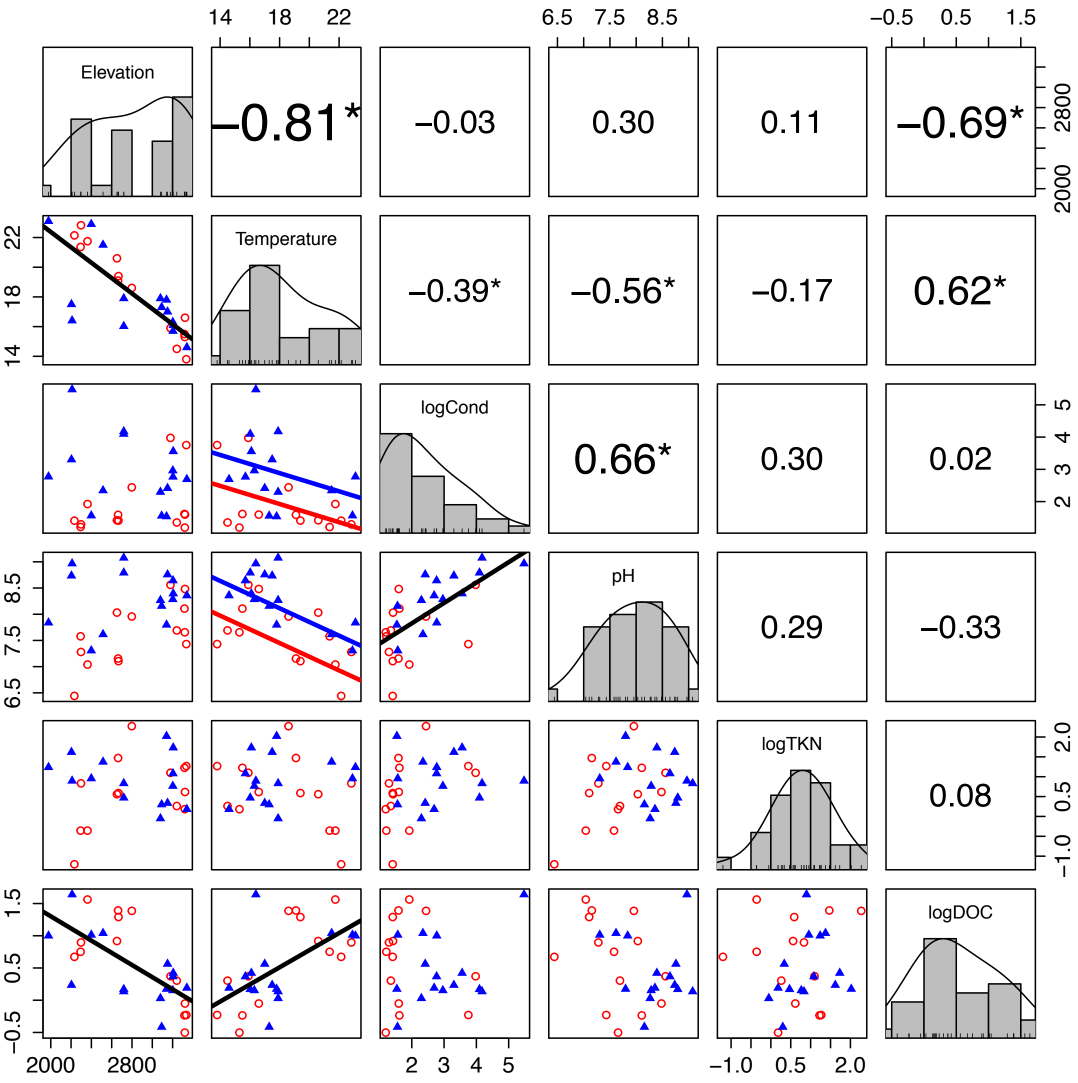

Figure 1A.1: Correlations between temperature, elevation, log transformed conductivity, pH, log-transformed TKN and log-transformed DOC. Histograms along the diagonal represent the distribution of the variable. Numbers in the top right panels are the correlation coefficients, significant is denoted * with a p value <0.05 of a Pearson correlation test. Panels on the bottom right show the relationship between the variables. Lakes with fish are represented by blue triangles and fishless lakes are represented by red circles. Black lines are present on plots that have a significant correlation. Separate blue (fish lakes) and red (fishless lakes) lines are present when there was a significant fish effect.

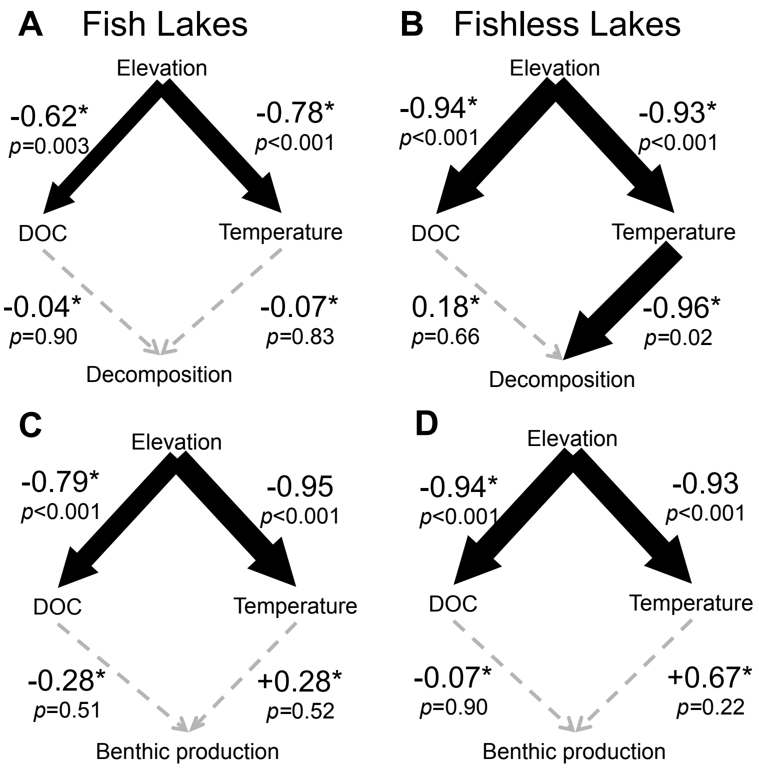

Figure 1A.2: The results of the SEM for (A, C) lakes with fish and (B, D) lakes without fish. (A, B) show results of the SEM for litter decomposition, and (C, D) show results for the benthic production. The width of the arrows are scaled to the standardized coefficients which are also reported with the corresponding p-values next to each arrow. Significant relationships are shown in black, while non-significant relationships are shown in grey. * represents path coefficients that are significantly different between fish and fishless lakes.

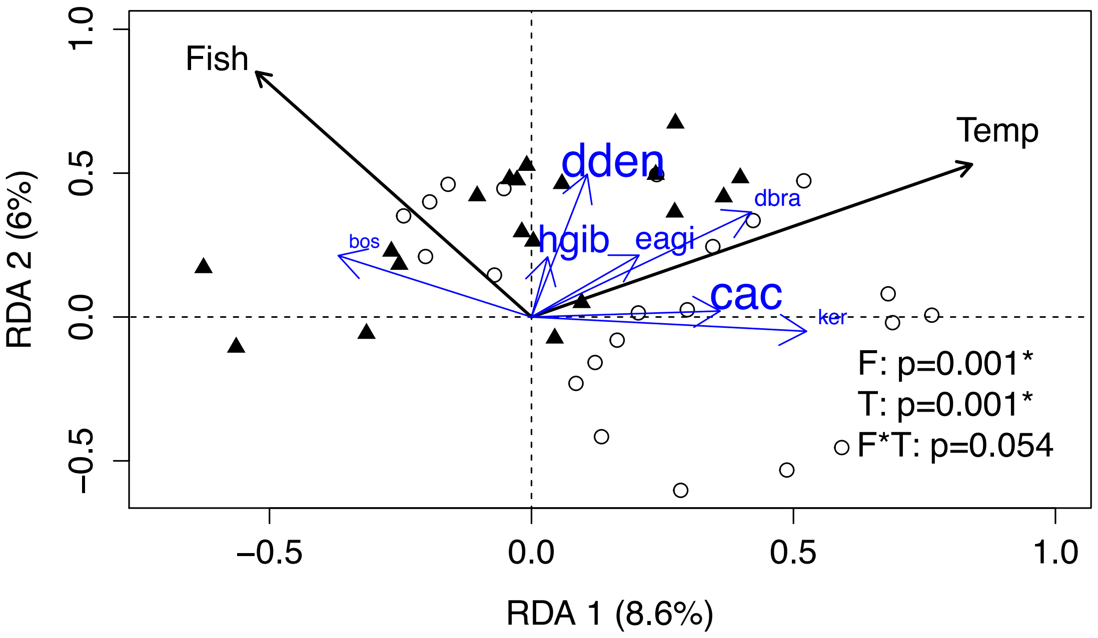

Figure 1A.3: A RDA of the zooplankton community data. The percent of variation explained by each axis is in parentheses. Black triangles are the site scores for lakes with fish, and open circles are site scores for fishless lakes. Black arrows represent the environmental loadings, and blue arrows represent species loadings. Only species loadings greater than 0.1 were included for clarity. The species included are: *Daphnia dentifera* (dden), *Diaphanosoma brachyurum* (dbra), *Holopedium gibberum* (hgib), *Eucyclops agilis* (eagi), calanoid copepidid (cac), *Keratella* sp. (ker) and *Bosmina longirostris* (bos). The names of the taxa are scaled according to their body size.

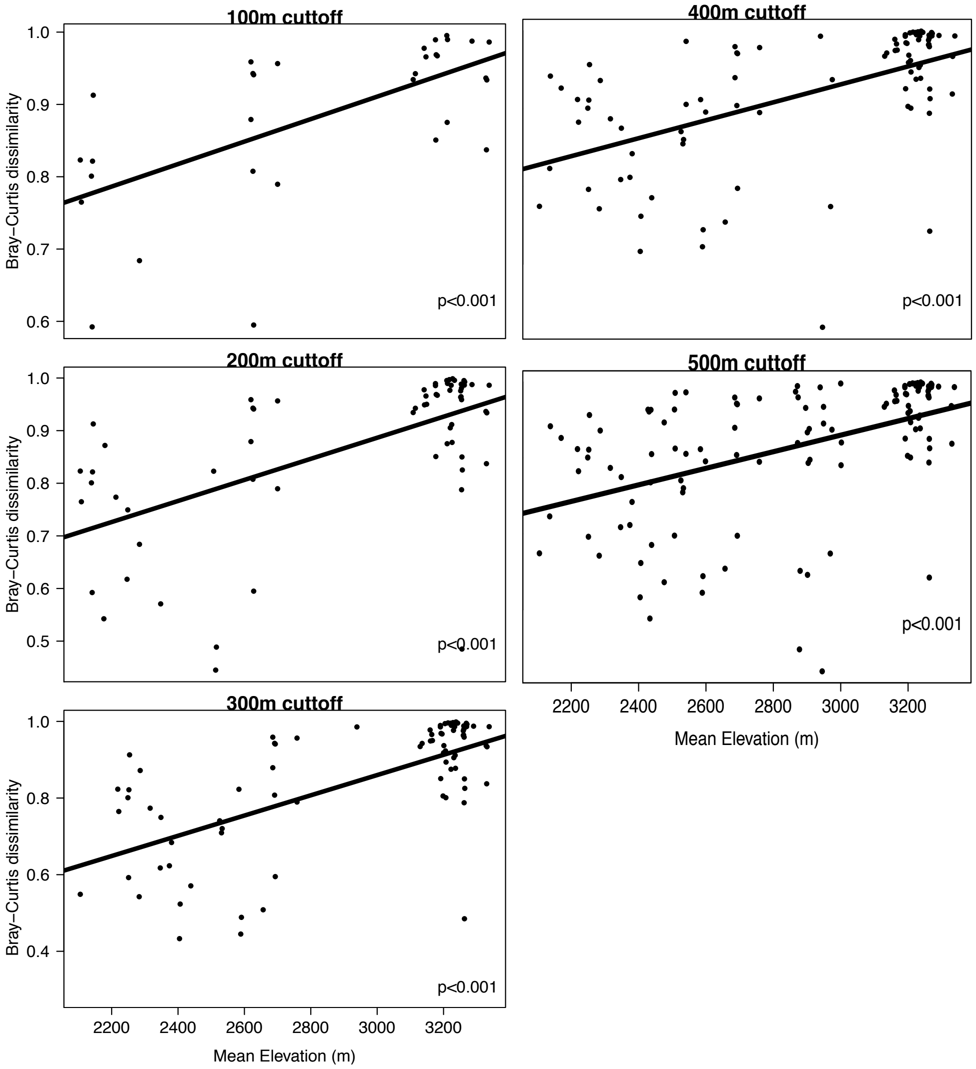

Figure 1A.4: The Bray-Curtis dissimilarity of zooplankton communities in fish-fishless pairs of lakes as a function of the mean elevation of the lakes. Pairs of lakes were used if they were within a certain elevational range of each other. The cutoff used is shown at the top of each plot. p-values represent linear regressions.

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CHAPTER 2

Gone but not forgotten: Non transitive effects of fish addition and removal on mountain lake plankton communities

Abstract

The impacts of global changes on ecosystems are shaped by evolution of organismal traits, plasticity and turnover in community structure. To test if phenotypic selection within and among species alters community responses to environmental change, we conducted a plankton community transplant experiment. We exposed communities that assembled and evolved at different elevations in the presence or absence of fish to different elevations and fish predation. Local adaptation predicts highest fitness in home environments, but instead we found that past selection by fish resulted in non-transitive effects of predator addition and removal. *Daphnia pulicaria* that evolved with fish reached greater biomass under fishless conditions than those from fishless lakes, resulting in greater zooplankton community biomass and average size. Eco-evolutionary effects were observed in response to predation but not elevation. These results indicate phenotypic evolution and community compositional turnover over broad environmental gradients can determine ecosystem responses to the extirpation of predators.

Keywords

resilience; life-history evolution; local adaptation; temperature; climate change; Daphnia pulicaria; elevation; historical contingency

Introduction

To persist under climate change, populations and communities must ‘migrate, acclimate, adapt or die’ (Gienapp et al. 2008). Adaptation can maintain population fitness in the face of environmental change by altering the frequency of phenotypes in response to selection (Bell and Gonzalez 2009). These shifts in species composition can stabilize ecosystem properties (e.g., community biomass, ecosystem function) against environmental change if sites are colonized by species and/or genotypes that possess traits that match the new conditions according to the “spatial insurance” hypothesis (Bell and Gonzalez 2011, Thompson and Shurin 2012, Symons and Arnott 2013). The ecological impact of environmental change therefore depends on phenotypic variability within and among species, and the distribution of this variability within local communities and across broad landscapes. The time scales of experimental studies of ecosystem response to environmental change are typically too short for ecological or evolutionary shifts to occur (Alexander et al. 2016; but see Zuppinger-Dingley 2014 for an example), thus the contributions of phenotypic selection within and among species to community resilience are largely unknown.

One mechanism by which ecological and evolutionary history influences community responses to environmental change is through local adaptation of populations to their environment. For example, prey populations sympatric with predators often evolve resistance to predation, which may dampen cascading effects of predation on lower trophic levels (Ingram et al. 2012, Martin et al. 2015). This type of standing genetic variation, including *via* phenotypic plasticity, throughout a species’ range may be an important source of resilience to environmental change (Jump et al.

2009, Lande 2009). Adaptation to the new environment can allow species to persist during environmental change, resulting in a more stable community structure.

Evolutionary processes are generally expected to maintain fitness under environmental change. However, local adaptation may also produce surprising population responses to novel forms of selection (Handelsman et al. 2013). Selection in one environment may result in traits that affect fitness under anomalous conditions that a population has never encountered. For example, under 'prodigal son' dynamics an environmental change that increases fitness (e.g., higher CO_2 for plants, predator removal) may transiently increase local abundance before it returns to a similar "pre-disturbance" abundance, despite the environment remaining in its new state (Collins 2016). One mechanism to explain this decline in abundance is a trade-off between the intrinsic rate of increase (r) and competitive ability (Gill 1974). Populations with an increased r may be invaded by slower growing, more competitive genotypes over time. For instance, Schaum and Collins (2014) found that *Chlamydomonas* that were exposed to high CO_2 initially increased cell division rates, but over time this rate decreased to the cell-division rate of their ancestors in low CO_2, likely to reduce damage associated with fast cell division rates. As a result, adaptive evolutionary responses may buffer populations and communities against changing environmental conditions, however the capacity of most populations for evolutionary rescue is largely unknown.

To test how evolutionary and ecological history influence community responses to environmental change, we conducted a transplant experiment that exposed plankton communities from mountain lakes to two ecologically relevant stressors: an elevational gradient in climate including temperature, and predation by a non-native fish. Our experiment is a community-level analog to a common garden, designed to measure the impact of the environment and genotype on the phenotype of an organism. We established communities of aquatic organisms (phytoplankton, zooplankton, bacteria and benthos) originating from four types of lakes in the California Sierra Nevada mountains: all factorial combinations of alpine and sub-alpine elevations, with and without introduced trout predators. The source lakes vary in temperature along an elevational gradient, and in history of fish stocking, thus some communities have evolved and assembled in the presence of fish. We grew these four types of plankton communities at three elevations crossed with the presence of fish predators in the experimental pond mesocosms. Our goal was to test the hypothesis that evolutionary and ecological history of elevation and fish predation would affect the contemporary population, community and ecosystem level responses of plankton to these same perturbations.

Materials and Methods

Experiment overview

To test the hypothesis that phenotypic selection within and among species buffers ecosystems to environmental changes, we conducted a plankton community transplant experiment across elevation in mesocosms (Figure 2.1). We collected communities of plankton and micro-organisms from lakes that varied in their environment due to elevation, and history of fish stocking. Thus, the treatments were:

- **History of elevation (H_{Elev}):** source community elevation (2 levels, sub-alpine [average of 2591m] and alpine [average of 3252m])

- **History of fish (H_{Fish}):** source community fish presence (2 levels, +/-)
- **Experimental elevation treatment (E_{Elev}):** transplant elevation (3 levels, montane [1200m], sub-alpine [2149m] and alpine [3093m])
- **Experimental fish treatment (E_{Fish})**: fish presence in the transplant environment (2 levels, +/-)

This experimental design allows us to partition the variance in the response of community and population variables to the present and historical environment and their interaction. The response of plankton species and aggregate community metrics to the experimental treatments was modeled as a function of the current ecological conditions in the experiment (E), the ecological history of the community from which they originated (H), and the interaction between the two (E*H), where $E = E_{Fish} + E_{Elev} + E_{Fish}*E_{Elev}$ and $H = H_{Fish} + H_{Elev} + H_{Fish}*H_{Elev}$. E_{Fish} is the presence of fish in the mesocosms, E_{Elev} is the elevation of the experimental environment, and $E_{Fish}*E_{Elev}$ is the interactive effects of contemporary conditions. The conditions in the community of origin are represented by history (H), where the presence or absence of fish predators in the source community is H_{Fish}, and its elevation is H_{Elev}. Each term represents a treatment or interaction in the mixed effects model table. The two-way interaction terms $E*H = E_{Fish}*H_{Fish} + E_{Fish}*H_{Elev} + E_{Elev}*H_{Fish} + E_{Elev}*H_{Elev}$ represents the eco-evo interaction, or the impact of selection history of the community on the outcome of contemporary ecological interactions.

Experimental set-up

We established mesocosm arrays at three elevations, located at three UC Natural Reserves (White Mountain [WM], 3093m, 37.499044, -118.171597; Sierra

Nevada Aquatic Research Lab [SNARL], 2149m, 37.613240, -118.830226; and Sierra Nevada Research Institute [SNRI], 1200m, 37.540008, -119.657737). Using mesocosms at three elevations allowed for natural seasonal and daily thermal regimes, and also for other environmental differences associated with elevation such as vegetation cover (Figure 2.1 and 2.2). We used three transplant elevations so that communities from each elevation were exposed to higher temperatures than the source lakes to simulate warming. We installed 40 mesocosms at three locations described above. The mesocosms were 1280 L, 2m in diameter and 1m in depth. Mesocosms were filled with well water for the low and high elevation sites, and a local stream (filtered through 63um mesh) for the sub-alpine (mid) elevation site. Initial water chemistry data are found in Appendix 2A in Supporting Information. To reduce evaporation and UV stress on trout, the tanks were covered with 60% shade cloth. In addition, three 6” inch long, 2” diameter PVC tubes were placed in each tank as a refuge for fish. Temperature loggers were installed in three haphazardly chosen tanks at each location to measure water temperature at 2 hour intervals throughout the experiment.

Next, we selected lakes that varied in their history of fish presence and elevation to collect the four different types of source communities (sub-alpine x alpine, fish x fishless; see Appendix 2A). Plankton communities were collected from three lakes within each of the four source community types. Nearly all lakes at these elevations are naturally fishless. Fish populations were stocked starting in the early 1900s and are now self-sustaining (Knapp and Matthews 2000). This has resulted in communities that differ in the presence or absence of fish predators over the order of

~100 years. Lakes are also arrayed along an elevational gradient where lower elevations have warmer temperatures and higher dissolved organic carbon (DOC) concentrations from more densely vegetated watersheds (Sadro et al. 2011, Piovia-Scott et al. 2016, Symons and Shurin 2016).

Plankton were collected at the deepest point in the lake by drawing a 30cm diameter zooplankton net through the water column, starting 1m above the lake bottom. We collected the volume of zooplankton required to inoculate each mesocosm at ambient lake density (see Appendix 2A). Plankton samples from the three lakes were combined in a 20L bucket, stirred, and stored at 4C until mesocosm inoculation which occurred within 9 days of collection (4-12 July 2014). In addition, 6L of sediment was collected at each lake, combined, and placed in three containers to be distributed at each mesocosm array. We chose three lakes in each source community category to ensure that we sampled a diversity of species representative of these conditions, and included sediment to ensure that resting stages would be present in the inoculum. Zooplankton, phytoplankton and sediment were inoculated into the mesocosms at each location over a nine-day period (4-12 July 2014). Four aliquots of each source community inoculum were preserved with 70% ethanol for later enumeration. The plankton communities had nearly one year to establish in the mesocosms.

We established the presence/absence of fish in the mesocosms (E_{Fish}) by the addition of 5 juvenile Rainbow Trout (*Oncorhyncus mykiss)* between May 13-16 2015 at the montane and sub-alpine elevations. Fish were added to the alpine elevation tanks on June 4 2016 as the mesocosm water surface was frozen before this date.

Triploid female juvenile rainbow trout from one hatching were obtained from Thomas Fish Company. After a 24-hour acclimation to ambient temperature at each elevation 5 juvenile fish (5.4±0.13 cm) were added to the tanks. Fish were monitored at one location (sub-alpine location, SNARL) every other day for signs of distress and at other sites opportunistically during sampling events. Fish survival was 88% overall; 67% at low elevation, 100% at medium elevation, 97% at high elevation. Five tanks in the E_{fish} treatment that did not contain any fish at the end of the experiment were excluded from our analyses.

The treatments were replicated 5x each for a total of 120 experimental units.

Mesocosm Sampling

We sampled the mesocosms monthly to quantify water chemistry, zooplankton community composition and abundance, and phytoplankton biomass. We sampled the zooplankton community using an integrated tube sampler. We collected 20L from haphazardly chosen locations from each mesocosm, condensed the sample on a 63μm mesh filter and preserved it with 70% ethanol. Zooplankton samples were counted by C.C.S. using a protocol designed to estimate the abundance of common species and also detect rare species. Two hundred individuals were identified to the lowest taxonomic resolution possible (generally species for crustaceans and genus for rotifers) with no more than 50 individuals of each species being counted toward the total. The remainder of the sample was scanned to detect rare species. Taxonomic keys used included Ward and Whipple (1959), Wilson and Yeatman (1959) and De Melo and Hebert (1994).

To calculate zooplankton community biomass, we measured the body length of

15 individuals of the three most common species in each of the sample. For rare species we used the average body length of all measured individuals of that species. Body size measurements were done only on the final set of samples (September); for September samples we used the mesocosm-specific measurements but for all other sample dates we used the average length of each species across all treatments. We then used published length-weight regressions to estimate zooplankton biomass (Dumont et al. 1975, McCauley 1984). To calculate average body size, we used abundance-weighted mean length. Total community biomass was determined by summing the population biomasses of each species.

To quantify the environment in our mesocosms we measured a series of water chemistry variables. First, the total nitrogen (TN) and total phosphorus (TP) in the tanks was measured by filtering water through 63um-mesh, collecting it in a triple-rinsed 20mL high-density polyethylene (HDPE) bottles, then preserving it with H_2SO_4 to a pH<2 and storing it at ~4C until later analysis. TN and TP were measured using an auto analyzer (LaChat QuikChem 8500, persulfate digestions, LaChat, Colorado, USA). To measure DOC water samples were filtered through precombusted glass fiber filters (Whatman GF/F, pore size 0.45um, Whatman, Maidstone, UK) into triple-rinsed 20 mL glass vials and preserved with HCl to a pH<2. DOC was measured using a total organic carbon analyzer (TOC-V CSN, Shimadzu Scientific Instruments, Kyoto, Japan). Chlorophyll-*a* concentration (chl-*a*), a proxy for phytoplankton biomass, was measured in a known volume of water filtered through a GF/F that was frozen until processing. Chl-*a* concentration was measured using a Turner Trilogy fluorometer (Turner, San Jose, USA) following a 24 hour ~4C methanol extraction.

Statistical Analyses

We modeled total zooplankton community biomass, chl-*a*, average body size and total abundance using a linear mixed effects model. The fixed effects included in the model are E_{Fish} and E_{Elev} (the contemporary effects of fish and elevation), H_{Fish} and H_{Elev} (the presence of fish and elevation of the source environment), and the two-way interactions among them. Here we present models with only two-way interactions and main effects to simplify interpretation. The results of the analysis with all higher order interactions is shown in Appendix 2C. Sample date and mesocosm were included as random effects to account for temporal pseudoreplication. Variables were transformed to improve normality and homoscedasticity. Models were run using the function *lme()* in the *nlme* package (Pinheiro et al. 2016). Individual species responses were modeled with a permutational LME due to non-normal distributions of data.

To examine how community structure responded to treatments we used a permutational multivariate analysis of variance based on a Bray-Curtis distance matrix (Adonis function in vegan package; Oksanen et al. 2016) on the species biomass at the end of the experiment. To visualize changes in species composition we used non-metric multidimensional scaling (NMDS). All analyses were performed in R (R Core Team 2016).

Results

Initial conditions

Mesocosms filled with water at different elevations varied in water chemistry (see Appendix 2A). Nutrients (TN and TP) were uniformly low at all three sites, but DOC was highest at the low elevation montane site and conductivity was greatest at sub-alpine elevation (see Appendix 2A). In addition, as the experiment progressed more detrital inputs to the mesocosms at low elevation resulted in higher nutrient and DOC concentrations over time (see Appendix 2B). These patterns are consistent with natural elevation gradients (Symons and Shurin 2016), which is why this treatment is described as an ‘elevation’ treatment instead of a ‘temperature’ treatment. In addition, climate warming is expected to increase lake water temperatures in addition to causing upward elevational expansion of vegetation and greater DOC loading into aquatic systems (Walther et al. 2005). Our elevation treatment is therefore a relatively faithful representation of the effects of climate warming at different elevations.

Treatments

Mesocosms at different elevations differed in mean temperature (nlme, $p<0.001$, Figure 2.2). The low, medium and high elevation mesocosms averaged 19.2, 16.7 and 13.4 C respectively. The community inoculum differed among lake types (ADONIS, $p<0.001$, see Appendix 2C). Six of the eleven species present in the inoculum were found in all lake types.

Chlorophyll-*a* throughout the experiment was highest in the mesocosms with fish (E_{Fish}) and at low elevation (E_{Elev}), and was unaffected by the other treatments or interactions (nlme, E_{Fish} $p<0.001$, E_{Elev} $p<0.001$).

Zooplankton community structure

Communities that originated from lakes containing fish showed different responses to the presence or absence of fish in the experiment in terms of biomass and size structure. Communities sympatric with fish increased in biomass compared to other communities when fish were absent from the mesocosms (Figure 2.3A). This pattern was driven mainly by changes in the biomass of the ecologically dominant species, *Daphnia pulicaria* (Figure 2.4A). Indeed, when examining community biomass without *Daphnia pulicaria* included we did not see the same pattern documented in Figure 2.3A. Biomass of *D. pulicaria* increased in the fishless tanks due to an increase in both body size and abundance, though each alone was not significant (LME *D. pulicaria* abundance E_{Fish}*H_{Fish} p=0.58, ANOVA *D. pulicaria* body length H_{Fish} p=0.60). In addition, the shift in total community biomass was not in response to a difference in total abundance (Table 2.1), but instead due to a shift in the mean body size of the community (Figure 2.3C; Table 2.1). Large bodied species, including *D. pulicaria*, were more abundant in communities from fish lakes in the treatment without fish present (Figure 2.3C and 2.4A). Experimental conditions influenced the biomass and abundance of zooplankton, which decreased in mesocosms at high elevation, and average body size varied with E_{Elev}, with the largest body size at the low elevation site (Figure 2.3B, 2.3D, Table 2.1). History also influenced body size, and we found significant interactive effects between H_{elev} and H_{fish} where in June, mean body size was greatest in communities originating from high elevation fishless lakes (Figure 2.3E).

Daphnia pulicaria biomass varied with experimental conditions and the history of exposure to fish (Figure 2.4). As described above, *D. pulicaria* biomass was highest in populations with a history of fish exposure in the tanks when fish were absent (Figure 2.4A). E_{Fish} had the greatest impact on *D. pulicaria* biomass at the montane site because the species obtained higher biomass in the absence of fish then at the other two sites (Figure 2.4B). Similarly, H_{Fish} had the largest impact on *D.*

pulicaria biomass at the montane site with populations with a history of fish exposure obtaining higher biomass (Figure 2.4C).

Zooplankton species composition

The source environment determined how zooplankton communities responded to contemporary experimental conditions (ADONIS, Table 2.1, Figure 2.5). There was an interactive effect of E_{Fish}*E_{Elev} due to a larger shift in the species composition in response to fish at high elevation compared to lower elevations (Figure 2.5A). The effect of H_{Fish} interacted with E_{Elev} in a similar way where the communities originating from lakes with different histories of fish presence are more distinct at high elevation than low elevation (H_{Fish}xE_{Elev}, Figure 2.5B). The effect of having fish in the mesocosms on zooplankton composition was in the opposite direction of the effect of having fish in the past environment, where E_{Fish}(+) caused a large shift towards smaller bodied species (Figure 2.5).

Table 2.1: *p*-values for mixed effects models and ADONIS permutational analysis of the community composition

	Community biomass	Abundance	Average body size	*Daphnia pulicaria* biomass	Community composition
Test	LME	LME	LME	Randomization	NMDS
E_{Fish}	0.06	0.98	**0.001***	--	**<0.001***
E_{Elev}	**<0.001***	**<0.001***	**<0.001***	--	**<0.001***
H_{Fish}	0.17	0.42	0.89	--	0.17
H_{Elev}	0.92	0.85	0.91	0.21	0.08
E_{Fish}*E_{Elev}	0.99	0.84	0.32	**<0.001***	**<0.001***
E_{Fish}*H_{Fish}	**0.01***	0.77	**0.008***	**0.02***	0.05
E_{Fish}*H_{Elev}	0.24	0.16	0.55	0.50	0.06
H_{Fish}*E_{Elev}	0.87	0.71	0.45	**0.001***	**0.02***
H_{Fish}*H_{Elev}	0.85	0.59	**0.007***	0.28	0.07
H_{Elev}*E_{Elev}	0.83	0.64	0.89	0.14	0.07

* denotes significance at $p<0.05$

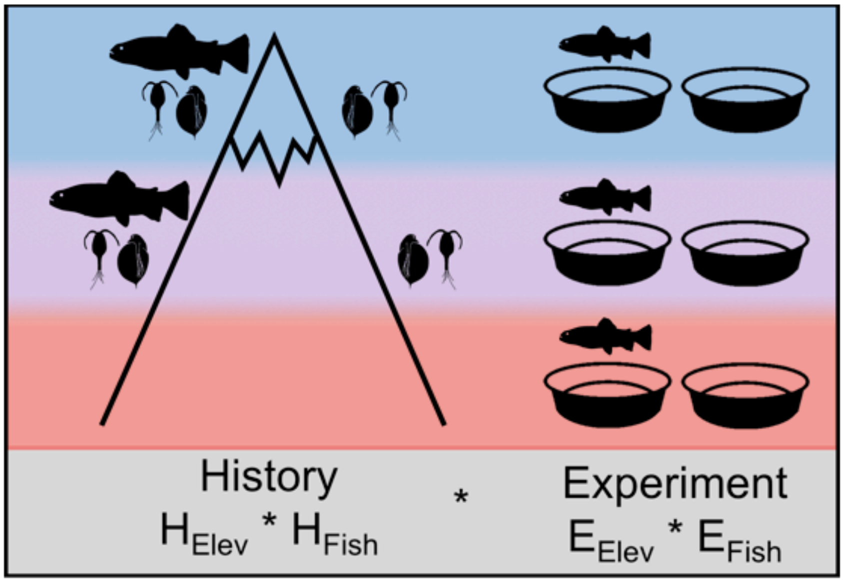

Figure 2.1: Schematic of the experimental design. Plankton communities were collected from lakes at two elevations, with and without fish (History) and exposed to different elevations and fish in mesocosms (Experiment).

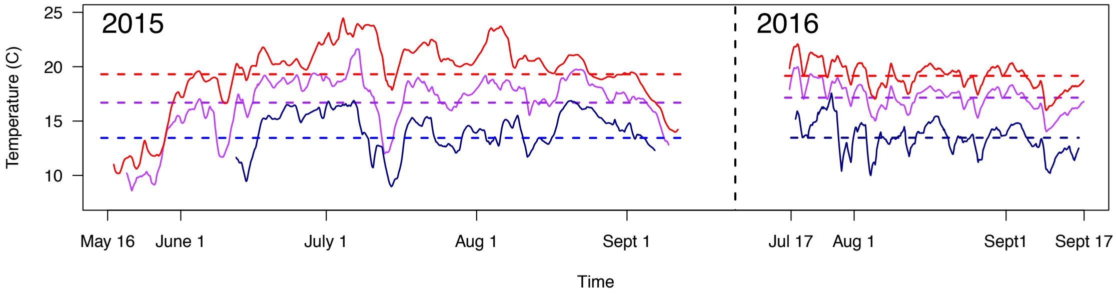

Figure 2.2: Daily average water temperature from a montane, sub-alpine and alpine elevation mesocosm in red, purple and blue respectively. Average temperature for the time period of temperature logger deployment within each year is denoted by the horizontal dashed lines

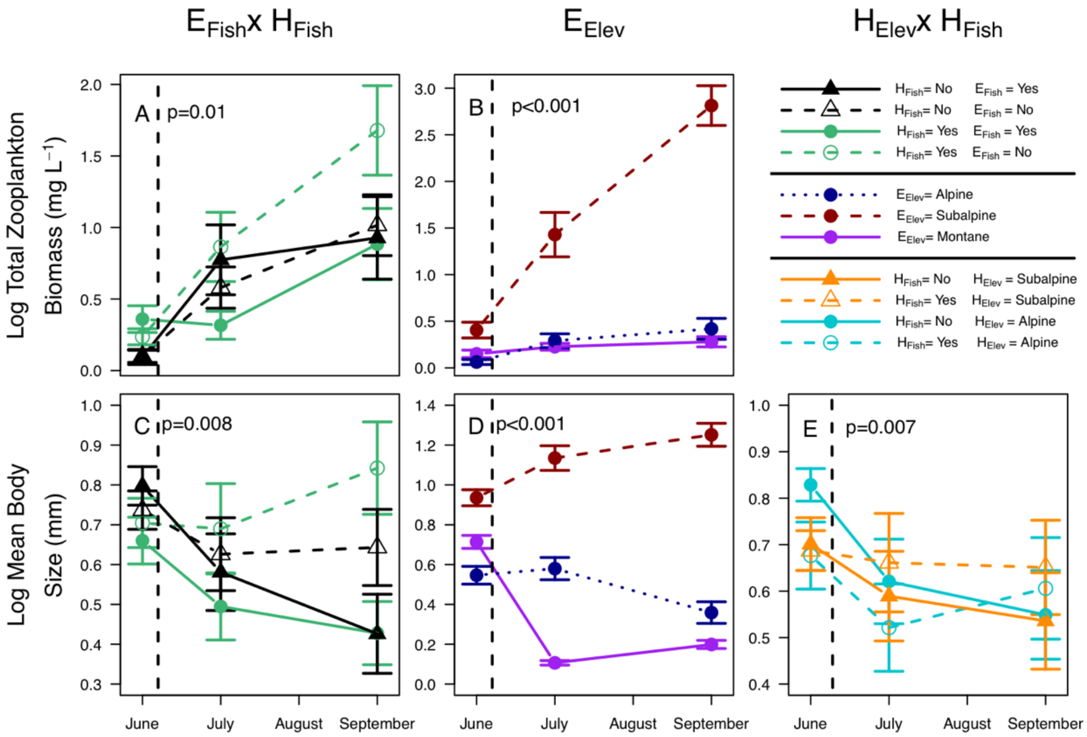

Figure 2.3: The response of (A, B) total zooplankton biomass, (C-E) mean community body size to experimental treatments. Vertical dashed lines represent the time fish were added to the mesocosms. Only significant results are presented, therefore data are averaged across non-significant effects for each panel

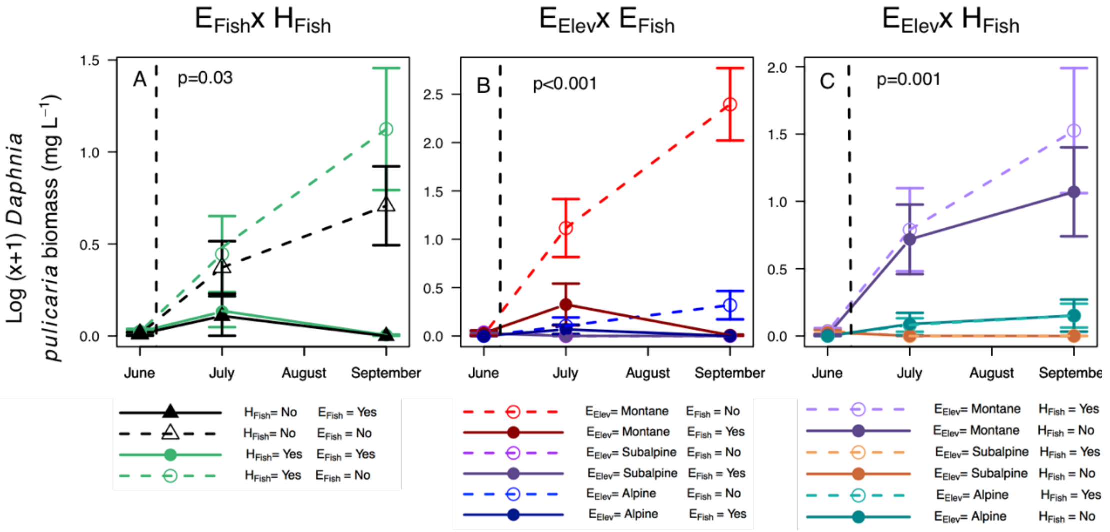

Figure 2.4: The response of *Daphnia pulicaria* biomass to experimental treatments. Vertical dashed lines represent the time fish were added to the mesocosms. Only significant results are presented, therefore data are averaged across non-significant effects for each panel

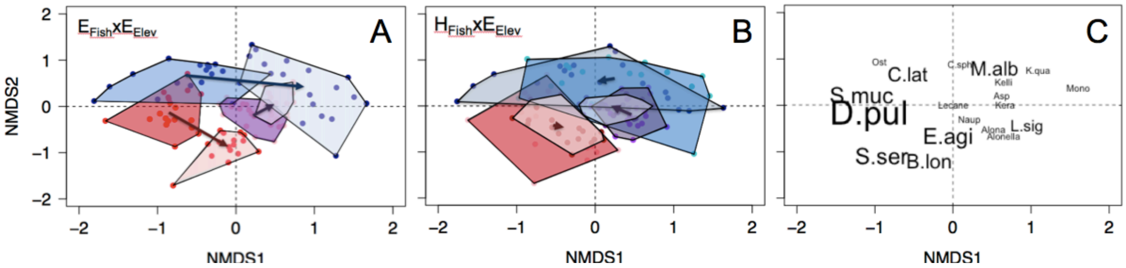

Figure 2.5: NMDS ordination results highlighting significant predictors of community composition. A) E_{Fish}xE_{Elev}, mesocosm elevation is denoted by color, red, purple and blue representing montane, sub-alpine and alpine sites respectively. Mesocosms that contained fish are denoted by lighter colors. Centroids are connected by arrows going from mesocosms without fish to mesocosms with fish. B) H_{Fish}xE_{Elev}, treatments are indicated exactly as in panel A, but represent source habitat conditions instead of experimental condition. Centroids are connected by arrows going from lakes without fish to lakes with fish. C) Species loading are shown, with the size of the text scaled to the average body size of each taxon. Species depicted are *Alona* spp., *Alonella* spp., *Asplanchna* spp. (Asp), *Bosmina longirostris* (B.lon), *Ceriodaphnia laticaudata* (C.lat), *Chydorus sphaericus* (C.sph), *Daphnia pulicaria* (D.pul), *Eucyclops agilis* (E.agi), *Kellicottia* spp. (Kelli), *Keratella* spp. (Kera), *Keratella quadrata* (K.qua), *Lecane* spp., *Leptodiaptomus signicauda* (L.sig), *Macrocyclops albidus* (M.alb), *Monostyla* spp. (Mono), nauplii (Naup), Ostracoda (Ost), *Scapholeberis mucronata* (S.muc), *Simocephalus serrulatus* (S.ser)

Discussion

We found that the response of communities to elevation and predators was contingent on the environment from which they originated. We expected that local adaptation would produce plankton with the highest fitness in their home environment, but this prediction was not supported. Instead, zooplankton that originated in lakes with fish obtained a higher total community biomass in the absence of fish than communities that were originally from fishless lakes. This pattern was largely driven by changes in *Daphnia pulicaria* biomass (increases in both abundance and body size) suggesting fish select for a faster intrinsic growth rate in *Daphnia* populations, or alter the community dynamics such that *Daphnia* increase in biomass. The history of fish predation played a greater role in contemporary community structure and response to environmental change than the history of elevation. Our experiment indicates that shifts in species composition and evolutionary history of populations along environmental gradients determine the aggregate response of communities to changes in predation and climate.

We found that past selection by fish increased the biomass of *Daphnia pulicaria* above naturally fishless populations. This result is particularly important because *Daphnia* spp. play a keystone role in lake food webs as preferred prey of fish and strong grazers of algae (Carpenter et al. 1987). This result runs counter to the expectation that prey evolve defense traits to reduce the effect of predation in fish-adapted communities (Ingram et al. 2012). We expected weaker top-down control in communities with a history of fish exposure due to local adaptation. However, fish and fishless lake plankton communities were equivalent in terms of zooplankton size, biomass and *Daphnia* biomass in the presence of fish in the experiment, indicating that past selection did not increase abundance when predators were present. Instead, the strongest effect was past selection by fish on the growth rate of *Daphnia* in experimental environments when fish are absent. This effect could be driven by shifts in the community that allow for greater biomass of *Daphnia*, or through shifts in *Daphnia* traits in response to fish, of which the latter has substantial empirical support.

Fish have been shown to select for changes in *Daphnia* life history parameters that result in increased population growth rates (earlier reproduction and smaller body size, (Riessen 1999), and genetic differences have been documented in *Daphnia melanica* in response to fish in Sierra Nevada lakes (Fisk et al. 2007). This selection is driven by fish-induced reduction in survival to maturity causing *Daphnia* to reproduce earlier and increase clutch size. Indeed, another *Daphnia* species (*Daphnia ambigua*) from lakes with higher planktivory can show a greater *r* than those from fishless lakes, in controlled lab experiments (Walsh and Post 2011). Our finding expands on this and shows that this type of effect lasts for many generations, and is sufficiently strong to alter zooplankton trophic level biomass and size structure. Selection on life history traits that result in higher *r* accounts for greater fitness upon release from predation pressure in our experiment. However, the reason for lower abundance of *Daphnia* from fishless lakes when grown in tanks without fish is less clear and raises new questions regarding the role of predation in shaping carrying capacities.

A mechanism that could explain the differences in *D. pulicaria* growth in fishless tanks with or without a population history of fish predation is countergradient selection (Conover and Schultz 1995, Conover and Baumann 2009). Countergradient selection is a form of local adaptation whereby selection counters the effect of the environment on fitness along gradients. For example, in response to temperature gradients many organisms have evolved a greater *r* at colder temperatures and this increase is present irrespective of the ambient temperature to which they are exposed (Conover and Baumann 2009). This may have influenced our results because behavioral adaptations and habitat preferences of *Daphnia* in the presence of fish affect ambient temperature. *Daphnia* exhibit diel vertical migration in response to fish where they inhabit deeper, colder portions of the water column during the day (Lampert 1989). Because *Daphnia* from lakes with fish may experience colder temperatures than individuals from fishless lakes, counter gradient selection could lead to increased *r* above *Daphnia* from fishless lakes. This type of selection has been detected in comparisons of *Daphnia* populations among lakes with anadromous fish which constrain *Daphnia* to the early, colder part of the growing season to *Daphnia* that are present for the whole growing season in lakes with landlocked fish (Walsh and Post 2011). Alternatively, countergradient selection due to increased mortality in lakes with fish could select for greater fitness in sympatric *Daphnia* that would only be evident when comparing populations in the absence of predators (Lankford et al. 2001).

Interestingly, our results are also consistent with a pattern found in a previous survey of Sierra Nevada lakes. Knapp et al. (2001) surveyed the biota of lakes in three categories: (1) naturally fishless lakes (2) lakes stocked with fish and (3) lakes where fish had been stocked, but have been restored to the fishless condition (stocked-now-fishless). They found that the stocked-now-fishless lakes were similar to the always-fishless lakes except in that they contained a marginally higher abundance of *Daphnia* spp. Our results suggest that this pattern may be due to the past selection by fish on *Daphnia* traits. The survey of (Knapp et al. 2001) suggests that these effects may persist for at least 10 years post fish-removal. The transient increase in *Daphnia* density following removal of fish could affect trophic dynamics and lake water clarity (Carpenter et al. 1987). Our results indicate that fish select for *Daphnia* traits such as fast growth rates that also increase biomass in fishless environments, but that growth rates become slower in the long term as evidenced by *Daphnia* from naturally fishless lakes.

Evidence from long-term evolution experiments suggests that we might expect the higher growth rates of *Daphnia* populations from fish lakes to diminish over time in the absence of fish (Schaum and Collins 2014). We may also expect a reduction in growth rates over time if there is a trade-off between r and competitive ability (Gill 1974). Selection by fish can increase r and R^*, the resource concentration a species requires to persist in a habitat, reducing their competitive ability (e.g., Litchman et al. 2009). Therefore, fish-selected *Daphnia* populations could be vulnerable to invasion by a slower growing, stronger competitor, or selection resulting in reduced r after fish removal. Because we did not compare the competitive abilities of the different *Daphnia,* we cannot test which populations are competitively superior; however, the lake survey suggests that the *Daphnia* that have been exposed to fish in the past may maintain higher abundance than fishless *Daphnia* for at least a decade (Knapp et al. 2001). Our results suggest that the rapid increase in *Daphnia* numbers upon removal of fish from their environment may be a transient phenomenon. Over time, abundance may be reduced by evolution toward, or invasion by, slower growing but competitively dominant clones.

Though zooplankton biomass depended on H_{Fish} there were no cascading impacts of community history on chl-*a*. Instead we found that mesocosms with fish had higher chl-*a* in a classic tri-trophic cascade where fish reduced zooplankton biomass, releasing phytoplankton from grazing pressure (Carpenter et al. 1985). We expected chl-*a* to be impacted by H_{Fish} because important determinants of zooplankton grazing rates, namely biomass and body size, were related to H_{Fish} (Table 2.1). However, we did not directly measure community grazing rates which may not have been related to these variables. This results contrasts with Ingram et al. (2012) who found that adaptation of sticklebacks to sculpin predators dampened the cascading trophic effects of sculpins on invertebrates. We found no evidence that zooplankton from lakes with fish performed better in the presence of fish in our experiment. In addition to the fish effects, we also found independent effect of experiment elevation on zooplankton. The mesocosms at the montane site (warmer temperatures, higher nutrients; see Appendix 2B) generally supported higher zooplankton abundance and biomass (Figure 2.1), consistent with surveys of lakes along an elevational gradient in the same region (Symons and Shurin 2016). The community composition in all treatments varied strongly with the elevation of the mesocosms (Figure 2.5A). Interestingly, although elevation affected composition and biomass, we saw little variation and fewer other treatment effects on community biomass, abundance, or average body size (Table 2.1). This suggests that species turnover with higher elevation resulted in species which fit in the role of species they replaced.

The response of community composition to our experimental treatments reflects patterns found in natural lakes in this region along elevational and predation gradients (Symons and Shurin 2016). Our survey of lakes found that fish had a larger impact on zooplankton species composition in high elevation lakes. Similarly, our experiment found an interactive effect of fish and elevation on composition, where we saw a greater shift in composition in response to fish at the high elevation site, whereas communities were more similar between the fish and fishless tanks at the low elevation sites (Figure 2.5A). We also found an interactive effect of community history of fish predation and experimental elevation (Figure 2.5B). Communities with different past exposure to fish remained the most distinct at high elevations and converged to more similar compositions at low elevation. This effect was largely driven by the higher abundance of *Daphnia pulicaria* in communities with a history of fish (Figure 2.5B, 2.5C). These results indicate that fish predation and elevation impose selection on many of the same zooplankton traits, including body size and growth rates.

We hypothesized that communities originating from different elevations would be locally adapted and therefore exhibit lower fitness in different climates. However, H_{Elev} did not have a significant independent effect on our response variables, or interactions with either of the E treatments (Table 2.1). This result was surprising given the large differences in temperature among the lakes from which our plankton communities originated. One possible explanation may be that zooplankton show high phenotypic plasticity in responses to temperature variation (e.g., Mitchell and Lampert 2000). Populations experience broad interannual, seasonal and vertical within-lake variation in temperature, and therefore may have evolved broad thermal niches (Miner et al. 2005). Therefore, our results could indicate that zooplankton populations in the Sierra respond to elevation with plasticity, but are more locally adapted to fish predation.

Our results show that contemporary conditions and past selection interact to determine zooplankton community response to changes in climate and predation regimes. We found a non-transitive effect of fish addition and removal in this experiment. Removing fish from the environment produced a community with greater biomass and larger individuals and species than a historically fishless community, while addition of fish resulted in a community with similar structure to those in fish lakes. This suggests that communities undergo transient dynamics after fish are removed due to past selection on life history traits of zooplankton. The legacies of past selection therefore influence community composition and trophic level biomass, leading to asymmetrical responses to the addition and removal of stressors over short timescales.

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Chapter 2, in full, is currently being prepared for submission for publication of the material. Symons C.C., M.A. Schulhof, H.B. Cavalheri and J.B. Shurin. The dissertation author is the primary investigator and author of this paper.

Appendix 2A

Species composition of the community inoculum & initial water chemistry

We selected lakes that varied in their history of fish presence and elevation to collect the four different types of source communities (sub-alpine x alpine, fish x fishless). Plankton communities were collected from three lakes within each of the four source community types. We collected the volume of zooplankton required to inoculate each mesocosm at ambient lake density (Table 2A.1; Table 2A.2).

To determine how these communities varied we conducted a permutational multivariate analysis of variance using distance matrices using the function *adonis* in the package '*vegan'*. We found that there was an interactive effect of H_{Elev} and H_{Fish} (ADONIS, p=0.001). We then conducted an NMDS on the species composition to visualize these results (Figure 2A.1). The fishless alpine lakes were the most distinct in composition due to the abundance of *Daphnia melanica* (Figure 2A.1). The biomass of each species in the inoculum can be found in Table 2.

The mesocosm water source varied among E_{Elev}, and therefore water chemistry varied among sites (Table 2A.3).

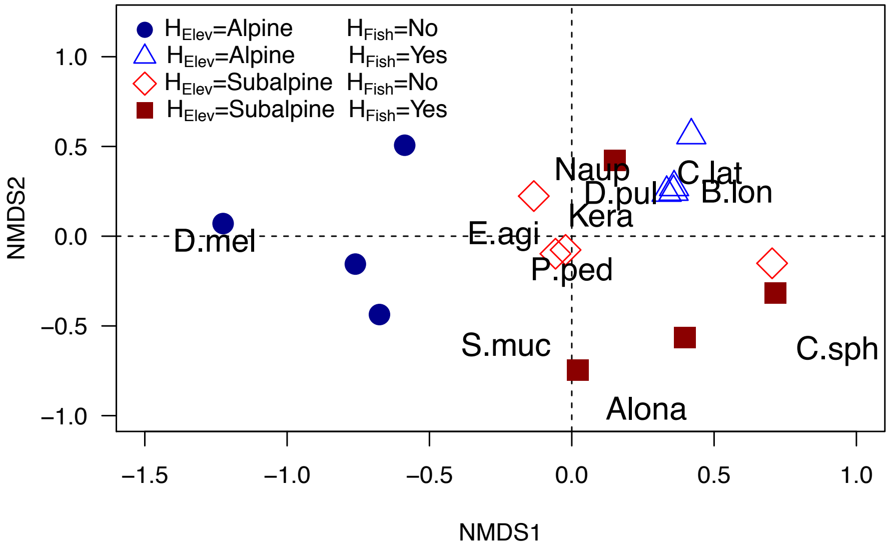

Figure 2A.1: NMDS ordination of the inoculum samples. Each point represents an aliquot of the inoculum and taxa names are placed according to their loading on the NMDS axes. Taxa depicted are *Alona* spp. (Alona), *Bosmina longirostris* (B.lon), *Ceriodaphnia laticaudata* (C.lat), *Chydorus sphaericus* (C.sph), *Daphnia pulicaria* (D.pul), *Daphnia melanica* (D.mel), *Eucyclops agilis* (E.agi), *Keratella* spp. (Kera), nauplii (Naup), *Polyphemus pediculus* (P.ped), and *Scapholeberis mucronata* (S.muc)

Table 2A.1: Lakes sampled for source communities and the abundance and biomass of the zooplankton used to inoculate mesocosms. Standard errors are in parentheses

Lakes	Lake type		Abundance (# L^{-1})	Biomass (mg L^{-1})
	H_{Elev}	H_{Fish}		
Lower Gaylor, Upper Gaylor, Helen	Alpine	Present	73.5 (35)	0.30 (0.01)
Lower Skelton, Upper Skelton, Secret	Alpine	Absent	235.5 (18)	0.71 (0.07)
Lukens, Harden, Lower Sunrise	Sub-alpine	Present	185.3 (51)	0.51 (0.11)
Dog, Polydome 1, Polydome2	Sub-alpine	Absent	407 (52)	1.55 (0.09)

Table 2A.2: The mean biomass of each species in the inoculum. Standard deviations are presented in parentheses.

Taxa	**Alpine Fish**	**Alpine No Fish**	**Subalpine Fish**	**Subalpine No Fish**
Alona spp.	0	0.2 (0.4)	0.8 (1.6)	3.2 (2.7)
Bosmina longirostris	182.8 (17.4)	1.6 (3.1)	51.6 (96.9)	180.4 (187.1)
Chydorus sphaericus	0	0	30.4 (60.9)	60.9 (82.2)
Ceriodaphnia laticaudata	24.8 (4.2)	0.3 (0.6)	7.3 (13.0)	0.6 (16.1)
Nauplii	48.8 (10.1)	14.4 (27.2)	53.9 (43.0)	16.1 (27.2)
Daphnia pulicaria	180.7 (132.3)	10.0 (12.8)	16.7 (20.1)	344.7 (302.3)
Eucyclops agilis	268.8 (11.3)	68.8 (39.1)	609.0 (364.6)	223.0 (88.1)
Keratella spp.	3.4 (2.5)	2.3 (4.3)	10.6 (4.5)	3.4 (2.1)
Scapholeberis mucronata	0	0.4 (0.9)	2.1 (2.6)	0.9 (1.0)
Daphnia melanica	0	202.7 (38.4)	0	0
Polyphemus pediculus	0	0	433.4 (155.4)	2.0 (3.9)

Table 2A.3: Initial water chemistry at the three experimental sites. Values are reported as means with standard errors in parentheses

Site	TN (mg/L)	TP (mg/L)	DOC (μM Carbon)	pH	Conductivity (μS cm^{-1})
Montane (SNRI)	0.38 (0.09)	<0.001	416 (12.6)	8.0 (0.03)	58.8 (0.9)
Sub-alpine(SNARL)	0.28 (0.02)	<0.001	212 (14.1)	8.7 (0.01)	203.6 (1.6)
Alpine (WM)	0.34 (0.12)	<0.001	315 (16.4)	8.3 (0.04)	87.1 (2.9)

Appendix 2B

Water chemistry

We measured the nutrients (total nitrogen, total phosphorus) in June, July and September of 2016. Dissolved organic carbon was measured once at the end of the experiment in September 2016. We modeled total nitrogen (TN) and total phosphorus (TP) using a linear mixed effects model. The fixed effects included in the model are E_{Fish} and E_{Elev} (the contemporary effects of fish and elevation), H_{Fish} and H_{Elev} (the presence of fish and elevation of the source environment), and the two-way interactions among them (Table 2B.1, Figure 2B.1 & 2B.2). Dissolved organic carbon (DOC) was modeled with an ANOVA with the two-way interactions and main effects of the four factors (Table 2B.1, Figure 2B.3).

We found that TN was unaffected by any of the imposed treatments, although there was variation over time, with highest TN in July (Figure 2B.1). TP was related to E_{Elev} with TP being highest at the low elevation site, and at the lowest elevation site the effect of H_{Fish} was the strongest with higher TP in mesocosms where the community came from a fishless lake (Figure 2B.2). Finally, DOC was highest in the low elevation site as was expected due to higher input of terrestrial detritus (Figure 2B.3).

Table 2B.1: p-values for mixed effects models and ANOVA of total nitrogen (TN), total phosphorus (TP) and dissolved organic carbon (DOC)

	TN	TP	DOC
Test	LME	LME	ANOVA
E_{Fish}	0.92	0.32	0.49
E_{Elev}	0.12	**<0.001***	**<0.001***
H_{Fish}	0.67	**0.03***	0.55
H_{Elev}	0.66	0.80	0.13
E_{Fish}*E_{Elev}	0.98	0.07	0.10
E_{Fish}*H_{Fish}	0.92	0.50	0.77
E_{Fish}*H_{Elev}	0.16	0.99	0.60
H_{Fish}*E_{Elev}	0.43	**0.009***	0.39
H_{Fish}*H_{Elev}	0.62	0.17	0.76
H_{Elev}*E_{Elev}	0.62	0.40	0.15

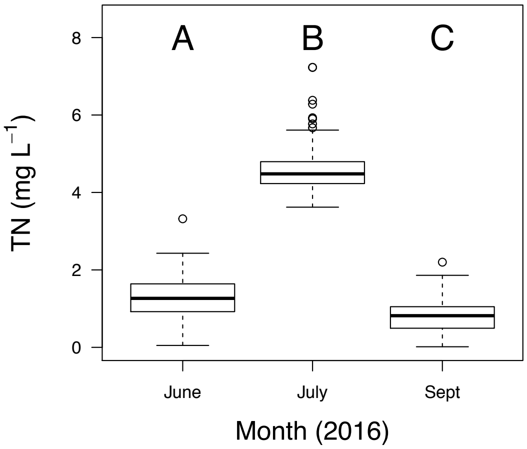

Figure 2B.1: Total nitrogen measured from the mesocosms over the summer of 2016. The letters denote which groups are significantly different from each other at $p<0.05$

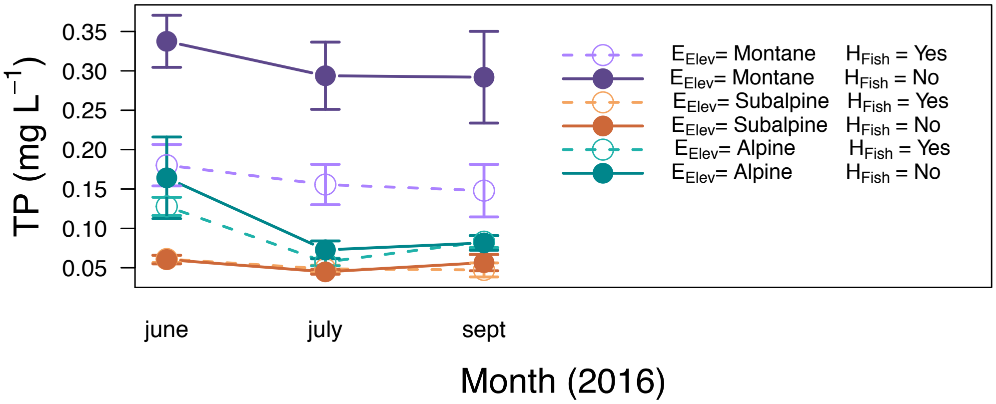

Figure 2B.2: Total phosphorus measured from the mesocosms over the summer of 2016

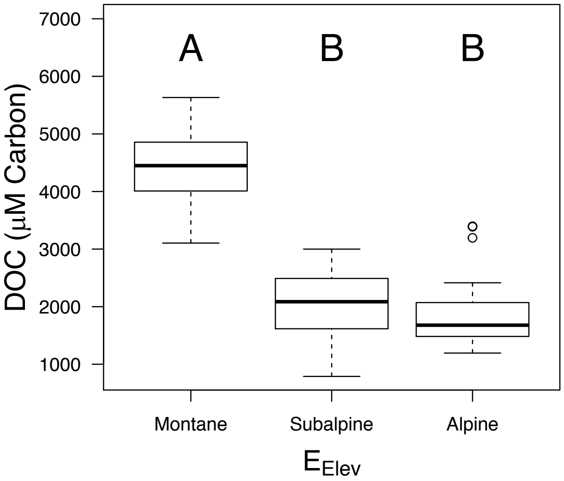

Figure 2B.3: The dissolved organic carbon in mesocosms at each of the three E_{Elev} sites. The letters denote which groups are significantly different from each other at $p<0.05$

Appendix 2C

Fully factorial analysis

We modeled total zooplankton community biomass, chl-*a*, average body size and total abundance using a linear mixed effects model. The fixed effects included in the model are E_{Fish} and E_{Elev} (the contemporary effects of fish and elevation), H_{Fish} and

H_{Elev} (the presence of fish and elevation of the source environment), and all interactions among them. Sample date and mesocosm were included as random effects to account for temporal pseudoreplication. Variables were transformed to improve normality and homoscedasticity. Models were run using the function *lme()* in the *nlme* package (Pinheiro et al. 2016). *Daphnia pulicaria* responses were modeled with a permutational LME due to non-normal distributions of data (Table 2C.1).

All analyses were performed in R (R Core Team 2016).

Table 2C.1: *p*-values for mixed effects and permutation models

	Community biomass	Abundance	Average body size	*Daphnia pulicaria* biomass
Test	LME	LME	LME	Permutation
E_{Fish}	0.059	0.98	**0.001***	--
E_{Elev}	**<0.001***	**<0.001***	**<0.001***	--
H_{Fish}	0.17	0.43	0.89	--
H_{Elev}	0.92	0.85	0.91	--
E_{Fish}*E_{Elev}	0.99	0.84	0.31	--
E_{Fish}*H_{Fish}	**0.01***	0.78	**0.007***	--
E_{Fish}*H_{Elev}	0.21	0.15	0.51	--
H_{Fish}*E_{Elev}	0.89	0.70	0.48	--
H_{Fish}*H_{Elev}	0.85	0.59	**0.007***	--
H_{Elev}*E_{Elev}	0.85	0.68	0.90	--
E_{Fish}*E_{Elev}*H_{Fish}	**0.03***	0.62	0.44	**0.001***
E_{Fish}*E_{Elev}*H_{Elev}	0.10	0.37	0.85	0.33
E_{Fish}*H_{Elev}*H_{Fish}	0.99	0.58	0.62	0.29
E_{Elev}*H_{Elev}*H_{Fish}	0.26	0.65	**0.007***	0.34
E_{Fish}*E_{Elev}*H_{Fish} *H_{Elev}	0.83	0.44	0.98	0.37

* denotes significance at p<0.05

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CHAPTER 3

Antagonistic effects of temperature and allochthony on fish growth in California mountain lakes

Abstract

Resources and temperature play major roles in determining biological production in lake ecosystems. Lakes have been warming and ‘browning’ over recent decades as a result of climate change and increased loading of organic matter of terrestrial origin. Conflicting hypotheses and evidence have been presented about whether these changes will increase or decrease production of fish. DOC may enhance fish growth by stimulating microbial production that is transferred up through food webs, or may reduce fish production if it provides poor quality food, and decreases aquatic primary production through shading. We sampled 20 trout populations in the Sierra Nevada mountains of California to examine how body condition and individual growth rates, measured by otolith analysis, varied across independent elevational gradients in temperature and dissolved organic carbon (DOC). We found that fish grew faster at warmer temperatures but slower in high DOC lakes. Additionally, spectral analysis of the source of DOC found that fish in lakes with more terrestrially-derived carbon compared to within-lake carbon production showed poorer body condition. The warming and browning of lakes in the future will likely have antagonistic impacts on fish growth in these high elevation lakes reducing the predicted independent impact of each stressor.

Keywords

Rainbow trout; Brook trout; *Salvelinus fontinalis*; *Oncorhynchus mykiss*; light; production; elevation; alpine lakes

Introduction

A dominant paradigm in freshwater ecology is that the level of primary and secondary production in lakes is largely determined by nutrient concentrations, mainly nitrogen and phosphorus. In addition to N and P, dissolved organic carbon (DOC) has emerged as another major determinant of the structure and function of lake ecosystems (Williamson et al. 1999). The role of terrestrial carbon sources in subsidizing aquatic consumers and limiting *in situ* primary production is currently under much debate (Pace et al. 2004, Wilkinson et al. 2013). The role of terrestrial carbon is important to determine as climate warming is altering the distribution of vegetation and accelerating detrital decomposition, thereby increasing the supply of organic matter to aquatic systems (Evans et al. 2006, Monteith et al. 2007, Larsen et al. 2011). Understanding how terrestrial carbon subsidies to lakes will influence fish production is critical to predicting how climate change will influence this important ecosystem service.

Dissolved organic carbon (DOC) quantity can have positive or negative effects on secondary production in lakes (Karlsson et al. 2009, Jones et al. 2012). DOC can increase secondary production in lakes by blocking harmful UV rays and by providing a source of organic carbon to aquatic micro-organisms that are resources for invertebrates (Hessen and Andersen 1990, Stasko et al. 2012). In oligotrophic lakes DOC is also a major source of phosphorus and nitrogen to lake production (Hessen et al. 2009). However, colored DOC can decrease production by reducing the amount of photosynthetically active radiation (PAR) in the water column, resulting in light limited phytoplankton and benthic algae growth decreasing energy available to higher trophic levels (Jones et al. 2012). A recent lake survey found that fish abundance was unimodally related to DOC in nutrient-poor lakes (Finstad et al. 2014). However, fish abundance may be a poor indicator of their productivity. Understanding how DOC will influence fish growth in lakes, particularly mountain lakes which are predicted to be the most impacted by browning, is of particular importance.

DOC that originates within (autochthonous) vs. outside of (allochthonous) lake waters differs in chemical characteristics, bioavailability and impacts on food webs. Terrestrially-derived allochthonous DOC contains the most recalcitrant, colored compounds which reduce water transparency, attenuate light, increase bacterial production, and suppress phytoplankton production (reviewed in Williamson et al. (1999). Terrestrially derived DOC may also provide lower quality resources to food webs than phytoplankton as the materials are mainly used by heterotrophic bacterioplankton, which are poor food for zooplankton (Wetzel 1995). Comparatively, autochthonous DOC has less structural carbon, and higher essential fatty acid content making them higher quality food for higher trophic levels (Brett et al., 2009). A recent study found that fish growth in a Canadian Boreal Shield lake was related to both DOC quantity and quality (Tanenzap et al. 2015). DOC quantity and quality may therefore exert different effects on lake food webs (Tanenzap 2017). As climate changes, we expect allochthonous inputs of carbon to increase disproportionately to autochthonous sources. The impact of DOC quality on biological production across trophic levels in lakes, including potential fisheries yield, remains an open question.

In addition to DOC, growth in fish is highly dependent on temperature (Elliott 1976). Within lakes, fish growth has been positively correlated to variation in temperature (Morrongiello et al. 2011). However, the effect of temperature among populations is shaped by the potential for local adaptive response over time. Reponses to temperature will depend on the thermal tolerance curve, which may be shaped by population-specific response to the local environment (Somero 2010). Fish can adapt to different thermal regimes over a few generations (reviewed in Crozier and Hutchings 2014). In fishes, evidence has been shown for countergradient variation among thermal environments where growth rates remain similar at different temperatures because genetic differences counteract the environmental effect (e.g., Conover and Present 1990). Determining how fish growth varies over broad temperature gradients where there has been opportunity for adaptation to temperature will help to understand the impact of climate change on this important ecosystem function.

Study location

Our study is focused on oligotrophic mountain lakes of the Sierra Nevada that vary in elevation from 2506 to 3337 m. Historically, California mountain lakes were fishless due to colonization barriers. However, the majority of lakes now contain trout (primarily brook trout *Salvelinus fontinalis* and rainbow trout *Oncorhynchus mykiss*) which were introduced approximately 100 years ago to create recreational angling opportunities (Knapp et al. 2001). Mountain lakes tend to be oligotrophic and clear making them especially sensitive to even small changes in DOC concentrations relative to darker lakes, with large impacts on thermal structure and light penetration

(Stasko et al. 2012). Despite the increasing interest in the effect of climate change on DOC concentrations there are very few empirical investigations into the role of DOC in oligotrophic, clear lakes that may show the greatest sensitivity to increased terrestrial carbon subsidies (but see Finstad et al. 2014). Here we chose lakes arrayed along independent gradients in temperature and DOC to examine how these variables, among others, influence individual fish growth rates and body condition.

Methods

We chose 20 lakes in the Sierra Nevada to test the effects of temperature and DOC on fish growth. The mountainous terrain provides a natural elevational gradient in temperature and DOC while water chemistry shows less variation due to similar underlying geology (Sadro et al. 2011). We chose lakes to have independent gradients in temperature and DOC to determine their independent effects (temperature and DOC correlation r^2=0.31, p=0.20). Lake fish communities are very low in diversity because the lakes are naturally fishless and were stocked with trout (Knapp et al. 2001). Brook trout (*Salvelinus fontinalis*), rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), cutthroat trout (*Oncorhynchus clarkii*), golden trout (*Oncorhynchus mykiss aguabonita*) were stocked starting in the late 1800s until cessation in the 1970s. Brook trout and rainbow trout are the most common species found in the lakes of the Sierra Nevada (Knapp et al. 2001). We sampled each lake for water chemistry, zooplankton, phytoplankton, macroinvertebrates and fish between July 2015 – September 2015 and June 2016 – August 2016.

Lake Sampling Methods

At the deepest point in each lake *in situ* measurements of temperature, conductivity, dissolved oxygen (DO) and pH were taken using a YSI probe (YSI Incorporated, Yellow Springs, Ohio, USA). Surface water samples were filtered through 63-um mesh to remove zooplankton and processed for chlorophyll-*a* (chl-*a*), particulate organic matter (POM), total nitrogen (TN), total phosphorus (TP) and dissolved organic carbon (DOC). For chl-*a* quantification, a known volume of water was filtered through 0.45μm glass fiber filters (GF/F fisher scientific) and frozen. Chl-*a*, a proxy for phytoplankton biomass, was measured using a fluorometer after a 24 hr cold methanol extraction. For POM isotope analysis a known volume of water was filtered through pre-weighed precombusted (7 hours, 500C) 0.45μm glass fiber filters. Upon returning to the lab, samples were dried for 24 hours at 60C, weighed and packaged in tin capsules for isotope analysis. Total nitrogen and total phosphorus samples were collected in HDPE vials and preserved with H_2SO_4 to a $pH<2$ and stored at ~4 C until analysis. TN and TP were measured using an auto analyzer (LaChat QuikChem 8500, persulfate digestions). Leaves of several common plant species were collected from shoreline and frozen until processing for isotopic analysis. Leaves were sorted into broad functional groups (grasses, shrubs, pine), and dried at 60C for two days. A mortar and pestle was used to grind the leaf samples before packaging in tin capsules for isotope analysis. Based on a subset (10 lakes) of the plant data we chose to process a grass and a pine sample to capture the maximum variation in isotopes within the terrestrial organic matter entering lakes.

To quantify DOC, water samples were filtered through precombusted glass fiber filters (Whatman GF/F, pore size 0.45μm) into triple-rinsed 20 mL glass vials and preserved with HCl to a pH<2. DOC was measured using a total organic carbon analyzer (TOC-V CSN, Shimadzu Scientific Instruments, Japan). To characterize DOC quality, we used fluorescence spectroscopy, which provides compositional and chemical information about the fluorescing DOM pool. We collected excitation emission matrices (EEMs) which are a 3-dimensional representation of fluorescence intensities scanned over a range of excitation/emission wavelengths (Chen et al. 2003). EEMs were collected with a JY-Horiba Spex Fluoromax-3 spectrophotometer at room temperature using 5nm excitation and emission slit widths and an integration time of 1.0s. All fluorescence spectra were collected in signal-to-reference (S:R) mode with instrumental bias correction. Instrument-specific corrections, Raman area normalization, and Milli-Q blank subtraction were conducted with Matlab (2009). From the EEMs data we calculated two indices of DOC quality: the freshness index (FI) and specific UV absorption (SUVA). FI (β:α) is a ratio of emission intensity at 380 nm to that of the region between 420 and 435 nm at an excitation of 310 nm and was developed to quantify recently produced algal organic matter (Parlanti et al. 2000). SUVA is a DOC-normalized index of aromaticity calculated as UV absorbance at 254nm/[(DOC(mg/L) x Path length (0.01m)] (Weishaar et al. 2003). FI increases with autochthonous carbon production whereas SUVA increases with allochthonous carbon production.

All fish, plant and POM isotope samples were analyzed by the University of California, Davis Stable Isotope Facility for ^{13}C and ^{15}N using an elemental analyzer interfaced to a continuous flow isotope ratio mass spectrometer.

Fish sampling

At each of the 20 lakes we caught fish by angling. Each fish was identified to species, weighed, photographed and measured (TL; maximum length). We collected a dorsal muscle sample from each individual which was frozen until processing for stable isotope analysis. Upon returning to the lab muscles samples were freeze-dried for 24 hours, ground with a mortar and pestle and packaged for ^{13}C and ^{15}N analysis. Otoliths were removed, cleaned, dried and stored in vials for age determination and growth rate analysis. We calculated catch per unit effort (CPUE) as the number of person-hours spent angling at each lake.

Fish sample processing

Fish in temperate regions can be aged by examining calcified structures called otoliths, which form annuli – rings that correspond to low winter growth. The width of the annuli is an indicator of annual growth. To determine age and annual growth the sagittal otoliths were mounted on a microscope slide and polished until a transverse cross-section remained and microstructures were visible. Annuli were counted by two independent readers in the absence of information about fish size or lake. Ages were in agreement for 84% of the otoliths, and never differed by more than one year. For otoliths where the age determinations disagreed the two readers examined the otoliths together and were able to reach consensus. The width of each annuli was measured using imaging software (Image J).

Calculations and statistical analysis

For body condition comparison we calculated condition using equation 1 (Fulton 1902).

$$\text{Condition} = (\text{wet body mass}/ \text{total body length}^3) \times 100 \tag{1}$$

To quantify DOC quality we conducted a PCA on the correlation matrix of two indices of DOC quality: freshness index, and SUVA. We first removed three outlier lakes for the SUVA index. Both SUVA and freshness loaded positively on PCA axis 1, and SUVA loaded negatively on axis 2 while freshness loaded positively (Figure 3A.1). The site scores along axis 2 were used as a measure of DOC quality for further analysis where low values of this quality variable are indicative of allochothonous DOC and high values indicate autochthonous DOC.

Trophic position for each fish was calculated using the $\delta^{15}N$ values of fish, plants and particulate organic matter (POM). We calculated fish trophic position as the number of trophic levels above the average plant and POM $\delta^{15}N$, assuming a trophic enrichment of $\delta^{15}N$ of 3.4‰ per trophic level (Post 2002).

To determine the best predictors of body condition we fit a mixed effects model with lake temperature, elevation, DOC, fish $\delta^{13}C$, fish trophic position, CPUE, chl-*a*, TN, date caught, species and DOC quality as predictors and lake as a random effect. TP was not included as a predictor because it consistently fell below detection limits. Variance inflation factors were calculated to determine the degree of multicollinearity and all VIFs were <4 suggesting that these predictors are appropriate to use (Quinn and Keough, 2002). We used a forward selection AIC-based procedure to fit the best models. In addition we calculated importance values for all predictors using the dredge() function in the R package “MuMIn”. Importance values for parameters are calculated by constructing models with all possible combinations of predictor variables and summing Akaike weights for each model that contains the predictor of interest. Importance values range from 0 (least important) to 1 (most important).

To examine individual-level growth rates we restricted our analysis to fish that were at least 4 years old to generate time series of comparable lengths similar to Romo-Curiel et al. (2015). Growth was represented as the length of the radii from the core to each annulus as a function of age (Figure 3.1A). To calculate a measure of individual growth rate we fit a linear model to the annuli radius as a function of age from age 1 to 4. The slope of this line was then used as a measure of individual growth rate for further analyses. We fit a mixed effects model as above to predict growth. We removed trophic position and date caught as predictors because these are not relevant to early growth. We added an additional predictor because fish of different ages experienced early growth during different calendar years. We were interested in having a measure of temperature experienced by the fish during the years they were between 1 and 4 years old. To this end, we calculated the average air temperature over this three-year period from the Virginia Lake weather station, the closest weather station to our sites, which is located at an elevation that is intermediate to our sites (NOAA Virginia Lake MCAS, CA US). Model selection and importance values were calculated as above. Results were consistent when we calculated growth over different durations (e.g., growth from age 1 to 3, or age 1 to 5; Table 3A.1).

For the condition and growth analysis we plotted the data as added-variable plots (AV plots; Figure 3.1, Figure 3.2). These plots show the effect of x on y without interfering effects from other explanatory variables, therefore more clearly depicting the relationships found by the model (Draper et al. 1966).

All analyses were done in R (R Core Team 2016).

Results

We caught 87 fish across the 20 lakes (range 1-12, average 4). We caught 77 rainbow trout and 10 brook trout, and the brook trout were always caught in lakes where we also caught rainbow trout. The mean length of fish varied between lakes and ranged from 12 to 36.0 cm, and their weight varied from 0.03 to 0.62 kg.

The lakes were arrayed along broad environmental gradients from 2506 to 3337 m in elevation. This allowed us to sampled lakes that varied in epilimnion temperature from 8.7 to 20.3 C and DOC concentration that varied from 0.83 to 3.6 mg L^{-1}. A summary of the predictor variables can be found in Table 3.1.

Forward-selection AIC on mixed effects models found that fish body condition increased with TN and DOC quality, and decreased with temperature, elevation and DOC quantity (Figure 3.1; Table 3.2). This model selection procedure identified the best model according to AIC. One term in the model (DOC) is marginally significant in the model, but was retained because it reduced model AIC (Figure 3.1). The five predictor variables selected by AIC also had the highest importance values when considering all possible reduced models (Table 3.2).

Otoliths

Fish ranged in age from 1 to 15 years, and averaged 4.8 years old. Growth curves varied among individuals (Figure 3.2A). Early growth was negatively related to the quantity of DOC, and the $\delta^{13}C$ of fish (Figure 3.2B, 3.2C; Table 3.2) and positively related to temperature and chl-*a* (Figure 3.2D, 3.2E; Table 3.2).

Table 3.1: Median and range of physical and environmental variables from the 20 lakes sampled

	Median	Range
DOC (mg L^{-1})	1.1	0.83–3.6
Elevation (m)	3120	2506–3337
TN (mg L^{-1})	0.3	0.02–0.58
Lake temperature (C)	15.9	8.7–20.3
SUVA	1.1	0.06–2.7
Freshness Index	0.58	0.34–0.77
δ^{15}N of fish (‰)	6.6	3.9–9.7
δ^{13}C of fish (‰)	-19.8	-30.9 – -14.4
Chl-*a* (µg L^{-1})	0.44	0.18–1.23
CPUE (fish hour^{-1})	2	0.04–4
Trophic position	3	1.88–3.75
Temperature (age 1 to 4, C)	5.7	4.5–6
Precipitation (age 1 to 4, mm yr^{-1})	20	19.4–28.3

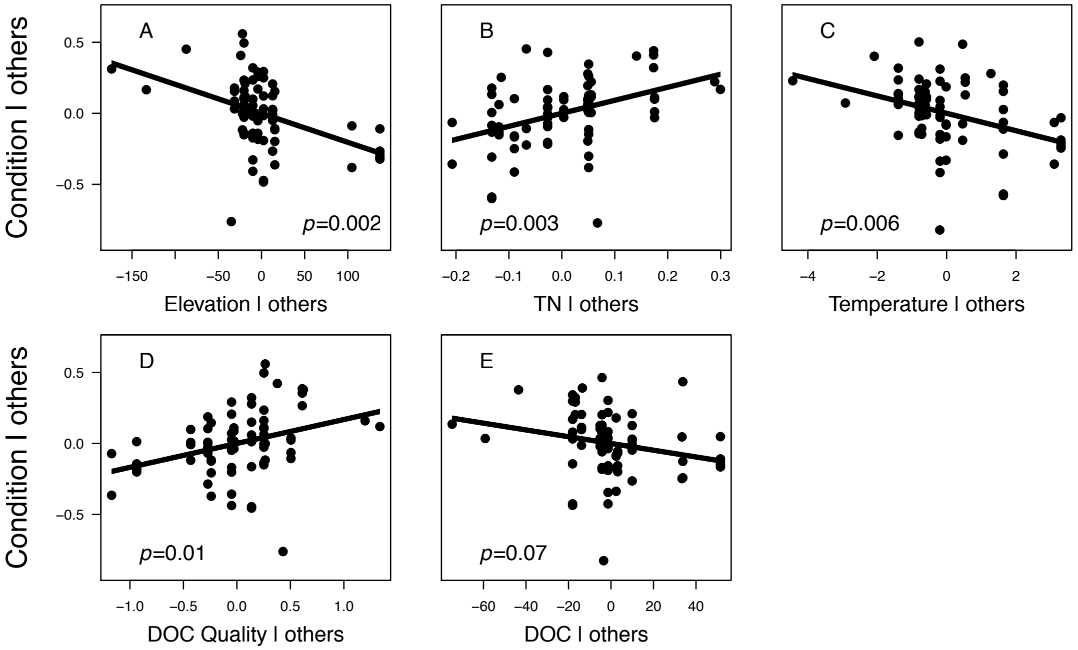

Figure 3.1: Added-variable plots for predictors of body condition in the final model selected by forward AIC selection.

Table 3.2: Importance values for predictors of fish condition (mg mm^{-3}) and fish growth (mm otolith year^{-1}) from mixed effects models. Bold values represent predictors that were included in the best model from forward AIC selection.

Predictor	Condition	Growth
DOC (mg L^{-1})	**0.34**	**0.72**
Elevation (m)	**0.57**	0.40
TN (mg L^{-1})	**0.44**	0.28
DOC quality	**0.40**	0.21
Lake temperature (C)	**0.39**	0.32
$\delta^{13}C$ (‰)	0.34	**0.60**
Chl-*a* (µg L^{-1})	0.27	**0.48**
Species	0.32	0.22
CPUE (fish hour^{-1})	0.24	0.22
Date	0.25	--
Trophic position	0.26	--
Temperature (age 1 to 4, C)	--	**0.56**
Precipitation (age 1 to 4, mm yr^{-1})	--	0.44

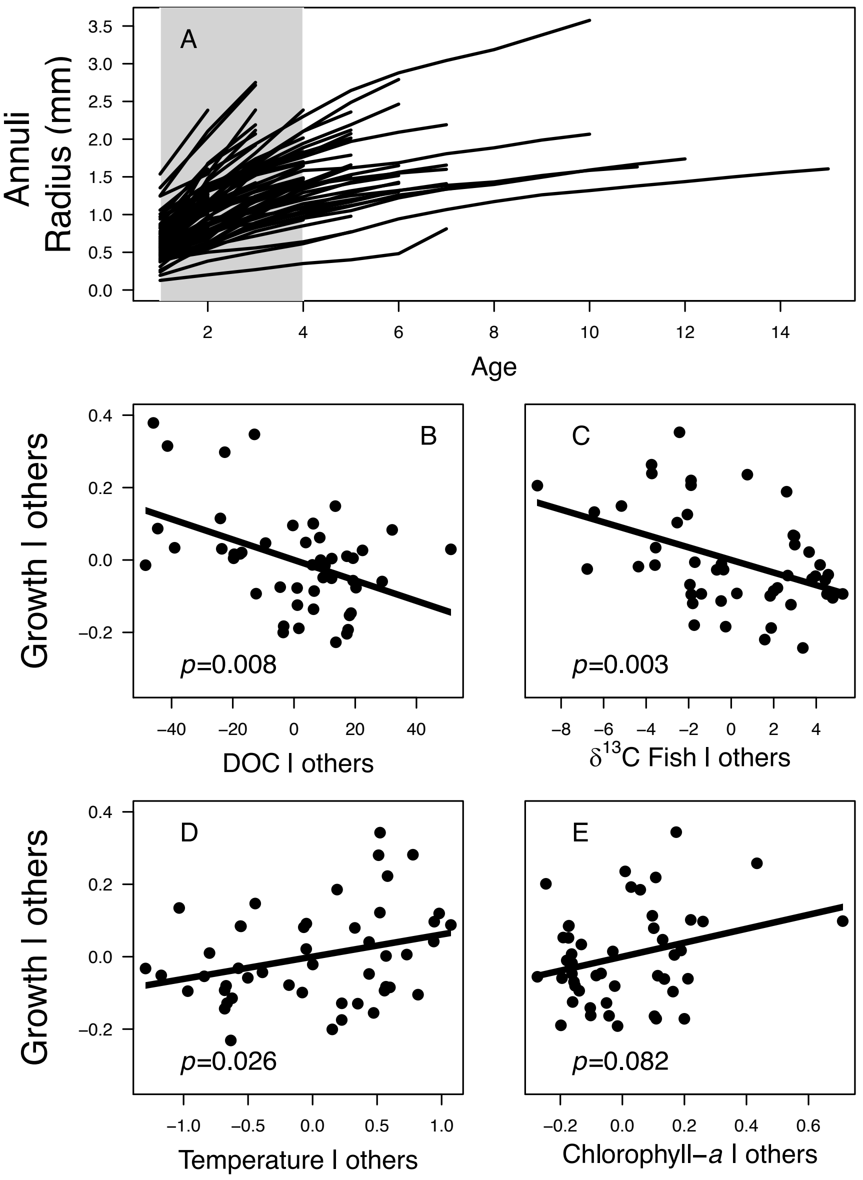

Figure 3.2: A) Growth trajectories for individual fish plotted as the otolith annuli radius as a function of age. Linear models were fit to the growth from age 1 to 4 for individuals that were at least 4 years old (shaded box) and used as the measure of growth for future analysis. B-E) Added-variable plots for predictors of individual growth in the final model selected by forward AIC selection.

Discussion

We found opposing effects of temperature and DOC on fish growth, with faster growth in warmer lakes, and slower growth in higher DOC lakes. Ours is one of the only studies of the influence of DOC on fish performance in oligotrophic lakes, where terrestrial subsidies are expected to act as a source of nitrogen and phosphorus to increase lake production, including fish (Hessen et al. 2009). However, we found that DOC was a strong, negative predictor of early individual fish growth rates (Table 3.2; Figure 3.2), even at these low concentrations (Table 3.1). Fish body condition was related negatively to DOC, but positively to DOC quality, a measure of DOC source (terrestrial or algal). Algal-derived carbon is associated with greater fish body condition, suggesting that the origin of DOC impacts food quality for fish. Overall, our results suggest that as lakes become warmer and browner, fish production will depend on the magnitude of the change in each of these stressors. A concurrent increase in temperature and DOC could buffer fish growth rates from predicted change in response to these individual stressors.

Two recent studies found that DOC is negatively related to fish abundance in European and North American temperate lakes (Karlsson et al. 2009, Finstad et al. 2014). However, abundance is not a proxy for growth. Benoît et al. (2016) hypothesized that a decrease in abundance with DOC may increase density-dependent fish growth rates. Despite this prediction they found a negative impact of DOC on growth rates, suggesting DOC was functioning to reduce production through shading (Benoît et al. 2016). Our study expands this result by examining lower DOC lakes, which are not currently represented in the literature (Benoît *et al*. 2016: 2.6-9 mg/L, current study 0.83-3.6 mg/L). Globally, most lakes are oligotrophic and clear, and are predicted to respond strongly to even small increases in DOC (Stasko et al. 2012). Therefore, determining if DOC will reduce or increase fish growth rates at these low concentrations is important to understanding how lake ‘browning’ will impact important ecosystem functions in the future in the majority of lake ecosystems.

We found a negative relationship between DOC and individual fish growth even at very low concentrations of DOC. This is potentially due to a negative effect of DOC on primary productivity via photon absorption (Carpenter et al. 1998, Jones et al. 2012, Thrane et al. 2014). DOC can absorb 10 times as many photons as phytoplankton, reducing light availability for primary production in phytoplankton and benthic algae (Thrane et al. 2014). Indeed, a precipitous drop in 1% PAR absorption depth was documented between 0.1 and 3 mg L^{-1} of DOC in Canadian Boreal Shield lakes (Gunn et al. 2001), similar to the range of DOC concentrations sampled in this paper (Table 3.1). Thus, although Sierra Nevada lakes appear very clear, it is apparent that even small changes in DOC can reduce the light energy available for in-lake production. Corroborating this, fish growth was positively related to chl-*a* concentration, a proxy for phytoplankton biomass and aquatic productivity (Figure 3.2E). Together this suggests that fish growth is regulated through bottom-up processes, where primary production at the base of the food web determines the energy available for higher trophic levels.

DOC can also alter the visual environment in which fish must operate. Lower light intensity can decrease the visual acuity of planktivorous fish (Vinyard and O’Brien 1976, Bramm et al. 2009), decreasing their consumption rates (Carter et al. 2010). Therefore, the negative relationship between growth and DOC could be mediated through changes in the efficiency of trout foraging in different light environments.

To model growth we measured DOC and chl-*a* concentrations during different calendar years than the growth of fish from age 1 to 4, implicitly assuming that measured DOC and chl-*a* represent difference among lakes that persist over the lifespan of fish. In Sierra Nevada lakes DOC and chl-*a* show distinct seasonal patterns associated with snow-melt (Piovia-Scott et al. 2016); however, on annual timescales DOC and nutrient-load to lakes is largely driven by characteristics of the terrestrial ecosystems such as primary production and vegetation structure which are likely stable at the timescale of interest (Larsen et al. 2011). Among lake variation in DOC and water chemistry may therefore be maintained despite interannual variability driven by weather conditions.

To examine the source of primary production used by fish we measured $\delta^{13}C$ in fish muscle, which was negatively related to fish growth rates. The fish $\delta^{13}C$ we measured was less negative than our measured plant or POM signatures (Symons and Shurin, *unpublished data*) even after accounting for trophic enrichment of ^{13}C (Post 2002). Therefore, we do not have appropriate endpoints for mixing models, and are unable to determine the carbon source fish. Resolving the explanation for the negative association between $\delta^{13}C$ and fish growth requires further study.

The effect of temperature on growth was more intuitive, with higher individual growth rates in warmer lakes. Within populations fish growth rates are related to temperature (Elliott 1976) and this growth is captured by variation in otolith width (Black et al. 2005). Higher growth rates in warmer lakes likely represent faster metabolic processes increasing growth in these ectothermic animals. Additionally, the seasonal duration of temperatures that permit physiological processing of food can limit growth in ectotherms (Sinervo et al. 2010). In colder, high elevation lakes there are shorter ice-free season, and likely shorter window of time that temperatures are optimal for growth. As temperatures warm fish growth rates will likely increase.

We did not find that fish density as measured by angling CPUE predicted growth rates or body condition (Table 3.2). However, angling estimates of fish density are not as reliable as other estimates, e.g. gill nets (Pierce and Tomcko 2003). Higher fish density can reduce individual growth rates through increased competition for food (Magnuson 1962), and has been documented in rainbow trout (Holm et al. 1990). It is possible that with a more accurate estimate of CPUE fish density may be important for individual growth rates.

Fish body condition was generally related to different lake variables than growth (Table 3.2). Body condition varies on shorter timescales than growth and is often indicative of recent prey availability and quality (Blackwell et al. 2000). We found that variables associated with aquatic productivity – low DOC quantity, high TN, and high DOC quality (Elser et al. 2000, Brett et al. 2017) – were related to better body condition (Figure 3.1). Our results agree with Tanentzap et al. (2014) who showed a positive influence of DOC quality on fish growth. Lower quality, terrestrially-derived organic matter lacks fatty acids required by zooplankton and other consumers that are found in algal matter (Brett et al. 2009). Although we did not find an impact of DOC quality on fish growth rates, the reduction in body condition with low quality DOC suggests that food quality at the base of the food web can impact higher trophic levels.

Conclusion

Understanding the role of temperature and DOC in structuring aquatic ecosystems is imperative as the climate warms and the influence of terrestrial production increases. This study adds to the body of evidence showing negative effects of terrestrial inputs on production of fish in lakes (Karlsson et al. 2009, Finstad et al. 2014, Benoît et al. 2016). Our survey is unique in adding a new geographic range and expanding the DOC concentration gradient to include lower DOC lakes. Even in these low DOC, clear lakes there was a negative impact of DOC on fish growth and body condition, which was likely driven by the negative effect of DOC on lake primary production and subsequently fish growth. Lakes will warm and brown at different rates depending on their geographical context, thus the response of fish growth to climate change will be context dependent. In lakes of the Sierra Nevada when warming and browning will occur together, these changes will likely have antagonistic impacts on the growth rates of fish and the productivity of an economically important recreational fishery.

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Chapter 3, in full, is currently being prepared for submission for publication of the material. Symons C.C., M.A. Schulhof, H.B. Cavalheri and J.B. Shurin. The dissertation author is the primary investigator and author of this paper.

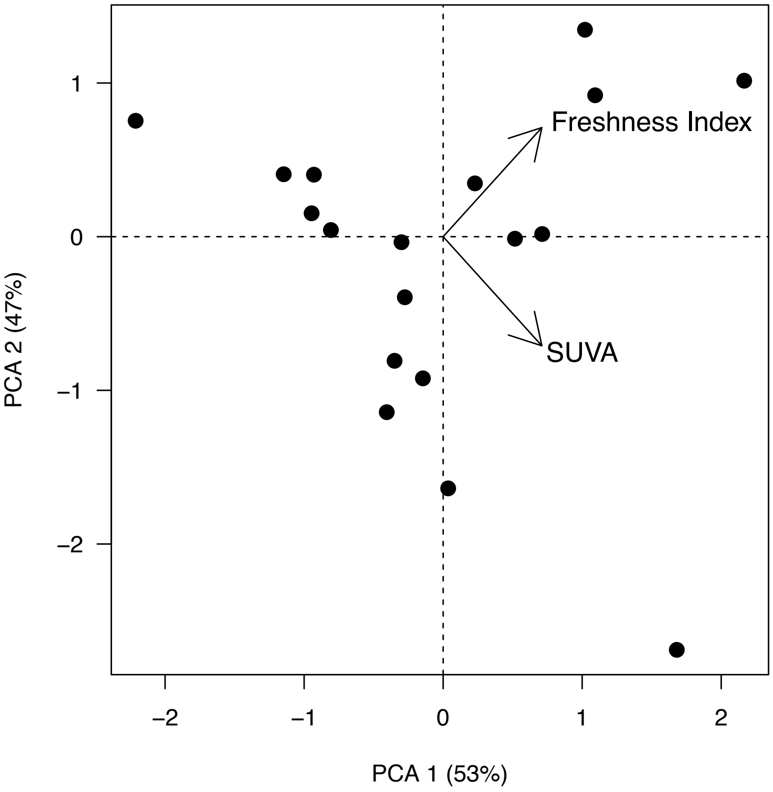

Figure 3A.1: A PCA of DOC quality metrics: Freshness Index and Specific UV Absorption (SUVA). Each point represents a lake. The percent of variation explained by each axis are in parentheses. The axis two scores were used as a metric of DOC quality.

Table 3A.1: Importance values for predictors of fish growth (mm otolith year^{-1}) from mixed effects models. Bold values represent predictors that were included in the best model from forward AIC selection.

Predictor	Growth (age 1 to 3)	Growth (age 1 to 4)	Growth (age 1 to 5)
DOC (mg L^{-1})	**0.42**	**0.72**	**0.78**
δ^{13}C (‰)	**0.52**	**0.60**	**0.48**
Temperature (age 1 to 4, C)	0.32	**0.56**	**0.61**
Chl-*a* (μg L^{-1})	0.22	**0.48**	**0.57**
Precipitation (age 1 to 4, mm yr^{-1})	0.29	0.44	0.44
Elevation (m)	0.48	0.40	**0.47**
Lake temperature (C)	0.29	0.32	0.38
TN (mg L^{-1})	0.28	0.28	0.31
Species	0.21	0.22	0.22
CPUE (fish hour^{-1})	0.21	0.22	0.23
DOC quality	0.21	0.21	0.20

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CONCLUSION

Large-scale anthropogenic disturbances such as changes in climate and the introduction or extirpation of top predators have the potential to alter community structure and function worldwide. Some effects may be buffered by species adapting to new conditions and/or tolerant species colonizing the habitat, allowing populations to be maintained in the face of these environmental challenges (Loreau et al. 2003, Hoffmann and Sgro 2011). Adaptation and colonization can stabilize ecosystem functions like biomass production during periods of environmental change (Gonzalez and Loreau 2009, Thompson and Shurin 2012, Gonzalez et al. 2013, Symons and Arnott 2013). However, predicting the impacts of novel environmental and biotic conditions is challenging because slow processes like species turnover or adaptation may dampen the direct effects of environmental change on ecosystems. (i.e., species turnover and adaptation Alexander et al. 2016). **This dissertation set out to elucidate how climate and predators shape aquatic communities over long time periods in order to understand how species turnover and local adaptation stabilize community responses to environmental change.**

I used a ‘natural experiment’ of lakes arrayed along an elevational gradient, where some lakes contain fish and others remain naturally fishless. This system therefore consists of communities that have assembled and evolved in response to different abiotic and biotic environments over the order of 100 years (fish) to millennia (temperature). Using this system, I have shown that ecological context and community history interact to determine how communities respond environmental change.

The effect of fish, i.e., strength of top-down control, was modified by plankton species turnover and environmental context. I found that species and trait turnover buffered the effects of top-down control in lake pelagic food webs, but only in high elevations lakes that are colder and have less dissolved organic carbon (DOC). High elevation lakes without fish contain large bodied zooplankton species that are excluded when fish are introduced. The replacement of the zooplankton community by the smallest bodied species in the regional pool may stabilize the effects of fish on community biomass, a mechanism not present in warmer lakes which already contain the smallest zooplankton. Models and experiments have examined how the cascading impact of top predators may be modulated by temperature. My result agrees with past research that suggests warming magnifies the strength of top-down control (Hoekman 2011, O'Connor et al. 2011, Shurin et al. 2012). However, in addition to the physiological responses to temperature, my dissertation shows that shifting species composition can also modulate the strength of top-down control (Chapter 1).

The warmer lakes were less resilient to the effects of top-down control, which is consistent with a growing body of literature showing that climate can impact community resilience to further abiotic and biotic changes. Resilience is defined as the capacity of a system to reorganize during a change to maintain the same function and structure (Walker et al. 2004). Evidence is accumulating that human-induced disturbances, such as warming, pollution and species extirpation erode ecosystem resilience, increasing the likelihood of regime shifts in response to a change that could previously have been absorbed (Folke et al. 2004). Understanding interactive effects of perturbations therefore requires a robust understanding of the mechanisms that confer community resilience, such as turnover in species composition and traits (Chapter 1).

In addition to species turnover, local adaptation can alter the effects of environmental change on populations and communities. My mesocosm experiment showed a legacy effect of selection by fish that resulted in non-transitive effects of predator addition and removal. Legacy effects are increasingly recognized by natural resource managers charged with conservation planning, as land-use history can continue to influence ecosystem structure and function well after the activities have ceased (Foster et al. 2003). The most well-studied legacy effects are influences on the abiotic environment that are difficult to reverse, such as enhanced recycling of phosphorus from anoxic sediments once a lake is eutrophic (Carpenter 2005). Chapter 2 shows that past selection on traits can also contribute to legacy effects, as selection by fish continued to influence plankton community composition and biomass for many prey generations after fish removal.

The potential for local adaptation can also complicate the ability to predict how populations and communities will respond to climate change. Models that use the current correlation between a species distribution and environmental variables to predict where it may occur in the future may overestimate species responses, because evolution generally reduces the impact of environmental change on phenotype (Ellner et al. 2011). By examining how phenotypes vary in nature along broad environmental gradients we can determine the effect of the environment after there has been time for local adaptation. Therefore, the use of the ‘natural experiment’ in Sierra Nevada lakes allowed me to investigate the impact of climate on fish (bottom-up processes) while allowing for differences among populations. I was able to separate the effect of temperature and DOC on fish growth rates and growth rates increased with temperature and decreased with DOC. This suggests that as warming and vegetation expansion in alpine watersheds increases the DOC concentrations in lakes, the response of fish growth will depend on the relative pace of the two changes. Fish growth should be reduced by greater terrestrial inputs and enhanced by warmer temperatures. The net effect of these two processes is unknown.

The effect of climate on fish in the Sierra raises questions about how to manage ecosystems to meet multiple conservation goals, as fish represent an economically important recreational resource (MEA 2005). The presence of introduced fish can extirpate endangered amphibians from lakes (Knapp and Matthews 2000), and depress the abundance of native birds *via* a reduction in emerging insects (Epanchin et al. 2010). The multiple competing management goals in the study area, particularly Yosemite National Park (YNP), require consideration of the different ecosystem services provided by the presence or absence of fish, e.g., recreation opportunities, water clarity, restoration to ‘natural’ conditions, and the conservation of species diversity. These decisions are made by balancing the values and drivers of human well-being in this social-ecological system (Nicholson et al. 2009). My thesis provides insight into the effect of fish on the biomass and composition of lower trophic levels at different elevations (Chapter 1). These results may help to guide decisions about where to remove fish (an active part of YNP management) to meet the goals of lake ecosystem management (e.g., water clarity or restoring high-elevation specialist zooplankton species). Additionally, the information about correlates of fish growth (Chapter 3) can be used to determine where fish will grow fastest in the future, and continue to provide the recreation ecosystem service to park visitors.

Making robust predictions about the dynamics of ecosystems undergoing environmental change remains a persistent challenge (Austin 2002, Carpenter 2002, Elith and Leathwick 2009). Many mechanisms can influence ecosystem responses to change, such as adaptation, species range shifts and drift. In addition, indirect effects of climate change mediated by species interactions may overwhelm the direct effect of the environment (Blois et al. 2013, Alexander et al. 2015). For example, temperature has pervasive effects on metabolic processes and physiology of organisms (Gillooly et al. 2001). Less is known about the adaptive capacity of species to respond to increases in temperature (Williams et al. 2008), and the least known about how temperature may influence species interaction strengths, especially in no-analogue communities that may emerge in the future as species ranges shift and new combinations of organisms are brought into contact with one another (Williams and Jackson 2007, Alexander et al. 2015, Alexander et al. 2016). Using natural environmental gradients to investigate how communities may respond to future environmental changes provides insights into how contemporary ecosystems vary along natural climatic gradients, and in response to different kinds of perturbations. By using a natural system, in this thesis I was able to investigate how top-down and bottom-up processes vary with climate focusing on the ecological and evolutionary effects of shifting composition and traits on the future resilience of Sierra Nevada lake communities to environmental change.

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