Water Resources Research

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Key Points:

- Lake and landscape features are better predictors of the composition of lake resource pools than elevation
- Allochthony gradients in mountain systems can vary substantially among different lake resource pools
- Aquatic producers are the dominant contribution to lake carbon pools across a large gradient in landscape vegetation cover

Supporting Information:

Supporting Information may be found in the online version of this article.

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Watershed and Lake Attributes Dictate Landscape Patterns of Resource Flows in Mountain Lakes

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Abstract The extent to which terrestrial organic matter supports aquatic consumers remains uncertain because factors regulating resource flows are poorly understood. We sampled 12 lakes throughout the Sierra Nevada (California, USA) spanning large gradients in elevation and size to evaluate how watershed attributes and lake morphometry influence resource flows to lake carbon pools and zooplankton. We found that the size and composition of carbon pools in lakes were often more strongly determined by watershed or lake features rather than by elevational position. Using three different tracers of resource origin (δ^{13}C, Δ^{14}C, C:N ratio), we found terrestrial contributions to most lake resource pools (dissolved organic carbon, particulate organic matter (POM), sediments) and pelagic consumers (zooplankton) were more strongly related to local-scale watershed features such as vegetation cover or watershed area: lake area rather than to elevation. Landscape patterns in multiple tracers indicated consistent contribution of within-lake C sources to bulk resource pools across elevations (POM, sediments, zooplankton). δ^{13}C-enrichment of lake C pools and overlap with δ^{13}C of terrestrial resources can arise due to reduced fractionation of ^{13}C by phytoplankton under CO_2 limitation, therefore we recommend careful consideration of potential environmental drivers when interpreting among-lake patterns in δ^{13}C. Our findings emphasize the importance of local-scale variation in mediating terrestrial contributions to lake food webs.

1. Introduction

The flow of energy within and across ecosystems has important implications for food web structure and ecosystem function (Caraco & Cole, 2004). In aquatic ecosystems, terrestrial inputs (i.e., allochthonous material) fuel substantial microbial biomass (Forsström et al., 2013), support secondary production (Berggren et al., 2010), and suppress aquatic primary production (i.e., autochthonous production; Carpenter et al., 1998; Jackson & Hecky, 1980). Terrestrial material (e.g., allochthony) can subsidize production at higher trophic levels in some lakes, but the extent to which this occurs and the mechanisms supporting it continue to be debated (Brett, Bunn, et al., 2017; Brett, Kainz, et al, 2009; Cole et al., 2010; Francis et al., 2011; Pace et al., 2004). This debate continues in part because of the complexity of making cross-system comparisons, which are vital for understanding drivers of resource flows in food webs (Tanentzap, Kielstra, et al., 2017). Although our understanding of allochthony in river and stream food webs has benefited from studies conducted at landscape scales (Junk et al., 1989; Marcarelli et al., 2011; Vannote et al., 1980), a lack of such studies in lotic systems (Babler et al., 2011; Grey et al., 2001; Tanentzap, Szkokan-Emilson, et al., 2014) has hindered understanding of mechanisms governing the role of terrestrial resources in lake food webs.

Landscape and lake attributes mediate terrestrial contributions to lake food webs by driving both the magnitude of external fluxes and their fate within water bodies (Lapierre et al., 2015; Rasmussen et al., 1989; Soranno, Cheruvelil, et al., 2015; Zwart et al., 2018). Relevant attributes that affect terrestrial carbon loading to lakes include land cover composition of the catchment, drainage area to lake area ratios, landscape position, and lake morphometry (Gergel et al., 1999; Rasmussen et al., 1989; Sadro et al., 2011; Soranno, Webster, et al., 1999). Lake food webs and resource abundance are also affected by the internal dynamics within lakes. Mixing dynamics within a lake control availability of nutrients and light to phytoplankton and exert controls over autochthonous contributions to lake food webs (Diehl, 2002). Extensive littoral zones, the presence of macrophytes, and benthic production also influence lake food web autochthony (Batt et al., 2012; Solomon, Carpenter, Cole, & Pace, 2008; Vander Zanden et al., 2011). Together, these factors complicate efforts to predict resource flows in lake food webs at spatial scales beyond individual water bodies.

Mountain lakes are conducive to investigating resource flows through food webs since overall carbon fluxes are small, community structure is relatively simple, and spatially compressed environmental gradients associated with elevation (e.g., vegetation cover, soil development, and length of ice-free season) should exert strong controls on the magnitude and composition of resources (Piovia-Scott et al., 2016). These unique attributes establish a context within which basic theoretical assumptions about food web resource flows can be evaluated. For instance, the prediction that allochthonous subsidies to secondary consumers increase with increasing terrestrial organic matter (t-OM) loading should be more easily evaluated in oligotrophic lakes where in situ production is comparatively low.

In mountainous terrain, it is typically assumed that the flow of terrestrial carbon through lake food webs scales with the magnitude of terrestrial fluxes and should therefore decrease with elevation as tree and soil cover decline (Piovia-Scott et al., 2016; Vlah et al., 2017). Other studies have detected an allochthony-elevation gradient in mountain lakes for dissolved organic matter (DOM) and particulate organic matter (POM) at elevations above the montane-subalpine transition zone (Rose et al., 2015). However, it remains unclear if elevational gradients in allochthony are a general feature of mountain lake ecosystems, or if other factors exert similar or stronger controls on lake resource pools. A second assumption is that terrestrial support of secondary consumers scales with lake features that affect the balance between pelagic and benthic resources, or between lake and catchment influence (Tanentzap, Kielstra, et al., 2017). Vlah et al. (2017) demonstrated that the size of high elevation lakes relates to the degree of terrestrial subsidies to aquatic consumers: only small, forested lakes, and ponds showed significant terrestrial support of aquatic consumers, while larger lakes both above and below tree-line showed minimal terrestrial contribution to food webs. However, these lakes occurred within a relatively narrow elevational band (1,200–1,500 m), and an explicit comparison of the importance of elevation-driven gradients versus watershed or lake-specific factors for resource flows in mountain lakes is currently lacking.

Because of the difficulty of sampling lake food webs and energy sources at the temporal and spatial scales required for accurately characterizing resource flows, stable isotopes of bulk resource pools and consumers are often used as tracers of temporal and spatial integration in resource acquisition (Peterson & Fry, 1987; Post, 2002). Physical, chemical, and biological processes discriminate against heavy or light isotopes, theoretically resulting in different isotopic ratios among resources that can be used to estimate their contribution to bulk pools (sediment, POM, DOC) or consumers. Differences in δ^{13}C between t-OM and algae or phytoplankton have frequently been used to estimate terrestrial contribution to river and lake food webs (Solomon, Carpenter, Clayton, et al., 2011; Thorp et al., 1998). More recently, natural abundance radiocarbon (Δ^{14}C) has been used as an additional tracer of carbon sources in aquatic food webs, because in many freshwater systems the isotopic separation between terrestrial resources and aquatic primary producers can be substantially greater for Δ^{14}C than for δ^{13}C (>100‰ separation; Ishikawa, Finlay, et al., 2020; Ishikawa, Hyodo, & Tayasu, 2013).

Despite their potential utility for food web studies, especially in remote or inaccessible ecosystems where labor-intensive sampling is infeasible, isotopic tracers are subject to a number of methodological assumptions that constrain ecological interpretations. Two of the most significant of these assumptions are: (1) that terrestrial and aquatic energy resources exhibit distinguishable isotopic signatures and (2) that these signatures are well characterized within the study system. Resource signatures are often assumed to be invariant among species, locations, and time. For example, phytoplankton and periphyton are assumed to exhibit constant isotopic signatures (Peterson & Fry, 1987; Post, 2002), while in reality each can vary at short time scales (weeks to months; Finlay, 2004; Syväranta et al., 2006) and small spatial scales (e.g., stream riffles vs. pools, Finlay et al., 1999; lake littoral vs. pelagic zones; Syväranta et al., 2006). Adding to potential uncertainty in the isotopic signature of resource pools is that direct measurement of aquatic primary producers is difficult and rarely done. Instead, fractionation factors are applied to isotopic measurements of CO_2 (for δ^{13}C) to predict the signature of algae or phytoplankton. Nevertheless, isotopic tracers remain one of the only feasible ways to establish food web linkages in aquatic systems, especially at landscape or regional scales.

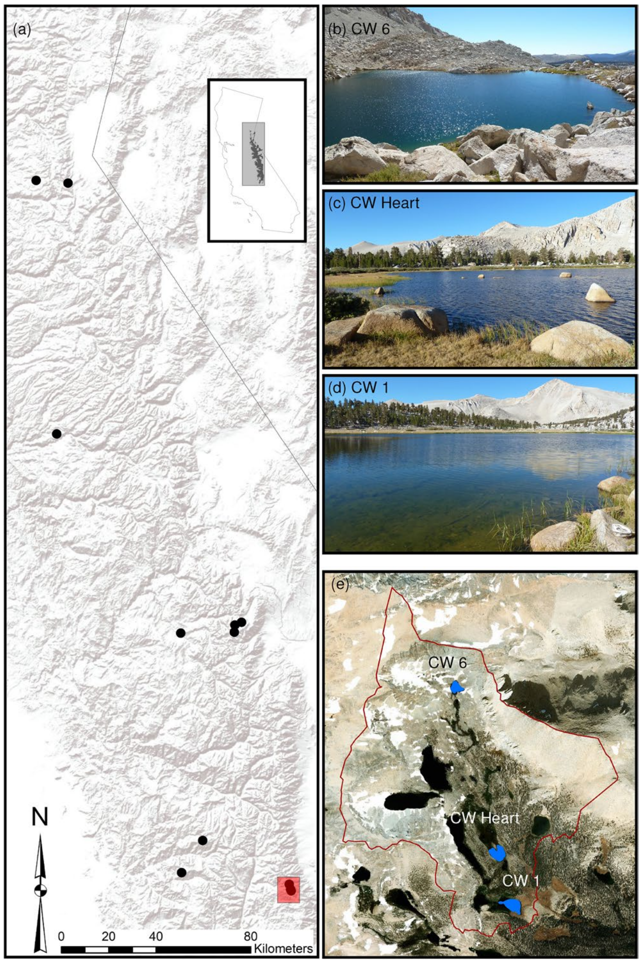

Figure 1. (a) Study sites (black dots) span the Sierra Nevada, California. (b–d) The three Cottonwood lakes (red inset in panel a), (e) located within the same drainage basin.

Understanding controls on energy flows in lakes at landscape scales is essential for developing a generalizable framework of aquatic food web structure and predicting the consequences of ongoing anthropogenic change. The high natural variation found in mountain landscapes provides a natural laboratory in which to test our theoretical understanding of resource flows in lake food webs. This study asks two questions focused on clarifying our understanding of resource flows in lakes: (1) How does the composition of basal resource pools (e.g., vegetation, DOM, POM, and sediments) vary in relation to the changes in landscape and lake characteristics found in mountain systems? and (2) Does a landscape gradient of increasing terrestrial inputs result in increased allochthony of lake C pools and pelagic consumers (zooplankton)? To answer these questions, we sampled 12 lakes in the Sierra Nevada (California, USA) that span large gradients in watershed attributes (elevation, land cover) and lake characteristics (lake area, depth, lake area: watershed area), and evaluated the composition of lake C pools using three tracers: molar C:N ratio, δ^{13}C, and Δ^{14}C.

2. Study System and Methods

2.1. Site Descriptions

Study lakes were distributed along the latitudinal extent of the Sierra Nevada (Figure 1), a distance of approximately 300 km, and spanned large gradients in elevation (1,500–3,600 m.a.s.l). Lakes also varied in maximum depth (1–31.3 m), surface area (0.5–14.6 ha), and watershed area (0.08–26.7 km^2). Watershed characteristics around each lake generally reflect elevation-driven differences associated with montane, subalpine, and alpine zones, with vegetation cover ranging from <10% in alpine catchments to >90% in montane catchments (Table 1; Figure 2). Lakes were sampled once between August and mid-September of 2014, which was a drought year with historically low winter snowpack (Margulis et al., 2016).

Table 1
Study Site Locations and Attributes

Lake	Lat/long	Elevation (m)	Max depth (m)	Surface area (m^2)	Watershed area (km^2)	Vegetation cover (%)	Fish presence
Swamp	37.950,−119.829	1,554	19.2	60,403	1.65	97.12	Fishless
Oriole	36.460,−118.736	1,722	6.9	5,001	1.74	99.22	Fish
Lily	38.876,−120.081	1,996	9.2	31,843	26.71	82.00	Fish
Doris	37.337,−119.014	2,088	8.5	25,658	0.54	80.27	Fish
Beauty	38.856,−120.236	2,148	2	21,496	0.08	86.70	Fish
Emerald	36.597,−118.675	2,800	10	27,206	1.10	32.17	Fish
Eastern brook	37.431,−118.742	3,154	7.4	44,039	2.14	53.73	Fishless
Cottonwood one	36.490,−118.210	3,362	1.2	33,761	7.38	34.17	Fish
Cottonwood heart	36.495,−118.214	3,389	1	20,402	0.35	93.88	Fishless
Ruby	37.415,−118.770	3,397	31.3	146,187	4.49	9.52	Fish
Treasure	37.388,−118.765	3,407	7.3	24,848	0.50	22.14	Fishless
Cottonwood six	36.513,−118.226	3,559	12.5	19,856	1.27	9.36	Fishless

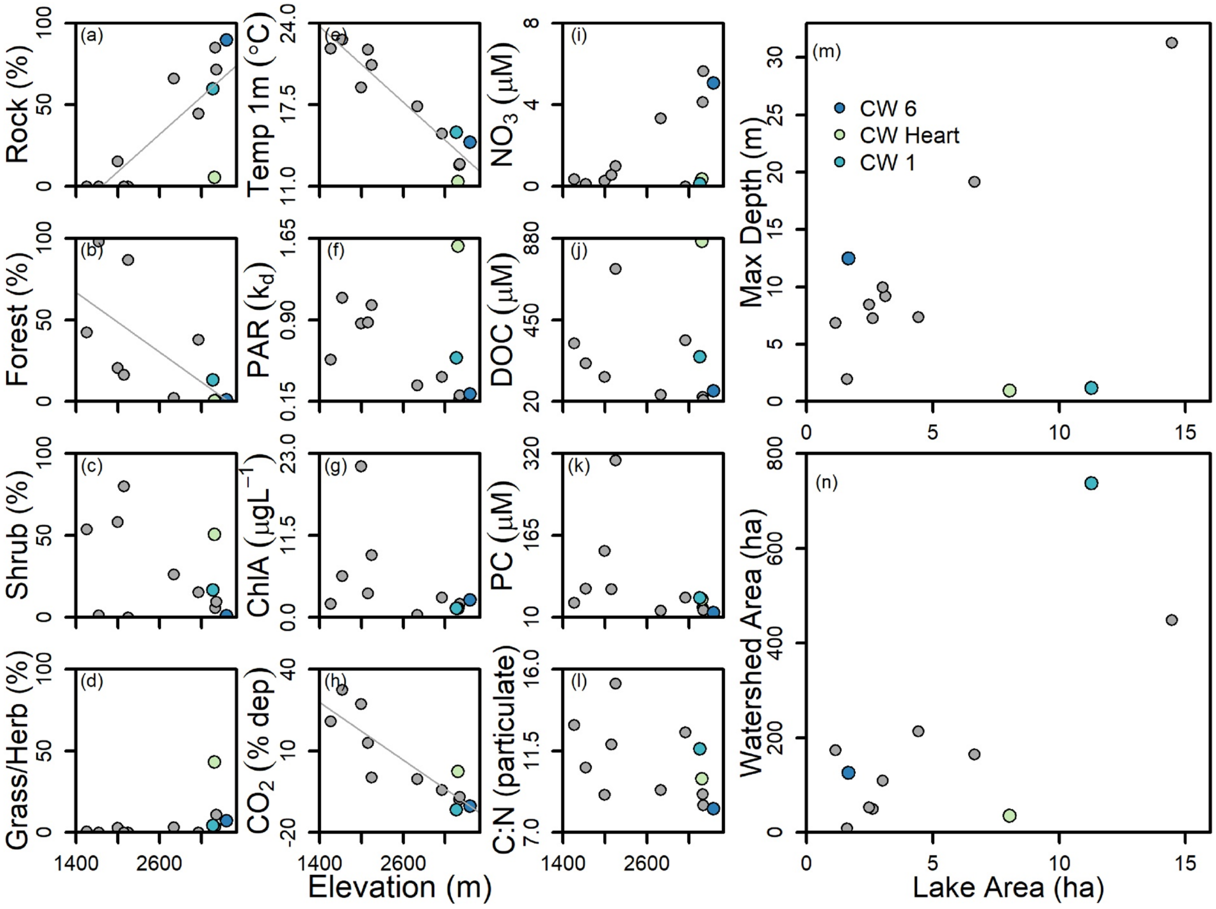

Figure 2. (a–d; %) Elevational patterns in watershed land cover, (e) epilimnion temperature, (f) diffuse light attenuation coefficient, and (g–l) epilimnion water chemistry. Variation in lake area (*x*-axes, hectares), maximum lake depth (panel m, meters), and watershed area (panel n, hectares). The Cottonwood lakes (CW 6, CW Heart, CW 1) are designated by colored dots in each panel. In panel h, CO_2 concentration is reported as percent departure from atmospheric saturation (% dep). Solid gray lines show significant linear relationships between elevation and the *y*-axis variable ($p < 0.05$).

2.2. Sample Collection and Processing

At the deepest location in each lake we collected profiles of water temperature, dissolved oxygen concentration (DO), and photosynthetically active radiation (PAR) at 0.5–1.0 m intervals to a maximum depth of 30 m using a hand held optical sonde (ProODO, YSI; ±0.1°C temperature and ±0.1% DO) and a PAR sensor (LiCor LI-250A with a LI-192 quantum sensor). Water samples for chemical and isotopic analysis were collected from within the epilimnion of each lake (0.75–3.0 m) using a Van Dorn sampler and stored in low-density polyethylene cubitainers for <4 h prior to processing in the field. Hypolimnetic water samples were only collected from Emerald and Oriole lakes. In all cases, water samples were filtered on site for dissolved organic carbon (DOC), colored dissolved organic matter (CDOM) absorbance (abs440), nitrate (NO_3), chlorophyll a (Chl-a), and particulate carbon, nitrogen, and phosphorus (PC, PN, and PP). Because substantial inorganic PC inputs to lakes are unlikely in the Sierra Nevada, we use the terms PC and POM interchangeably.

Samples for DOC and abs440 were filtered through glass fiber filters (Whatman GF/F, 0.7 μm nominal pore size) into amber borosilicate vials with Teflon-coated septa; filters and vials were pre-combusted at 450°C for 2 and 12 h, respectively. DOC samples were immediately acidified with HCl to a pH of <2 and measured on a total organic carbon analyzer (Shimadzu TOC-V) using high precision methods adapted for low concentrations (Carlson et al., 2010). CDOM absorbance (abs440) was measured on a spectrophotometer (Shimadzu) at a wavelength of 440 nm using a 5 cm cuvette. NO_3 samples were filtered through 1.0 μm polycarbonate filters into 60 mL low density polyethylene bottles and concentrations determined by ion chromatography (Sickman et al., 2003). Chl-a samples were filtered onto 0.45 μm nitrocellulose filters and analyzed on a Turner 10-AU Fluorometer after 24 h extraction in 90% acetone (Sadro et al., 2012).

All particulate samples were captured on pre-combusted glass fiber filters. PC and PN were measured through combustion on an elemental analyzer (Costech) and PP was measured using the Valderrama (1981) digestion method measured on a Latchet autoanalyzer using the phosphomolybdate method (Strickland & Parsons, 1972).

We measured surface water CO_2 concentrations, an indicator of terrestrial C loading, using a modification of the headspace equilibrium method (Kling et al., 1991). Headspace gas mixtures and replicate air samples collected at each lake were injected into pre-evacuated 12 mL glass exetainers with double-butyl septa and analyzed by gas chromatography (Shimadzu GC-8A) within 3 months of collection. pCO_2 was computed on the basis of Henry's Law and the fugacity-pressure relationship for CO_2 (Kling et al., 1991; Raymond, Caraco, & Cole, 1997; Weiss, 1974).

We collected terrestrial and aquatic resources that could contribute to lake food webs for isotopic analysis at each site. Terrestrial source pools included leaf material from representative plant species in relative proportion to their abundance around each lake based on visual assessment, and soil samples collected and aggregated from three locations around each lake. Alpine plant communities were dominated by *Carex* sp., *Salix* sp., *Ribes* sp., and *Phyllodoce* sp., subalpine by *Pinus* sp., *Juniperus occidentalis*, *Abies magnifica*, and *Salix* sp., and montane by *Carex* sp., *Pinus* sp., *Alnus* sp., *Abies* sp., *Arctostaphylos* sp., and *Salix* sp. Aquatic source pools included a variety of submerged and emergent aquatic plant and algal taxa. We collected living leaf or blade tissue from three to five representatives of each type of plant or algae growing near or within each lake. Periphyton was collected from hard substrates by scrubbing three to five locations along shore with a stiff bristled brush followed by collection using a 140 mL syringe and filtration onto quartz fiber filters (Whatman QM-A).

Samples for isotopic analysis were collected for the following lake carbon pools: dissolved inorganic carbon (DIC), DOC, POM, lake sediments, and zooplankton. We collected replicate water samples for isotopic analysis of DIC in 12-mL glass exetainers with double-butyl septa that had been pre-washed with soap and water, ashed at 500°C, coated with 80 μL of saturated zinc chloride as a preservative, and flushed with helium to remove atmospheric O_2. Water for DOC isotope analysis was filtered through glass fiber filters as described above into duplicate 1 L acid-washed polycarbonate bottles. We collected replicate POM samples by filtering 1–2 L of water that was pre-sieved through a 64 μm Nitex mesh to remove zooplankton through quartz fiber filters (Whatman QM-A). Duplicate samples of lake sediments were collected by modifying a Van Dorn sampler and allowing it to rest on the lake bottom prior to triggering. Replicate zooplankton samples were collected by taking vertical tows over the deepest point of each lake using a 30 cm diameter plankton net (64 μm). Live zooplankton was placed in 4 L low-density polyethylene cubitainers filled with Whatman GF/F filtered lake water and held for ~12 h in order to clear their guts prior to being collected. With the exception of DIC, all isotope samples were frozen in the field using dry ice and stored at −80°C until processing. Zooplankton were sorted into three major taxonomic groups (rotifers, cladocerans, and copepods). Individual zooplankton was pooled within each taxon to obtain a sufficiently large sample for isotope analysis, with composites ranging from 50 to 500 individuals depending on the mass of individual zooplankton. In addition, an aggregate sample reflecting the unsorted zooplankton pool of each lake was collected.

We conducted a dilution growth experiment in Emerald Lake to develop a pure phytoplankton sample for comparison with POM isotopic values. On July 9, 2014 water was collected from 6 m depth, corresponding to the chlorophyll-a maximum, and filtered through Whatman GF/F into triplicate 2 L polycarbonate bottles. Each bottle was filled with 1.5 L of filtered lake water and 0.5 L of whole water sieved through a 64 μm Nitex mesh to remove zooplankton. Bottles were incubated in the lake at 4 m depth for 10 days after which 500 mL triplicate 500 mL aliquots from each bottle were filtered onto quartz fiber filters (Whatman QM-A).

2.3. Stable Isotope Analyses

All food web materials were lyophilized prior to preparing the samples for isotopic analysis. Dried sediment, aquatic vegetation, soil, and terrestrial vegetation were ground to a fine powder with a mortar and pestle to improve homogeneity of subsamples.

Stable carbon isotope analyses were performed by the Facility for Isotope Ratio Mass Spectrometry (FIRMS) at the University of California, Riverside, using a Thermo Delta V Advantage isotope ratio mass spectrometer. A Costech 4010 elemental analyzer, operated in continuous flow, was used for δ^{13}C measurements and %C and %N determination. The international isotope standards USGS 40 and USGS 41 were included throughout each analytical run; isotope data are reported in delta notation relative to the Vienna PeeDee-Belemnite (PDB) standard. Carbon and nitrogen content are referenced against NIST peach leaves (SRM 1547).

To estimate the theoretical δ^{13}C signature of phytoplankton, we predicted ε_p, the photosynthetic discrimination factor by aquatic producers, from lake CO_2 concentration, as in Smyntek et al. (2012). Predicted ε_p was subtracted from δ^{13}C-CO_2 (corrected from measured δ^{13}C-DIC using fractionation factors in Zhang et al. [1995]) to estimate the theoretical δ^{13}C of phytoplankton in each lake.

2.4. Radiocarbon Analyses

Radiocarbon (Δ^{14}C) analysis of DOC, POC, and zooplankton was performed at the National Ocean Sciences Accelerator Mass Spectrometry (NOSAMS) laboratory at the Woods Hole Oceanographic Institute. DOC samples were pretreated for analysis of carbon isotopic composition (Δ^{14}C and δ^{13}C) using high-temperature oxidation and UV oxidation methods at Yale University (Raymond, McClelland, et al., 2007). All radiocarbon results are reported as Δ^{14}C, adjusted for sample δ^{13}C to account for mass-dependent fractionation (Δ in Stuiver and Polach [1977]). Δ^{14}C is in per mil units (‰), where $\Delta^{14}C = \delta^{14}C - 2 \times (\delta^{13}C + 25) \times (1 + \delta^{14}C/1{,}000)$, $\delta^{14}C = 1{,}000 \times (\text{Fmod}-1)$, and Fmod = fraction modern (Stuiver & Polach, 1977). Δ^{14}C greater than 0‰ reflects the presence of radiocarbon released by nuclear weapons testing in the 1950s and 1960s, though it does not preclude the presence of aged carbon fractions in a sample. Negative Δ^{14}C values imply the presence of pre-modern C (by definition before 1890) in a sample: if highly aged (i.e., ^{14}C-dead; $\Delta^{14}C = -1{,}000$‰) carbonate minerals or fossil carbon are present, sample Δ^{14}C may become depleted with even small contributions of these sources. Terrestrial resources such as leaf litter reflect the Δ^{14}C signature of atmospheric CO_2 and thus should be enriched above 0‰; Δ^{14}C of atmospheric CO_2 varies seasonally, regionally, and locally, but average values for the Northern Hemisphere in summer were +30‰ for Δ^{14}C during the study period (Hua et al., 2013). Δ^{14}C of aquatic primary producers such as phytoplankton reflects the signature of DIC and is often substantially depleted below 0‰ if carbonate minerals or aged OM in sediments contribute to the DIC pool.

2.5. Landscape and Lake Morphometric Analysis

Maximum lake depths were determined by taking multiple soundings with a hand-held sonar (Hawkeye). We determined watershed attributes and lake areas using ArcMap (v. 10.6.1, Esri). Lake area and perimeter were quantified using United States Geological Survey (USGS) digital orthophoto quadrangles (3.75 min USGS EROS Archive DOQs). We used 10 m digital elevation models (USGS National Elevation Data Set) to delineate watershed boundaries and determine watershed elevation. Land cover analysis for each lake's watershed (e.g., catchment) was done using the National Land Cover Database (USGS NLCD 2016).

2.6. Statistical Analyses

To assess relationships between landscape or lake variables and the magnitude and composition of lake resource pools, we fit simple linear regression models using maximum likelihood and compared model fits using Akaike's Information Criterion for small sample sizes (AIC_c; Burnham & Anderson, 2002). A difference in AIC_c (ΔAIC_c) greater than four between two models indicates moderate support for the model with lower $AIC_{c,}$ whereas $\Delta AIC_c > 10$ indicates strong support. We compared all regression models to an intercept-only null model—we considered any models within two AIC_c units of the null model as insignificant. Response variables included metrics related to the magnitude of lake C pools (CO_2 saturation, DOC concentration, PC concentration) as well as metrics related to C pool composition and origin (DOC, littoral and profundal sediments, POM, zooplankton). For DOC these metrics included abs440, $\delta^{13}C$, and $\Delta^{14}C$, whereas for the other C pools they included molar C:N ratio, $\delta^{13}C$, and $\Delta^{14}C$. Sediments did not have $\Delta^{14}C$ measurements. We did not perform taxon-specific linear regressions for zooplankton because in many lakes certain taxa were insufficiently abundant for successful isotopic analyses. We tested relationships with the following predictor variables: elevation, maximum lake depth, lake surface area, percent vegetation cover within the watershed, and the ratio of lake area: watershed area. Model fits were done using the "AICcmodavg" package in *R* (Mazerolle, 2020; R Core Team 2020), and are reported in Table S1.

3. Results

3.1. Landscape Patterns in Watershed Attributes and Lake Chemistry

The lakes in this study spanned large gradients in physical, chemical, and biological properties (Data Set S1; Sadro, 2021). Whereas some lake and watershed attributes varied linearly with elevation, in some cases there were outliers to this pattern, or no pattern at all (Figures 2a–2l). Linear relationships with elevation were strongest for percent rock cover within watersheds ($R^2 = 0.58$, df = 10), which increased, and total vegetation cover ($R^2 = 0.57$), water temperature ($R^2 = 0.87$), and CO_2 (percent departure from saturation; $R^2 = 0.75$), which decreased. Chl-a, DOC, NO_3, and PC concentrations varied widely but did not exhibit clear linear relationships with elevation, indicating that lake or watershed features exerted considerable influence. For example, three lakes within the same high-elevation drainage (Cottonwood lakes; >3,300 m a.s.l.) spanned the entire range of variation among all sites for light attenuation (k_d), DOC, and NO_3 (Figure 2).These three lakes varied in depth (1–12 m), lake area (1.6–11.2 ha), watershed area (35–737 ha), and percent vegetation cover (9%–93%; Figure 2).

Higher CO_2 concentration (above atmospheric saturation) in lower elevation lakes suggests greater terrestrial carbon loading and respiration rates. Watershed vegetation cover was also positively associated with CO_2 saturation ($\Delta AIC_c > 6$ compared to intercept-only model; Table S1). Elevation was not a significant predictor of DOC or PC concentrations ($\Delta AIC_c < 2$ compared to intercept-only model). Of the lake or watershed attributes considered, only the percent total vegetation cover (forest, shrub, herb/grass) and the ratio of lake surface area to watershed area were significantly related to DOC concentration (positive relationships; $R^2 = 0.41$, df = 10, $\Delta AIC_c > 4$; $R^2 = 0.36$, $\Delta AIC_c > 2$). Vegetation cover was not significantly associated with PC concentration.

3.2. Changes in the Composition of Terrestrial and Aquatic Resources Across Landscape Gradients

Isotopic composition and C:N ratios of terrestrial and aquatic resources (vegetation, soil, periphyton), bulk aquatic carbon pools (sediments, DOC, POM), and zooplankton differed, and also varied among lakes (Data Set S2; Sadro, 2021). These differences indicate that the degree of terrestrial contribution also varied among carbon pools and across landscape gradients. The isotopic composition of DOC and littoral sediments showed stronger linkages to vegetation cover than did the composition of profundal sediments, POM, or zooplankton (Table S1).

3.2.1. Terrestrial and Aquatic Vegetation and Soils

$\delta^{13}C$ of terrestrial resources varied among lake catchments and resource types (Figure 3 column 1). Mean $\delta^{13}C$ of terrestrial vegetation, including grasses, shrubs, and tree species, was −28.06‰ (±1.83; 1 SD) and became slightly enriched with elevation (Figure 3 row 1 column 1; $R^2 = 0.14$, $p < 0.01$). $\delta^{13}C$ of soil was similar to $\delta^{13}C$ of nearby terrestrial vegetation but was less variable among watersheds than terrestrial vegetation and unrelated to elevation (−27.98‰ ± 1.12‰; Figure 3 column 1). Aquatic vegetation, including both emergent and submerged macrophytes, was more enriched and more variable in $\delta^{13}C$ compared with terrestrial vegetation (−23.83‰ ± 5.70‰), and lacked an elevational trend. $\delta^{13}C$ of periphyton was similar to aquatic vegetation (−21.30‰ ± 7.02‰) and lacked an elevational trend.

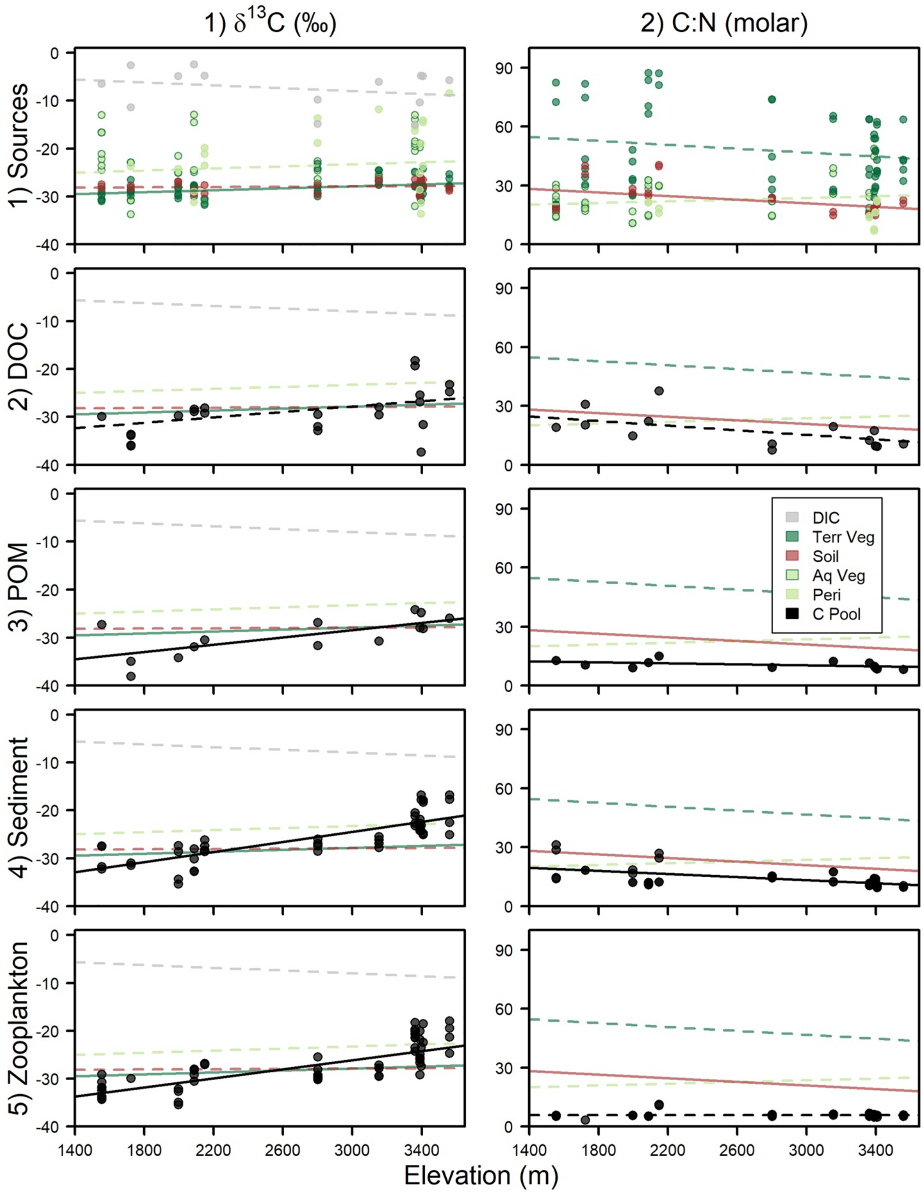

Figure 3. Elevational patterns in $\delta^{13}C$ (‰ vs. PDB; column 1), and molar C:N ratio (column 2) of terrestrial or aquatic resource pools (row 1; "Sources") and aquatic bulk carbon pools or pelagic consumers (rows 2–5). Row 1 shows data (filled circles) and regression relationships (colored lines) between elevation and $\delta^{13}C$ or C:N ratio of each source pool (terrestrial vegetation, aquatic vegetation (Aq Veg) and periphyton (Peri), soil, DIC ($\delta^{13}C$ only)). Regression lines between elevation and the composition of source pools are also plotted in panels in rows 2–5 for reference. In rows 2–5, black filled circles correspond to the carbon pool named on the *y*-axis (DOC, POM, Sediment, Zooplankton). Black lines show regression relationships between elevation and the $\delta^{13}C$ or C:N ratio of the lake carbon pool. Significant regression relationships are shown as solid lines ($p < 0.05$), non-significant as dashed lines.

The molar C:N ratio of terrestrial vegetation was higher and more variable (mean = 47.6 ± 19.4) than C:N of soils (22.6 ± 8.1), aquatic vegetation (21.6 ± 8.0), or periphyton (16.32 ± 5.17), and decreased slightly with elevation (Figure 3 row 1 column 3). Soil C:N also declined with elevation, though neither trend was significant.

3.2.2. Bulk Aquatic Carbon Pools

Bulk aquatic C pools (sediments, DOC, POM) showed $\delta^{13}C$-enrichment at higher elevations that generally exceeded the degree of enrichment in $\delta^{13}C$ of terrestrial vegetation or riparian soils with elevation, though the strength of the pattern was greater for POM and sediments than for DOC (Figure 3 column 1). C:N ratios of aquatic bulk C pools were lower than C:N of terrestrial vegetation (Figure 3 column 2) but often overlapped with C:N of soil and littoral primary producers (aquatic macrophytes and periphyton).

δ^{13}C of both littoral and profundal sediments became enriched with elevation ($\Delta AIC_c > 6$). Though δ^{13}C did not differ among habitats (mean = −25.7‰ ± 4.7‰), sediments from littoral zones had slightly higher C:N ratios than profundal sediments (16.1 ± 6.1 vs. 12.1 ± 1.7). C:N ratios of profundal sediments were unrelated to elevation or watershed vegetation cover ($\Delta AIC_c < 2$; Table S1), whereas littoral sediment C:N ratios declined with elevation ($R^2 = 0.47$, $p < 0.01$; $\Delta AIC_c > 4$) and were weakly related to vegetation cover ($R^2 = 0.25$, $p < 0.1$).

δ^{13}C-DOC was highly variable and only weakly enriched at higher elevations (mean = −28.5‰ ± 4.7‰; $\Delta AIC_c < 2$). Δ^{14}C-DOM was also highly variable (−110‰ ± 183‰; Figure 5b), ranging from extremely depleted to enriched above 0‰, indicative of modern terrestrial inputs. Δ^{14}C-DOM was more enriched in watersheds with high terrestrial vegetation cover ($R^2 = 0.44$, $p < 0.01$, $\Delta AIC_c > 6$, Table S1), and was more depleted in high elevation watersheds, though the relationship was not significant ($\Delta AIC_c < 2$; Figure 5b). Δ^{14}C-DOM was also more enriched in shallow lakes ($R^2 = 0.36$, $p < 0.01$, $\Delta AIC_c > 4$). Abs440 was un-related to elevation but positively associated with percent vegetation cover ($\Delta AIC_c > 2$).

Unlike DOC, POM- δ^{13}C became strongly enriched with elevation ($R^2 = 0.44$, $p < 0.001$, df = 10, $\Delta AIC_c > 6$). There was greater isotopic separation between POM and terrestrial vegetation and soils in low elevation lakes, whereas δ^{13}C signatures overlapped substantially in mid to high elevation lakes (Figure 3 column 1, row 3). Δ^{14}C-POM was more enriched in watersheds with higher percent vegetation cover ($R^2 = 0.38$, $\Delta AIC_c > 4$), and in low elevation lakes ($R^2 = 0.33$; $\Delta AIC_c > 2$; Figure 5c; Table S1). The C:N ratio of POM (mean = 10.7 ± 2.0) was substantially lower than that of terrestrial vegetation or soils and was not significantly associated with elevation or vegetation cover ($\Delta AIC_c < 2$).

The δ^{13}C signature of POM was more strongly associated with lake CO_2 concentration than with elevation (Figure 4c), whereas δ^{13}C of terrestrial resources showed little variation associated with elevation (Figure 3 column 1, Figure 4c). Lake CO_2 concentration was below atmospheric saturation in many of the high elevation study lakes (Figure 2h), potentially causing decreased δ^{13}C-discrimination (ε_p) by aquatic producers under conditions of CO_2-limitation (Figure 4b). This phenomenon has been documented in other freshwater systems (Smyntek et al., 2012) and may explain the observed δ^{13}C-enrichment of aquatic resources pools linked to pelagic production in higher elevation lakes. Applying a regression model based on CO_2 concentration predicted a decline in ε_p, and an enrichment in the theoretical δ^{13}C of phytoplankton, in lakes with lower pCO_2 (Figures 4b and 4c). Importantly, since there was a strong negative CO_2-elevation relationship (Figure 4a), theoretical δ^{13}C of phytoplankton increased with elevation, aligning with the elevational trends in aquatic carbon pools such as POM and zooplankton (Figure 3).

In Emerald Lake, phytoplankton were isolated from bulk POM for isotopic analysis, and Δ^{14}C -phytoplankton was similar to Δ^{14}C-POM (−226‰ vs. −210‰, respectively), suggesting phytoplankton make up the majority of bulk POM in mid to high elevation lakes in the Sierra Nevada. δ^{13}C-phytoplankton also closely matched δ^{13}C-POM in Emerald Lake (−31.5‰ vs. −31.6‰, respectively).

3.2.3. Zooplankton

Zooplankton δ^{13}C became enriched with elevation ($R^2 = 0.62$, $p < 0.001$, df = 51, $\Delta AIC_c > 10$; Figures 3 and 5g), concurrent with enrichment in δ^{13}C-POM (Figures 3 and 5f). However, zooplankton δ^{13}C was highly variable, and in some lakes, zooplankton were more depleted than any other sampled terrestrial or aquatic resources (Figure 3 column 1, Figure 5a) , a common finding in food web studies of lakes (Brett, Holtgrieve, & Schindler, 2018). Cladocerans were slightly enriched in δ^{13}C (−25.9‰ ± 4.5‰) compared to copepods (−27‰ ± 4.4‰). Lack of separation in δ^{13}C signature between aquatic and terrestrial resources in most study lakes, as well as δ^{13}C-zooplankton that fell outside of potential resource signatures, precluded its use as an indicator of lake-specific food web structure using mixing models. Zooplankton were occasionally more Δ^{14}C-depleted than POM, though zooplankton also frequently fell within the range of terrestrial vegetation across elevations (mean = −81.0‰ ± 167.6‰; Figure 5d). Δ^{14}C-zooplankton was not related to elevation ($\Delta AIC_c < 2$) or vegetation cover ($\Delta AIC_c < 2$), but was more depleted in deeper lakes ($\Delta AIC_c > 2$; Table S1). Δ^{14}C of cladocerans (−116.1‰ ± 214.7‰) was slightly more depleted than Δ^{14}C of copepods

(−101.2‰ ± 181.1‰), and more depleted than the overall mean for zooplankton (including composite samples from lakes lacking taxon-specific samples). Zooplankton C:N ratios were lower than all available resource pools (5.8 ± 1.2) and did not vary with elevation or watershed vegetation cover, or between major taxa (cladocerans and copepods).

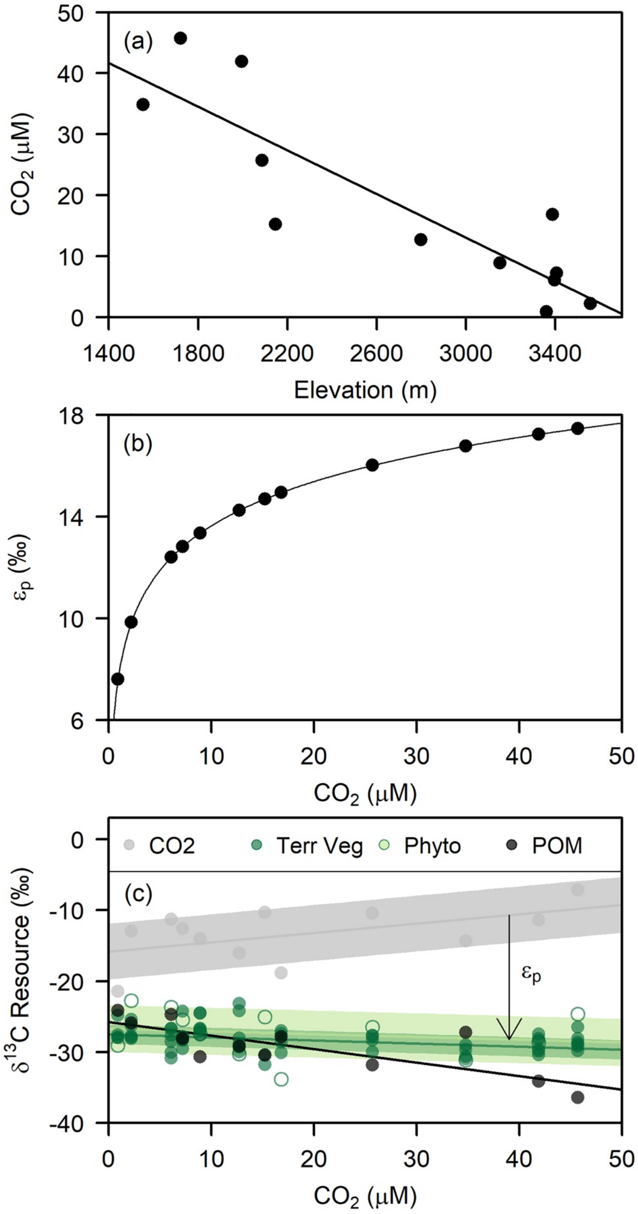

Figure 4. (a) Negative relationship between elevation and epilimnetic carbon dioxide (CO$_2$) concentration. (b) Predicted isotopic discrimination against δ^{13}C (ε_p) by aquatic primary producers during photosynthesis. ε_p increases as the available pool of dissolved CO$_2$ increases (Smyntek et al., 2012). (c) Predicted ε_p was subtracted from δ^{13}C-CO$_2$ (gray circles; corrected from measured δ^{13}C-DIC using fractionation factors in Zhang et al. [1995]) to estimate the theoretical δ^{13}C of phytoplankton in each lake (light green circles). Dark green circles represent δ^{13}C of terrestrial vegetation at each lake. Filled polygons represent one standard deviation (calculated from sample data or predictions) above and below the model prediction (line).

4. Discussion

4.1. Lake and Watershed Features Drive Allochthony Gradients in Mountain Landscapes

Elevation-associated decreases in vegetation cover are a classic feature of mountain landscapes that are presumed to generate corresponding spatial patterns in resource flows to mountain lake food webs (Piovia-Scott et al., 2016; Rose et al., 2015). Our study confirmed general elevational trends in vegetation cover and declines in terrestrial C loading to lakes (e.g., CO$_2$; Figures 2 and 4) in the Sierra Nevada, consistent with previous regional lake surveys (Sadro et al., 2011; 76 lakes in 14 lake chains). However, the concentration and composition of other bulk resource pools, such as DOC, POM, and sediments, often showed weak or no relationships with elevation, indicating that local variation in terrestrial loading or within-lake processes can dominate over elevational landscape gradients to create a mosaic-pattern of resource flows in mountain ecosystems. For variables corresponding to DOM concentration or composition (DOC concentration, abs440, Δ^{14}C), lake area: watershed area or vegetation cover were significantly better predictors than elevation (ΔAIC$_c$ > 6 compared to elevation model), and elevation either worsened or failed to improve model fits relative to an intercept-only null model (Table S1). Zooplankton Δ^{14}C was significantly related to lake depth (ΔAIC$_c$ > 3 compared to null model), but elevation was the worst predictor out of the set we tested (Table S1). Of the major carbon pools we examined, only POM composition (Δ^{14}C) showed a significant relationship to elevation, though vegetation cover was a slightly better predictor, and PC concentration was unrelated to elevation (Table S1). We also found that the strength of allochthony gradients in mountain systems can vary substantially among different resource pools. Overall we observed gradients in terrestrial contribution to DOC in Sierra Nevada lakes that corresponded to watershed vegetation cover and the potential for terrestrial C-loading, but much weaker linkages between watershed vegetation and lake sediments, POM, or zooplankton (Table S1; Figure 6).

4.2. DOM Reflects Landscape Patterns in Vegetation Cover

Watershed-level variation in vegetation cover influenced both the magnitude and composition of DOM in lakes, yielding a detectable allochthony gradient that was only partially related to elevation. DOC concentration, abs440, and Δ^{14}C-DOM were all more strongly associated with watershed vegetation cover than with elevation (ΔAIC$_c$ > 6 compared to elevation model; Table S1; Figures 6a–6c). Δ^{14}C-DOM varied extensively among lakes but was frequently enriched above 0‰ even in high elevation lakes, indicating contributions by modern primary production (e.g., terrestrial or aquatic vegetation; Figure 5b). While a more exhaustive sampling effort may have revealed a linear or threshold pattern of terrestrial C loading to lakes with elevation (as in Sadro et al., 2011), our limited sampling (12 lakes) instead highlighted the importance of local watershed attributes for controlling the concentration and composition of DOM. Our study spanned a larger elevation gradient (~2,000 m) than

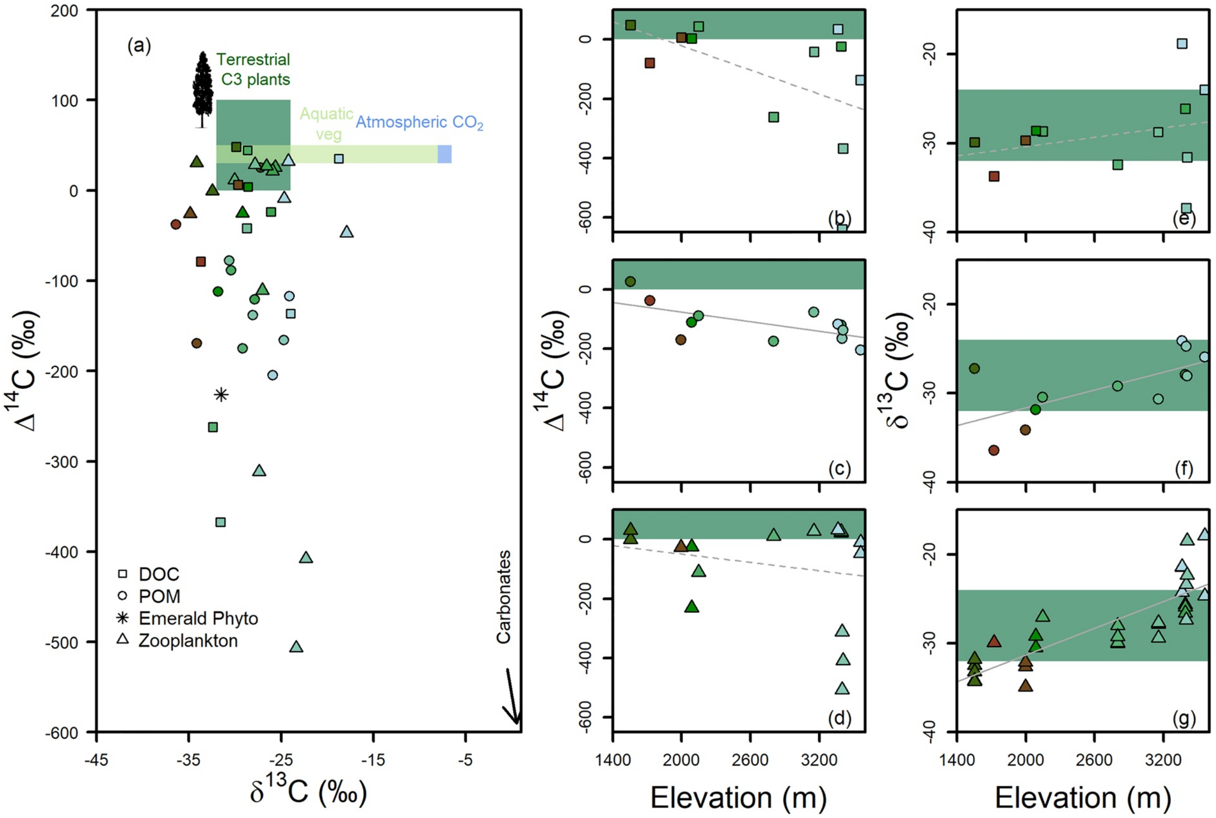

Figure 5. (a) Isotopic signature ($\Delta^{14}C$, $\delta^{13}C$) of DOC (squares), POM (circles), and zooplankton (triangles) from all lakes. Symbol color corresponds to lake CO_2 concentration (µm), from low (1 µm; blue) to high (45 µm; brown). The star symbol corresponds to cultured Emerald Lake phytoplankton. Filled polygons show the range in isotopic signatures of potential resources contributing to lake carbon pools, including terrestrial vegetation, aquatic vegetation (macrophytes), and atmospheric CO_2. The range in $\delta^{13}C$ of terrestrial and aquatic vegetation reflects observed values from this study, whereas $\Delta^{14}C$ ranges are "expected" values for recent terrestrial primary production (see Methods). (b–d) Changes in $\Delta^{14}C$ (‰) of lake carbon pools (DOC, POM, zooplankton) with elevation. (e–f) Changes in $\delta^{13}C$ of lake carbon pools across elevation.

comparable lake surveys in other mountain ranges (Rose et al., 2015 ~900 m; Vlah et al., 2017 ~170 m), yet our findings were similar in that DOM concentration and composition were determined by local variation in terrestrial vegetation cover rather than by explicit elevational position.

The three Cottonwood lakes, all situated above 3,300 m elevation, illustrate the potential variation in lake-watershed linkages that can exist irrespective of elevational gradients (Figures 1, Figure 2 colored dots): vegetation cover ranging from 9% to 93% among watersheds yielded a 10-fold variation in lake DOC concentration. Vegetation cover and the presence of low gradient wetland areas within mountain watersheds are often highly predictive of DOC concentrations (Winn et al., 2009), yet the scope of among-watershed land-cover variation at high elevations (see Piovia-Scott et al., 2016; Figure 1b) is perhaps an under-appreciated feature of mountain systems with important consequences for lake chemistry and food webs. Comparative studies of land cover variation within the world's mountain ranges will clarify the spatial scales at which elevation-driven allochthony gradients are a reasonable null hypothesis for understanding resource flows in mountain lakes (Moser et al., 2019).

4.3. POM, Profundal Sediments, and Zooplankton Reflect Primarily Autochthonous Sources Across Elevation

In contrast with DOM, terrestrial contributions to other lake resource pools, such as sediments or POM, were less clear and varied depending on the isotopic tracer examined. Unlike for DOM, concentrations of particulate C were unrelated to watershed vegetation cover (Figure 6d; Table S1). Variation and overlap in the $\delta^{13}C$ of basal carbon pools (terrestrial vegetation, predicted phytoplankton values; Figure 4c) precluded

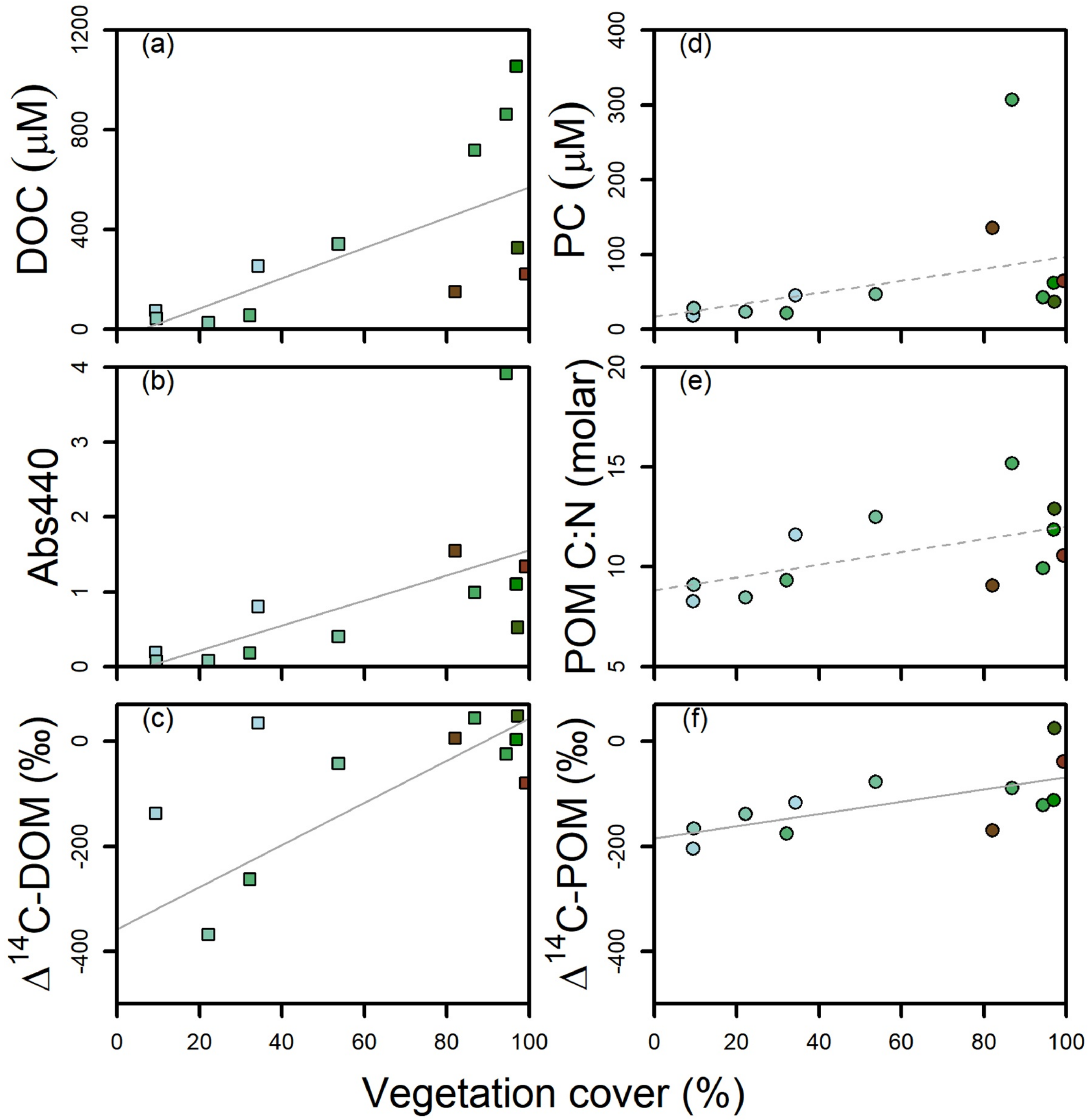

Figure 6. (a–c) Increasing watershed vegetation cover corresponds to increases in the magnitude (concentration) and terrestrial signature (Abs440, Δ^{14}C) of DOC in lakes. (d–f) Watershed vegetation cover was only weakly related to the concentration and terrestrial signature (C:N ratio, Δ^{14}C) of POM. Solid lines denote statistically significant linear relationships ($\Delta AIC_c > 2$ compared with intercept-only model), dashed lines are non-significant. Colors correspond to lake CO_2 concentration as in Figure 5.

quantitative estimation of terrestrial contribution to individual food webs using mixing models. However, these same landscape patterns also revealed important controls on resource composition in Sierra Nevada lakes, and considering multiple tracers simultaneously (δ^{13}C, Δ^{14}C, C:N ratio) suggests that POM, profundal sediments, and zooplankton are primarily of autochthonous origin irrespective of elevation or watershed vegetation cover, whereas DOM and littoral sediments are more clearly influenced by terrestrial sources (or their absence). We outline two main lines of evidence below.

First, we observed consistent δ^{13}C-enrichment of POM, sediments, and zooplankton with elevation (Figure 3 column 1), concurrent with declines in CO_2 concentration, and in contrast to relatively weak elevational trends in terrestrial vegetation or soil δ^{13}C. Rather than interpret this result as evidence for greater terrestrial contribution to food webs at higher elevations (e.g., convergence toward a terrestrial vegetation δ^{13}C signature), which is unlikely given watershed land cover trends (Figures 2a–2d), we instead interpret these patterns as evidence for consistent autochthonous contribution to lake resources and pelagic consumers. A plausible alternative mechanism for δ^{13}C-enrichment of bulk carbon pools with elevation is a decline in fractionation against ^{13}C by phytoplankton (ε_p) in lakes with low pCO$_2$. Decreased ε_p at low CO$_2$ concentrations is a well-established phenomenon in the ocean (Burkhardt et al., 1999; Hinga et al., 1994), streams (Finlay, 2004), and lakes (Smyntek et al., 2012). Applying an empirical regression model to predict ε_p demonstrated that landscape patterns in lake CO$_2$ concentration could partially explain the trends in δ^{13}C-POM (Figure 4c), assuming POM is primarily comprised of phytoplankton, which is supported by the phytoplankton culture experiment conducted in Emerald Lake. δ^{13}C-POM in the lakes with highest CO$_2$ concentration (>40 μm; Oriole and Lily lakes) was even more depleted than the predicted phytoplankton signatures, suggesting that the model under-estimates ε_p in certain lakes, perhaps unsurprising as the model was developed in a lake with a different plankton community (Smyntek et al., 2012).

Assuming invariant ε_p yields paradoxical conclusions about food webs in high elevation lakes. For example Pulido-Villena et al. (2005) interpreted enriched values of δ^{13}C-POM relative to theoretical phytoplankton values (calculated from δ^{13}C-CO$_2$ and a literature-derived $\varepsilon_p = 20‰$) as evidence for allochthonous inputs to POM in a high elevation lake in Spain (>3,000 m elevation), despite a lack of inlet streams, watershed vegetation cover, or substantial soil development in the watershed. Interpreted similarly (e.g., assuming invariant ε_p among lakes), our δ^{13}C-POM data also indicate an increase in terrestrial contribution to POM with elevation, contrary to trends in catchment vegetation cover and soil development, and contrary to the results of the phytoplankton culture experiment. Though phytoplankton community composition and community-level ε_p are unknown for our study sites, others have demonstrated considerable taxonomic variation in ε_p (Taipale, Brett, et al., 2012). Variation in community-level ε_p, coupled with predominantly autochthonous contribution to bulk carbon pools, is therefore a plausible mechanism for the observed δ^{13}C enrichment of POM, sediments, and zooplankton with elevation, and we consider this hypothesis more likely than increasing terrestrial contributions in lakes above tree-line.

Δ^{14}C and C:N ratios provide a second line of evidence for widespread in situ contribution to lake C pools across elevation and vegetation-cover gradients in the Sierra Nevada. Molar C:N ratios of POM (8.3–15.2) and profundal sediments (9.4–15.3) were lower than that of terrestrial vegetation (20.1–87.3) in all lakes regardless of elevation, and were similar to reported C:N ratios of aquatic primary producers in Finnish lakes (mean = 6.70 ± 1.51, $n = 151$, Vuorio et al., 2006). Littoral sediments had higher C:N ratios than profundal sediments, suggesting that pelagic phytoplankton make up a large portion of the POM deposited in deeper waters, whereas terrestrial OM or aquatic macrophytes contribute more to littoral sediments. Importantly, Δ^{14}C-POM matched the value of in situ cultured phytoplankton in Emerald Lake, and was depleted below the range of "modern" terrestrial primary production (<0‰) at all sites except Oriole lake (elevation = 1,722 m), despite overlap in the δ^{13}C signatures of POM and terrestrial vegetation in most lakes (Figure 5f). However, Δ^{14}C-POM and watershed vegetation cover were positively associated (Figure 6f; Table S1), suggesting a weak allochthony gradient for POM in Sierra Nevada lakes.

None of the tracers used in this study demonstrated a clear gradient in terrestrial contribution to zooplankton. Zooplankton showed large variation in Δ^{14}C (−506‰ to +39‰; Figures 5a and 5d), and overlapped with expected signatures for modern terrestrial vegetation in both high elevation and low elevation lakes (Figure 5d). Δ^{14}C-zooplankton was un-related to watershed vegetation cover, but was more depleted in deeper lakes (Table S1), suggesting greater allochthonous support of zooplankton in small lakes. This result is consistent with observations of greater t-OM assimilation by zooplankton in small versus large montane lakes (Vlah et al., 2017), and may reflect the higher ratio of littoral to pelagic habitat in small lakes.

Fish are also likely an important factor influencing resource flows to zooplankton in Sierra Nevada lakes, though the small number of lakes and the limited taxonomic resolution of zooplankton samples in this study constrained our ability to formally test hypotheses related to the role of fish. Nearly ubiquitous fish introductions to Sierra Nevada lakes (80%–95% of historically fishless lakes; Moyle et al., 1996) have drastically restructured the species and size composition of invertebrate communities toward small-bodied taxa (Knapp et al., 2001), likely relieving grazing pressure on phytoplankton. Fish also enhance nutrient availability, increasing phytoplankton and periphyton productivity in oligotrophic mountain lakes (Schindler et al., 2001). Lack of elevation or vegetation-associated allochthony gradients in zooplankton may therefore result in part from an increased supply of high quality algal food resources due to fish introductions.

Because we focused our sampling on pelagic consumers (zooplankton), we cannot fully assess allochthony patterns in Sierran lake food webs. Benthic invertebrates may have shown stronger linkages with landscape patterns in vegetation cover than did zooplankton given their proximity to shoreline and diversity of feeding behaviors. However, in one of the few studies to assess food web resource flows to a benthic consumer (Trichoptera) in high elevation lakes, reliance on t-OM was lower for benthic invertebrates than zooplankton (Vlah et al., 2017), likely a result of taxon-specific feeding preferences or temporal variation in resource availability. Resource flows to benthic consumers in mountain lakes are mostly unstudied but likely relevant to overall carbon fluxes, especially in small lakes and ponds where benthic invertebrate biomass may exceed zooplankton biomass, and should therefore be a focus of future work.

4.4. Δ^{14}C as a Food Web Tracer in Lakes

In aquatic ecosystems where δ^{13}C of terrestrial and aquatic C sources overlap, Δ^{14}C may provide a more robust tracer of resource composition and consumer resource use because DIC taken up by phytoplankton during photosynthesis can exhibit an extremely depleted Δ^{14}C-signature, generating greater isotopic separation among aquatic and terrestrial resources. Stream food web studies have already deployed natural abundance ^{14}C as an effective tracer of algal carbon in watersheds lacking aged organic carbon deposits (Ishikawa, Finlay, et al., 2020; Ishikawa, Hyodo, & Tayasu, 2013; Smits et al., 2017). While aged OM within watershed soils can directly contribute ^{14}C-depleted DOM or POM to lakes, in Sierra Nevada watersheds where soils are generally thin and low in organic matter, the Δ^{14}C-depleted signature of POM or DOC likely reflects DIC from internal lake sources. Profundal lake sediments represent a reservoir of aged organic carbon extending back ~10,000 years to the last ice age that may be respired as DIC. Bicarbonate fluxes from profundal sediments in Emerald Lake have historically ranged up to 2 ± 1 mmol $\mathrm{m}^2\,\mathrm{d}^{-1}$ (Melack et al., 2021), which given the low background concentrations in the lake, represents a substantial portion of the total DIC pool available for uptake by phytoplankton. An alternative source of ^{14}C-depleted DIC in lakes is mineral weathering within catchments; however in the Sierra Nevada, acidic soil water weathers plagioclase and other plutonic rocks, with the dominant incongruent weathering reaction being the production of kaolinite, whereas calcite accounts for only 0.5% of the total $\mathrm{HCO_3}$ produced (Garrels & Mackenzie, 1967). Thus mineral weathering is not likely a major contributor of ^{14}C-depleted DIC to Sierra Nevada lakes.

Without characterizing among-lake variation in Δ^{14}C-DIC (e.g., Δ^{14}C-phytoplankton) we cannot use Δ^{14}C as a quantitative tracer of terrestrial contribution to DOC, POM, or zooplankton, or to definitively describe elevational patterns in allochthony. For example, enriched Δ^{14}C-POM in low elevation or highly vegetated watersheds such as Oriole Lake could reflect either increased terrestrial contribution to POM, or simply uptake of Δ^{14}C-enriched DIC (derived from respiration of modern t-OM) by phytoplankton. When examined in tandem with landscape patterns of other tracers, however, the consistently depleted Δ^{14}C signature of POM and zooplankton lend support for the hypothesis that in situ producers are the dominant contribution to these carbon pools across lakes. ^{14}C analysis may prove useful for quantifying terrestrial contributions to lake C pools if a larger subset of potential C pools is analyzed, particularly Δ^{14}C-DIC or Δ^{14}C-phytoplankton to reflect the aquatic end-member.

4.5. Interpreting Snapshot Isotopic Data in the Context of Spatial and Temporal Variation

A major limitation, both of this study and other food web studies in mountain lakes (Rose et al., 2015; Vlah et al., 2017), is that sampling across environmental gradients and potential resource pools is prioritized over temporally resolute sampling or sampling among different within-lake habitats. While understandable due to the effort required to sample in mountainous terrain and the high degree of spatial variation that must be adequately characterized, the magnitude and composition (e.g., isotopic signature) of lake C pools is probably seasonally and spatially variable, but the magnitude of that variation is still uncertain relative to among-lake differences.

In order to assess how potential temporal and vertical variation in resource composition compares to the among-lake differences we observed, we compiled studies that published multiple measurements of δ^{13}C-POM in lakes during the ice-free season (Data Set S3; Sadro, 2021), many of which were previously aggregated in Gu et al. (2011). To examine temporal variability of δ^{13}C-POM within lakes we extracted means and

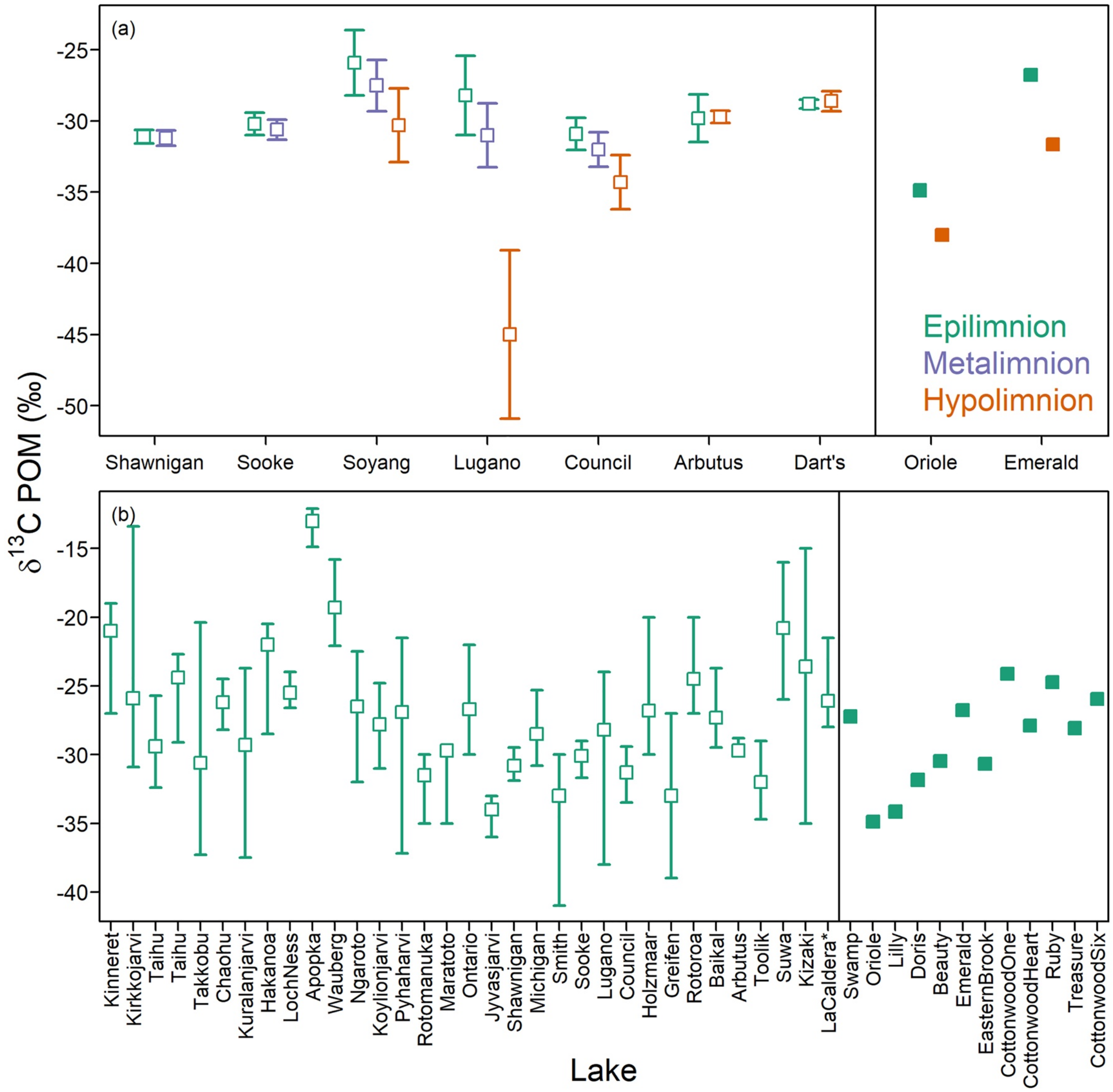

Figure 7. (a) Vertical and (b) temporal variation in δ^{13}C-POM. In each panel, data from the literature search are displayed (left; open squares) alongside data from this study (right; filled squares). Error bars in (a) represent the standard deviation around the mean for each depth strata during the stratified period. Error bars in (b) represent the amplitude (maximum-minimum) of the δ^{13}C-POM in the epilimnion through time. Lakes are arranged by elevation along the *x*-axis, but only one lake was above 800 m (La Caldera*, Sierra Nevada mountains, Spain).

amplitudes (maximum minus the minimum) in δ^{13}C-POM collected within the epilimnion. To examine variability with depth within lakes we extracted means and standard deviations for δ^{13}C-POM for at least two depth strata (e.g., epilimnion, metalimnion, hypolimnion) during the period of summer stratification. While not exhaustive, our literature review demonstrates that, as expected, δ^{13}C-POM varies within lakes with depth and through time (Figures 7a and 7b; Data Set S3). δ^{13}C-POM decreased with depth (Figure 7a), but vertical variation in δ^{13}C-POM was generally less than seasonal variation. Productive lakes had greater temporal variability in δ^{13}C-POM than oligotrophic or mesotrophic lakes (Gu et al., 2011). However, temporal variation in δ^{13}C-POM in the high elevation Lake Caldera (5‰) spanned almost half the total variation we observed among lakes in our study (Figure 7b).

Lakes in the Sierra Nevada probably exhibit a similar degree of temporal variation in the isotopic signature of major C pools as other oligotrophic lakes, thus the landscape patterns we observed for the composition of DOM and POM could differ substantially across seasons or among years. Zooplankton isotopic signatures may be less temporally variable than those of DOM or POM because they represent an integrated signal of feeding across seasons. DOM signatures are probably the most responsive to short term weather patterns and terrestrial OM inputs from rain events (Sadro & Melack, 2012). However, the results from other lake isotopic studies indicate that future sampling efforts should include a temporal component to better constrain this source of variation.

In this study we collected POM and DOM samples from the hypolimnion in only two lakes, Oriole and Emerald. Hypolimnetic POM was δ^{13}C-depleted relative to POM in the epilimnion in Oriole (−38.0‰ vs. −34.8‰ respectively), and the pattern was similar in Emerald Lake (−31.6‰ vs. −26.7‰). Interestingly, Δ^{14}C-POM also differed substantially across depth in both lakes: hypolimnetic samples were enriched in Δ^{14}C relative to epilimnetic samples (>50‰), a substantial difference relative to the observed range in Δ^{14}C-POM among lakes (−210‰ to + 25‰). For DOM, δ^{13}C was similar across depths in both lakes (mean difference = 2‰), whereas Δ^{14}C-DOM was enriched by > 100‰ in the hypolimnion in both lakes. Vertical variation in isotopic signatures of POM likely explains why zooplankton isotopic signatures frequently fell outside of the ranges for resources sampled within the epilimnion. Zooplankton migrate vertically on diel time scales, and do not necessarily feed at the depths where they are collected. While differences across depth appear to be smaller than seasonal variation, in Sierra Nevada lakes these differences can be large and merit further sampling in order to better characterize lake food webs.

5. Conclusions

Our study examined how elevation-driven gradients and spatially heterogeneous factors influence the concentration and composition (δ^{13}C, Δ^{14}C, C:N) of lake resource pools in the Sierra Nevada mountains. Although some lake C pools showed elevation-or-vegetation-associated gradients in magnitude and composition (e.g., DIC, DOC, littoral sediments), others appeared to be largely derived from in situ production regardless of elevation or watershed land cover (e.g., POM, profundal sediments, zooplankton). We found that δ^{13}C alone failed to distinguish terrestrial from aquatic food resources. However, when considered in tandem with Δ^{14}C and C:N ratios at the landscape level, these tracers provided important information on resource composition. Though more expensive than stable isotope analysis, radiocarbon presents a potentially more robust tracer of allochthony in lakes if lake C pools are sampled thoroughly.

These results highlight the need to account for spatial variation within and among lakes in the composition of lake C pools and underscore the importance of capturing seasonal or within-lake spatial variability to constrain uncertainty in isotopic values of basal resources. Fractionation against δ^{13}C during photosynthesis likely varies with community composition of primary producers, which are poorly described in Sierra Nevada lakes, and for mountain lakes more broadly. Taipale, Vuorio, et al. (2016) found significant differences in ε_p among phytoplankton taxa, among lakes, and among the epilimnion and hypolimnion in some lakes. We recommend measurements of ε_p at the community level if δ^{13}C is to be used as a quantitative food web tracer, or development of in situ cultures to isolate producers from bulk POM. Given the large observed differences between epilimnetic and hypolimnetic isotopic signatures of POM, studies of zooplankton resource use should account for differences in community composition or seasonal variability which might affect feeding behavior, as well as the role of fish predation on feeding behavior. If we are to predict how climate change or other anthropogenic influences will alter resource flows in lakes, we must better characterize the inherent scope of variation introduced by physical and temporal heterogeneity.

Data Availability Statement

Water chemistry (Data Set S1), isotopic data (Data Set S2), and compiled literature δ^{13}C-POM values (Data Set S3) are archived on the Environmental Data Initiative repository (EDI; https://doi.org/10.6073/pasta/6222e47f2eaca962c922f39e3fc2711a).

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