

1 **Seasonal changes in the biomass, distribution, and patchiness of zooplankton and fish in four**
2 **lakes in the Sierra Nevada, California**

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12 Running head: Zooplankton and fish in Sierra Nevada Lakes

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15 **Abstract**

16

17 We measured acoustic backscatter from zooplankton and fish in four peri-alpine lakes in the
18 Sierra Nevada Mountains of California, USA (Independence Lake, Lake Tahoe, Cherry Lake, and Lake
19 Eleanor) with a dual-frequency echosounder and converted these measurements to lake-wide estimates
20 of biomass density of zooplankton and fish, as well as quantitative descriptors of zooplankton spatial
21 distribution and patchiness. In two of the lakes, Cherry and Eleanor, surveys were repeated four times
22 at seasonal intervals between fall 2013 and fall 2014. Zooplankton abundances in these lakes were
23 highest in the spring and summer of 2014, with peak wet-weight biomasses estimated at 51 t in Lake
24 Eleanor in April, and 110 t in Cherry Lake in June. The biomass and vertical distribution of fish also
25 varied, increasing and moving shallower in the water column in June in both Cherry Lake and Lake
26 Eleanor. Zooplankton density displayed horizontal trends at the lake-wide scale, and the residuals from
27 these trends were spatially autocorrelated to distances over 1 km. While it is well-known that the
28 distribution of zooplankton is often patchy, this aspect of their ecology has not been thoroughly
29 quantified in most lakes, let alone in remote, high-altitude locations. These results illustrate how
30 acoustic sampling can rapidly measure the biomass of multiple trophic levels in small lakes. The
31 ability to measure changes in the spatial distribution of predators and prey simultaneously can provide
32 unique opportunities to study the processes which generate and maintain gradients and patchiness in
33 these components of the ecosystem.

34 **Introduction**

35 Zooplankton play a number of important roles in lake ecosystems. They influence water clarity
36 and nutrient cycling through grazing on primary production. They are also the conduit through which
37 primary production reaches larger predators such as fish, which often have commercial, recreational,
38 and cultural importance for humans. In lakes at high elevations, the biomass of middle and upper
39 trophic levels has been measured only rarely (McNaught et al. 1999), in contrast with more common
40 measurements of lower trophic level biomass (e.g. Pugnetti and Bettinetti 1999, Higley et al. 2001,
41 Sarnelle and Knapp 2005). The spatial distribution of that biomass within high-elevation lakes has
42 almost never been measured (Masson et al. 2001). Alpine and sub-alpine lakes differ in several
43 important ways from low-elevation lakes. They typically have lower inputs of sediment and nutrients
44 than lowland lakes, and are clearer and more oligotrophic. As a consequence, different environmental
45 factors, such as ultraviolet radiation, may be more important in structuring their pelagic ecosystems
46 (Williamson et al. 2016). Alpine and sub-alpine lakes may also be more sensitive to human
47 disturbance, including eutrophication, pH changes, deforestation, and introductions of non-native plant
48 and animal species (Bradford et al. 1998; Knapp et al. 2001; Schabetsberger et al. 2009).

49 For the sake of simplicity, most models of aquatic food webs assume, explicitly or implicitly,
50 that the spatial distributions of their component species can be ignored (Grünbaum 2012). However,
51 this may not always be a valid assumption, since patchiness is common in nature, and large fractions of
52 total predation can occur in small patches over short timespans (Tessier 1983; Temming et al. 2007).
53 In aquatic environments, sharp vertical gradients are common, and the distributions of predators and
54 prey often overlap to varying degrees, for instance due to diel vertical migration (DVM). Horizontal
55 gradients and patchiness may also be important, though these are measured less often. While the
56 potential importance of patchy distributions of zooplankton in lakes has been recognized fairly widely,
57 these distributions have rarely been measured at high temporal or spatial resolutions.

58 The lack of high-resolution measurements of zooplankton is largely a consequence of sampling
59 techniques. The most common methods for sampling zooplankton are net tows and traps. Even when
60 closing nets are used for vertically stratified tows, spatial resolution is limited, and all nets and traps
61 involve a degree of spatial or temporal blurring. Automated optical techniques (Finlay et al.
62 2007) have better spatial resolution than traps or nets, though observations are still limited to the
63 instrument's towed path through the water, and they lose taxonomic resolution relative to direct
64 samples.

65 In contrast, active acoustics (i.e., scientific echosounders) can measure the density of animals
66 through the water column quickly and at high (sub-meter) resolution. Acoustics are regularly used to
67 survey fish in lakes (e.g. Brandt et al. 1991, Rudstam et al. 2009, Simonin et al. 2012), but have rarely
68 been used for zooplankton. This is chiefly due to the fact that most lake zooplankton scatter sound
69 very weakly at the acoustic frequencies used for fish surveys, with the notable example of some larger
70 genera such as *Mysis* (Rudstam et al. 2008) and *Macrohectopus* (Melnik et al. 1993), and gas-bearing
71 larvae of midges in the genus *Chaoborus* (Northcote 1964; Teraguchi and Northcote 1966). Only a few
72 studies have used high-frequency (i.e. > 200 kHz) acoustics to measure the vertical or horizontal
73 distribution of small (< 2 mm) zooplankton (Roman et al. 2001; Hembre and Megard 2003; Parks et al.
74 2012). Likewise, few studies in lakes have examined the joint distribution of zooplankton with their
75 fish predators at the same fine spatial scale (Pinel-Alloul et al. 1999; Masson et al. 2001). Acoustic
76 methods are uniquely suited to address these questions, though they do have limitations. Most
77 importantly, echoes return limited information on the identity of scattering organisms, so that direct
78 sampling is still necessary to identify them and as ground-truth for acoustic density estimates.
79 Acoustical techniques are a powerful tool for measuring the distribution of zooplankton, especially
80 when higher frequencies enable the detection of small size classes or abundances of organisms (Warren
81 et al. 2016).

82 We surveyed the zooplankton and fish in four lakes in the Sierra Nevada mountains of
83 California, USA, between autumn 2013 and autumn 2014. Our primary tool was a two-frequency
84 acoustic system which allowed us to measure the vertical and horizontal distribution of these animals at
85 high (meter-scale) resolution. Acoustic observations were augmented with net samples to identify the
86 zooplankton scatterers and measure their sizes, to parameterize models of their acoustic target strengths
87 (TS). Fish TS were measured in situ. TZooplankton and fish TS values were used to convert acoustic
88 backscatter to biomass, yielding estimates of total biomass at two trophic levels. The high-resolution
89 nature of the acoustic data also let us compare the vertical profiles and horizontal trends in of
90 zooplankton and fish density among lakes. Changes in the distributions of zooplankton and fish from
91 one season to another were also examined. Finally, we quantified their spatial patchiness across scales
92 by calculating empirical variograms.

93

94 **Methods**

95 *Study lakes*

96 Surveys were conducted in four lakes in the Sierra Nevada: Cherry Lake, Lake Eleanor,
97 Independence Lake, and Lake Tahoe (Figure 1). Our main focus was on Cherry Lake and Lake
98 Eleanor, located at the border of Yosemite National Park near 38° 0' N, 119° 52.6' W (Figure 1). Both
99 are reservoirs of the San Francisco Public Utilities Commission. Cherry Lake is artificial, created by
100 the damming of Cherry Creek in 1956 (Eckart 1940). Lake Eleanor was formed naturally, but enlarged
101 and deepened by the construction of a dam in 1918 (Eckart 1940). Both lakes are approximately 1,420
102 m above sea level, and have areas of 6.3 km² (Cherry) and 3.9 km² (Eleanor). Both lakes have been
103 stocked with fish, including rainbow trout (*Onchorynclus mykiss*), brown trout (*Salmo trutta*), and, in
104 Cherry Lake, eastern brook trout (*Salvelinus fontinalis*) (Bingaman 1961; United States Forest Service
105 2016). Cherry and Eleanor were surveyed in October 2013, April 2014, June 2014, and September
106 2013 (Figure 1). In addition to our repeated surveys of Cherry and Eleanor, we surveyed Independence
107 Lake, located at 39° 26.4' N, 120° 18.6' W, and Lake Tahoe, at 39° 10' N, 120° 0' W once each in
108 October 2013. Independence is a natural lake, 2,127 m above sea level and 2.6 km² in area. It has
109 never been stocked with fish, and is one of only two lakes in the world with a self-sustaining
110 population of Lahontan cutthroat trout, *Oncorhyncus clarkii henshawi* (Nielsen and Sage 2002). Lake
111 Tahoe, at 1,897 m elevation, is much larger and deeper than the other three lakes, with a surface area of
112 490 km² and maximum depth of 501 m. It is also oligotrophic, in contrast to the three smaller lakes,
113 which are mesotrophic. The watersheds of the three smaller lakes are undeveloped, although portions
114 of the Cherry and Eleanor Creek watersheds were burned during the 2013 Rim Fire (National Wildfire
115 Coordinating Group 2013). Lake Tahoe is bordered by several towns, with a total permanent
116 population of approximately 50,000. All four watersheds are on granitic substrate.
117

118 *Acoustic data collection*

119 Surveys were run from outboard-powered boats trailered to each lake, and took place during
120 daytime. Acoustic volume backscatter was recorded at two frequencies, 120 and 710 kHz. Volume
121 backscatter can be expressed either in logarithmic form as “mean volume backscattering strength,” S_v ,
122 or a linear form as “volume backscattering coefficient,” s_v (MacLennan et al. 2002). The latter
123 quantity is proportional to the density of sound-scattering objects in the water. The 120 kHz
124 echosounder was a Simrad ES60 with a split-beam transducer (7° beam width), which can accurately
125 measure the target strength of individual fish in situ. The 710 kHz echosounder was a Simrad EK60
126 with a single-beam (2.8° beam width) transducer. This high-frequency system could detect small (<1

127 mm) zooplankton (Holliday and Pieper 1995; Warren et al. 2016), but its effective range was limited to
128 approximately 30 m due to attenuation in water. Both transducers were deployed on a pole mount off
129 the side of the survey boat at depths of approximately 30-50 cm depending on wave conditions.

130 Both systems were calibrated in Lake Tahoe on 21 October 2013 with a 38.1 mm tungsten
131 carbide standard target sphere (Foote et al. 1987). Because of the 710 kHz transducer's narrow beam
132 width, we were unable to center the sphere in the beam in the field, and so performed an additional, ex-
133 situ calibration for this instrument in a tank on land. A 166 L barrel, 80 cm deep and 50 cm across
134 (Rubbermaid, Atlanta GA), was filled with fresh water and the transducer mounted at the barrel's
135 center just below the water's surface. The calibration sphere could then be suspended in the center of
136 the beam beyond the transducer's 40 cm near field.

137 Independence Lake was sampled on 20 October 2013, and Lake Tahoe was sampled on 21
138 October. Cherry Lake and Lake Eleanor were each sampled four times. Cherry was sampled on 29
139 October 2013, and on 2 April, 24 June, and 10 September 2014. Eleanor was sampled one day later, on
140 30 October 2013, and 3 April, 25 June, and 11 September 2014. In the three smaller lakes, we
141 attempted to perform a lengthwise transect from one end of the lake to the other. In Independence
142 Lake, we were also able to add a series of zig-zag transects across the main axis of the lake. The April
143 2014 transects in Cherry and Eleanor were shorter due to snowfall, which required slow travel on the
144 mountain roads and reduced the time available for sampling.

145

146 *Zooplankton sampling and target strength models*

147 Zooplankton were collected on each sampling day near the center of the lake with a vertical tow
148 from 50 m to the surface using a ring net with 0.3 or 0.73 m diameter and 153 μm mesh. Due to an
149 equipment problem with the ring net during the October 2013 trip to Cherry and Eleanor, we instead
150 used an open Van Dorn bottle (10 cm diameter) with an elastic nylon mesh ($\sim 100 \mu\text{m}$) over one end.
151 This was hauled vertically through the water column with its uncovered end up, acting like a small-
152 diameter net. Samples were preserved for later analysis in 10% buffered formalin. In the lab, the total
153 biovolume of each sample was measured after allowing it to settle in a graduated cylinder. Because of
154 the small diameter of the Van Dorn sampler, the biovolumes in the samples from Cherry and Eleanor in
155 October 2013 were smaller than the finest graduation on our cylinder, preventing a precise
156 measurement. We estimated them at 0.1 mL; our analyses did not appear sensitive to these estimates
157 when they were in the range of 0-1 mL. A subsample of 200-300 animals was split from each original

sample and counted under a compound microscope. Animals were identified to the lowest possible taxonomic level. In addition, the lengths of the first 30 animals counted were measured to the nearest 0.1 mm.

To convert acoustic backscatter to animal densities it is necessary to know the backscattering cross-section, σ_{BS} , of the scattering organisms. The backscattering cross-section is also expressed in its logarithmic form, the target strength, $TS = 10 \log_{10}(\sigma_{BS})$ (MacLennan et al. 2002). We calculated these values using the stochastic distorted-wave born approximation (DWBA, Stanton et al. 1998, McGehee et al. 1998), implemented as a package, SDWBA.jl (Urmy 2016) in the Julia language (Bezanson et al. 2012). This package uses models for the body shapes of cladocerans and calanoid copepods from Warren et al. (2016), and we assumed density and sound-speed contrasts of 1.04 (Stanton and Chu 2000). For each lake, sampling date, and taxonomic group (i.e., cladocerans and copepods), we calculated the mean body length and its standard deviation (s.d.). We then drew 1000 random lengths from a normal distribution with these parameters (i.e., a parametric bootstrapping procedure, Efron and Tibshirani 1993). The generic body shape was scaled to each length and its backscattering cross-section (σ_{BS}) calculated using the DWBA. We also calculated its dry weight, W_d using a published regression for calanoid nauplii, the calanoid *Diaptomus oregonensis*, or *Daphnia galeata* (Culver et al. 1985), and converted the dry weight to a wet weight, W_w using a relationship from Wiebe et al. (1975).

The backscattering cross-sections and wet weights were averaged to get representative values for each survey date, lake, and taxonomic group. We also calculated the mean backscattering cross-section and wet weight across all three classes of scatterers using the weighted sums,

$$\langle \sigma_{BS,tot} \rangle = \sum_{i=1}^m p_i \langle \sigma_{BS,i} \rangle$$

$$\langle W_{w,tot} \rangle = \sum_{i=1}^m p_i \langle W_{w,i} \rangle$$

where p_i is the proportional numerical abundance of scattering class i in the net sample and the angled brackets denote an average or expected value. The total numerical density of all zooplankton (number m^{-3}) is then given by $n_{tot} = s_V / \langle \sigma_{BS,tot} \rangle$, and the overall biomass density ($g m^{-3}$) is given by $b_{tot} = n_{tot} \langle W_{w,tot} \rangle$.

184

185 *Acoustic data processing and analysis*

186 Acoustic data were processed using Echoview Software version 7.0 (Myriax Pty Ltd 2016).

187 Background noise was estimated and subtracted following De Robertis and Higginbottom (2007). Data

were manually scrutinized to correct bottom detection lines, exclude echoes from net and other instrument casts, and eliminate intermittent interference, such as multipath and sidelobe echoes from the steep rocky sides of the lake when close to shore. Acoustic data were integrated in bins 1 m deep and 10 m wide along-track and exported for further analysis.

Single fish targets were detected in the 120 kHz data using Echoview's individual target detection operator (split-beam method 2), with an uncompensated TS threshold of -70 dB, pulse length determination level of -6 dB, and minimum and maximum normalized pulse lengths of 0.5 and 2.0. Targets were rejected if their beam-pattern compensation was greater than 6 dB or if their angular standard deviation was greater than 0.5°. In Independence Lake, only the 710 kHz single-beam echosounder was operated, so we did not measure fish TS in this lake.. Fish target strengths were averaged (in the linear domain) by lake and survey.

Acoustic integration cells were classified as fish if their backscatter was higher at 120 kHz than at 710 kHz, since resonant scattering from fishes' swim bladders makes them stronger targets at the lower frequency. Zooplankton backscatter at 710 kHz in each lake on each sampling date was apportioned to copepods, cladocerans, and nauplius larvae using the proportional abundances in the net samples and converted to numerical and biomass densities based on the representative values for the overall zooplankton community, as described above.

Fish densities were calculated from the integrated 120 kHz backscatter, using the mean TS of the individual fish targets to convert backscatter to fish densities. To obtain approximate estimates of fish biomass, we first converted each fish target's TS to a length (in cm) by solving the relationship $TS = 20\log_{10}(L) - 67.4$ for physoclist fishes from (Foote 1987). These lengths were then converted to approximate wet weights using published scaling relationships. Length-weight relationships for fish are usually assumed to follow a power law of the form $\log_{10} W = a + b \log_{10} L$, where a and b are fitted empirically for a particular species or population. Because we could not identify fish targets to species, we averaged the parameters for rainbow trout ($a = -4.898$, $b = 2.99$, Simpkins and Hubert 1996), brook trout ($a = -5.186$, $b = 3.103$, Hyatt and Hubert 2001), and brown trout ($a = -4.867$, $b = 2.96$, Milewski and Brown 1994) to get a single length-weight equation with $a = -4.98$ and $b = 3.02$. These lengths and weights were averaged into mean values for each lake and survey.

Zooplankton and fish biomass densities were averaged across the survey track to give depth profiles of zooplankton and fish density. Additionally, they were integrated through the water column and multiplied by each lake's area to give estimates of the total biomass of fish and zooplankton in each

219 lake and survey. We also calculated the ratio of zooplankton biomass to fish biomass in each lake and
220 survey.

221

222 *Comparison of net and acoustic biomass*

223 To test the agreement between acoustic estimates of zooplankton biomass and the direct net
224 sampling, we regressed the acoustic estimate of biomass density for each lake on the biovolume from
225 the corresponding net sample. Net biovolumes were normalized by the total volume of water filtered to
226 give a biovolume density, in mL m^{-3} . The intercept in the linear regression was fixed at the origin,
227 since a preliminary model showed it was not significantly different from zero (at the $p=0.05$ level), and
228 because it is physically reasonable. Fitting the model without an intercept also added a degree of
229 freedom, increasing power and precision for the slope estimate, which was advantageous given the
230 small sample size ($n=10$). When examining preliminary results, one data point (from Lake Eleanor in
231 April 2014) appeared to be an outlier exerting undue influence on the slope, so we also fit the model
232 without this point for comparison. The significance of the slopes was assessed at the $p=0.05$ level.
233 These analyses were run using R (R Development Core Team 2016).

234

235 *Distribution of zooplankton and fish*

236 Vertical profiles of fish and zooplankton density were constructed for each lake and date by
237 averaging values horizontally within each depth bin. We also investigated horizontal spatial trends and
238 patchiness of zooplankton by averaging their densities vertically through the water column. The
239 densities in this horizontal dataset were \log_{10} -transformed and regressed on their distance from the
240 shoreline and from each lake's main stream inlet. This was done to test whether there were any spatial
241 trends in the density of zooplankton. Spatial autocorrelation was assessed by calculating empirical
242 variograms for the residuals of each regression. Two key features of a variogram are its *sill* and *range*.
243 The sill is the variogram's maximum value, indicating the expected absolute differences between
244 biomass densities at widely separated locations. The range is the spatial lag at which the variogram
245 reaches its sill, and characterizes the decorrelation distance. Because we calculated the variograms for
246 \log_{10} -transformed units, they imply multiplicative differences (\times/\div) in zooplankton density in the linear
247 domain. Variograms were calculated at spatial lags from zero to half the distance spanned by the
248 transect in each lake, in bins 0.25 km wide. Lake Tahoe was omitted from these spatial analyses,
249 because it is much larger and fed by many small streams at inlets around its perimeter, and because the

250 sampling schedule did not permit extended transects.

251

252 Results

253 The zooplankton communities of the four lakes differed, both among lakes and, in the case of
254 the repeated samples at Cherry and Eleanor, through time. Lake Tahoe's zooplankton were numerically
255 dominated by the calanoid copepods *Leptodiaptomus tyrelli* (56%) and *Epischura nevadensis* (22%),
256 with another 20% made up by unidentified copepods and copepodites (Figure 2). The zooplankton in
257 Independence Lake were split more evenly between the cyclopoid copepod *Diacyclops thomasi* (46%)
258 and the cladoceran *Daphnia middendorffiana* (44%), with the remainder composed of *Bosmina*
259 *longirostris* (6%) and unidentified rotifers (4%).

260 The zooplankton communities in Cherry Lake and Lake Eleanor were more diverse than those
261 in Independence and Tahoe, with four to ten species present in each sample (Figure 3). In October
262 2013, the communities in both lakes were approximately 60% cladocerans in the genera *Daphnia* and
263 *Diplostraca*, with the remainder mostly composed of cyclopoid copepods in the genus *Euryyclops*.
264 The following April, the community in Cherry Lake remained similar, but in Lake Eleanor it had
265 shifted to 59% Copepods, mostly *Epischura nevadensis*. During the final two surveys, in June and
266 September 2014, the communities in both lakes were between 59 and 77% copepods, a large proportion
267 of which were copepodites of unknown calanoid species. The cladocerans which composed 22-41% of
268 the communities in June and September were again a mix of *Daphnia* and *Diplostraca* (Figure 3).
269 Biovolumes of zooplankton estimated from the nets ranged from 0.1 mL m⁻³ in Lake Tahoe to 2.5 mL
270 m⁻³ in Lake Eleanor in April 2014 (Figure 4). Biovolumes in both Cherry Lake and Lake Eleanor were
271 highest in June 2014 and lower in the other months.

272 Target strengths for the different classes of zooplankton scatterers, as calculated using the
273 DWBA, varied widely (Table 1). The strongest scatterers were copepods in Cherry Lake in April 2014,
274 with an average TS of -111 dB. The weakest were nauplius larvae in Cherry Lake in October 2013,
275 with a mean TS of -148 dB. Cladoceran target strengths fell between -111 and -127 dB. Adult copepod
276 target strengths fell in the same broad range, from -104 to -128 dB. Nauplii, due to their much smaller
277 size, were predicted to scatter much less sound, with their mean TS falling between -120 and -148 dB
278 (Table 1). After averaging across all scattering classes, overall mean TS ranged from -125 dB, in
279 Cherry Lake in September 2014, to -105 dB, in Lake Tahoe in October 2013 (Table 1). There were no
280 systematic trends in TS between the lakes, or through time.

281 Mean fish target strengths, measured in situ, ranged between -39 and -36 dB re m²,
282 corresponding to mean lengths from 21 to 31 cm, and mean weights from 198 to 719 g (Table 2). In
283 October 2013, the mean TS (and the mean lengths and weights derived from them) were roughly equal
284 in Lake Eleanor and Lake Tahoe and slightly higher in Cherry Lake. In the following three surveys,
285 however, mean TS was 1-3 dB higher in Lake Eleanor, with corresponding length and weight
286 differences of 2-8 cm and 140-380 g.

287 The 710 kHz echosounder was able to detect the small zooplankton in the lakes, and the
288 frequency-differencing procedure could clearly separate them from fish echoes (Figure 5). Mean
289 zooplankton wet-weight biomass densities measured acoustically were relatively low (< 20 g m⁻³) in all
290 lakes, and varied seasonally (Figure 4). In October 2013, the mean zooplankton density in all four
291 lakes was low, with less than 5 g of zooplankton wet-weight biomass m⁻³ (Figure 4). Lake Eleanor had
292 a weak sound-scattering layer extending from the surface to 15 m, corresponding to an estimated peak
293 zooplankton biomass density of just over 4 g m⁻³ (Figure 6). In April 2014, Cherry Lake contained
294 zooplankton at similarly low densities, but Lake Eleanor had a denser zooplankton layer near the
295 surface, increasing from near-zero density at 10 m depth to a maximum of 125 g m⁻³ at 2 m depth, the
296 bottom of the echosounder's blind zone (Figure 6). Two months later in June, this layer was still
297 present, though not quite as deep as in April. During this time, a similar layer had also appeared in
298 Cherry Lake, with a maximum density, at 2 m depth, of 200g m⁻³ (Figure 6). By September, the surface
299 zooplankton layer in Lake Eleanor had mostly disappeared. The layer in Cherry Lake was much less
300 dense (maximum 4 g m⁻³, Figure 6).

301 Peak fish densities in the lakes ranged between 0.007 and 1.6 fish per 1000 m⁻³, corresponding
302 to biomass densities of 0.04 to 0.7 g m⁻³ (Figure 6). These fish were mostly found below the
303 zooplankton layers (Figure 6). In the first surveys in October 2013, fish in Cherry Lake were
304 concentrated in a layer centered at 35 m depth, with much higher densities than the other three lakes
305 (Figure 6). The overall mean fish density in October in Cherry Lake was 1.6 per 1000 m⁻³, compared to
306 0.007 in Lake Eleanor. The next April, the fish in both lakes were grouped in two layers. These layers
307 were shallower in Cherry Lake, at depths of 10 and 25 m, than in Lake Eleanor, where they were at
308 depths of 20 and 40 m (Figure 6). In June, fish in both lakes were concentrated in the upper 10-15 m
309 and were more abundant overall than in April, with mean densities of 0.3 (Cherry) and 0.5 (Eleanor)
310 fish per 1000 m⁻³. In September, the fish in each lake were in one broad layer, between 5 to 20 m depth
311 in Lake Eleanor and from 10 to 30 m in Cherry Lake. Overall densities were lower than in June, at 0.2

312 fish per 1000 m³ in Cherry Lake and 0.1 fish per 1000 m³ in Lake Eleanor.

313 When depth-integrated and scaled by their respective lake areas, these densities yielded a wide
314 range of estimates for the total biomasses in the different lakes. In October 2013, Lake Tahoe
315 contained an estimated 7,500 kg of small zooplankton. Zooplankton in the three smaller lakes was 60-
316 240 times denser than in Tahoe, but their much smaller areas led to similar or smaller total biomass
317 estimates (Table 3). In April 2014, the zooplankton wet-weight biomass density in Lake Eleanor had
318 increased to 13 g m⁻³, raising its total biomass estimate to over 51,000 kg, higher than that of Lake
319 Tahoe in October 2013. Total zooplankton biomass in Cherry Lake in April was 3,300 kg, 14% of its
320 level in the October survey. By June, however, it had increased to 110,000 kg, while the zooplankton
321 biomass in Eleanor dropped to 31,000 kg. During the September 2014 survey, zooplankton populations
322 in both lakes had dropped back to low levels, similar to the previous autumn (Table 3).

323 Estimates for total fish biomass were much lower than those for zooplankton. The highest
324 estimate was 2,200 kg in Lake Tahoe, followed by 1,700 kg in Cherry Lake, both in October 2013.
325 Fish biomass in Cherry Lake and Lake Eleanor was lowest the following April, increasing somewhat in
326 the following two surveys in June and September. Fish biomass did not vary as widely as zooplankton
327 biomass. In all surveys, zooplankton outweighed fish by a factor between 3 and 850.

328 Net and acoustic estimates of zooplankton density were positively related (Figure 7). The
329 regression of net-caught zooplankton biovolume on acoustically estimated biomass was not statistically
330 significant when all data points were included ($p=0.1$, $R^2=0.19$), though fitted slope was positive.
331 When the outlying measurement from Lake Eleanor in April 2014 was excluded, the fitted slope was
332 significantly different from zero, with a fitted value of 0.34 mL mg⁻¹, and a 95% confidence interval
333 from 0.21 to 0.46 mL mg⁻¹. This model fit the data fairly well, with an adjusted R^2 of 0.81.

334 Zooplankton biomass density displayed significant trends with respect to distance from the inlet
335 and shore in most surveys, though the directions of these trends were variable (Table 4). The most
336 pronounced trend was in Cherry Lake in June 2014, where zooplankton biomass density was an order
337 of magnitude higher near the lake's inlet than near the dam at the other end. In eight out of the nine
338 surveys, the signs of the coefficients for distance from shore and distance from the inlet were the same.
339 The single survey in Independence Lake was the exception, with biomass density increasing closer to
340 the inlet and decreasing closer to shore. In three of the four surveys in Cherry Lake, zooplankton
341 density increased towards the shore and inlet. In Lake Eleanor, the reverse was true: three out of four
342 surveys showed zooplankton density higher away from shore and the inlet (Table 4). These spatial

343 regressions explained a low-to-moderate amount of the variability in th data, with R^2 values ranging
344 from approximately zero in Lake Eleanor in October 2013, to 0.63 in Cherry Lake in June 2014 (Table
345 4).

346 The residuals from these regressions were spatially autocorrelated in some, but not all, lakes
347 and surveys. In September 2013, when biomass densities in all lakes were low, Lake Eleanor's
348 variogram reached its sill of 0.1 at a range of about 2 km. Independence Lake's variogram was flat,
349 showing little evidence for spatial autocorrelation, and in Cherry Lake, the variogram was higher at
350 shorter lags, suggesting short-range anticoncorrelation (Figure 8). In April, Lake Eleanor's variogram was
351 similar, with a sill of around 0.1 at a range of 1.5 km. Back-transformed to linear units, this implies an
352 expected difference in biomass on the order of 25% across distances of 500 m or greater. The short
353 transect in Cherry Lake in April limited the spatial information available for that variogram.

354 In June, the sill of the variogram in Lake Eleanor had increased to 0.15 at a range of 2 km
355 (Figure 8), implying an expected difference in biomass on the order of 50% when transformed back to
356 linear units. In Cherry Lake, the variogram was relatively flat (Figure 8), showing little evidence for
357 spatial structure other than the lakewide trends described above. Spatial variability in Lake Eleanor
358 decreased somewhat between June and August 2014. However, the variogram for Cherry Lake in the
359 final survey showed higher overall variability, peaking at 0.37 at a lag of 1 km and a sill near 0.2
360 beyond 1.5 km. Overall, the variogram sill values ranged from approximately 0.1 to 0.2 . These
361 values, in \log_{10} -transformed units, imply multiplicative differences (\times/\div) in zooplankton density from
362 0.25 to 1.6 at long ranges, where “long ranges,” as defined by the variograms, are between 1 and 2 km.
363

364 Discussion

365 Our acoustic measurements produced estimates of the total biomass of zooplankton and fish in
366 four peri-alpine lakes in the Sierra Nevada Mountains. To our knowledge, these are the first biomass
367 estimates (for any trophic level) ever made in Independence Lake, Cherry Lake, and Lake Eleanor. In
368 Lake Tahoe, our estimate of the mean density of small zooplankton (approximately 2,200 individuals
369 m^{-3}) was in good agreement with prior estimates (e.g. 0-23,000 individuals m^{-3} , Goldman et al. 1979).

370 A spring bloom of zooplankton occurred in both Cherry Lake and Lake Eleanor, with peak
371 biomass densities of 4-6 g m^{-3} . In spring and summer, the zooplankton were concentrated in the upper
372 5-10 m of the water column, probably associated with a stratified surface layer. In 2014, the bloom
373 appeared to begin earlier in Lake Eleanor than in Cherry Lake, since a near-surface zooplankton layer

374 was present in Eleanor, but not Cherry, during the early April survey. By June, both lakes had similar
375 zooplankton densities, and by September, zooplankton populations in both lakes had declined by an
376 order of magnitude. At this point there were still more zooplankton in Cherry Lake, however,
377 suggesting that the bloom there, which started later, also took longer to collapse in the fall. This
378 pattern, of a spring and summer increase in zooplankton as they respond to blooming phytoplankton, is
379 consistent with standard models of seasonal cycles in lake ecosystems (Sommer et al. 1986, 2012).

380 Fish biomass did not vary nearly as widely as zooplankton biomass, which is expected given
381 their much longer life spans and generation times. At the height of the zooplankton blooms,
382 zooplankton biomass was several hundred times that of fish, indicating that the former were effectively
383 released from predatory control at those times. In both autumns, the zooplankton:fish ratios were much
384 lower, suggesting a closer match between rates of zooplankton reproduction and fish predation. While
385 fish were scarce in Lake Eleanor in October 2013, our estimate of total biomass (7 kg, Table 3) is
386 probably extreme, reflecting error due to the patchy distribution of fish and our short surveys as much
387 as the true biomass. It should also be noted that our seasonal sampling interval may have caused us to
388 miss shorter-scale variability in zooplankton populations, due either to sub-seasonal population
389 dynamics, or responses to environmental forcings such as runoff from rainstorms or mixing of the
390 water column due to wind. This study also only covers one year, leaving longer-term trends unknown.

391 Two longer-term environmental changes were under way during this study which deserve
392 particular mention. The first was the Rim Wildfire, which started approximately 20 km southwest of
393 Cherry Lake and Lake Eleanor on 17 August 2013. The fire spread rapidly, becoming the third-largest
394 wildfire on record in California, and burned portions of both lakes' watersheds. The fire was not fully
395 contained until several days after the first surveys in October 2013 (National Wildfire Coordinating
396 Group 2013). Fires may have a number of effects on lakes and the animals in them, for instance by
397 increasing runoff from burned watersheds, depositing ash from the air, or altering the characteristics of
398 incident solar radiation via drifting smoke plumes (Urmy et al. 2016; Williamson et al. 2016).

399 The second major environmental trend was an ongoing drought affecting the western United
400 States. One consequence of the drought was a decline in the water levels of Cherry Lake and Lake
401 Eleanor, which were nearly 8 m lower in the final survey in September 2014 than they were in the first
402 survey, in October 2013 (United States Geological Survey 2017). Both lakes are reservoirs supplying
403 water and electricity to the San Francisco, so their levels are managed by that city's Public Utilities
404 Commission. The drought probably also played a role in the spread of the Rim Fire: most of

405 California's largest wildfires, including the Rim Fire, have occurred during droughts (Williamson et al.
406 2016). However, the drought may also have mitigated some of the fire's effects on Cherry and Eleanor:
407 precipitation during the winter of 2013-2014 was well below normal (California Department of Water
408 Resources 2014), meaning that runoff and erosion in the burned areas were much less than they might
409 have been in a more normal year. Both the drought and fire are likely to have affected the lakes in
410 some way, but the limited sampling schedule makes it impossible to separate these effects from the
411 expected seasonal cycle for a temperate lake.

412 Fish target strengths, and the corresponding estimated lengths, were in the expected range for
413 lake salmonids. The vertical distribution of fish in Cherry Lake and Lake Eleanor was qualitatively
414 similar in every survey but the first, suggesting similar dynamics in the fish community of both lakes.
415 These dynamics cannot be determined from the limited information available in this study, but the
416 similar vertical patterns of fish density, offset in some cases by up to 10 m, suggest that Cherry Lake
417 and Lake Eleanor could be an interesting setting for further comparative studies of fish behavior. The
418 vertical distributions of fish and zooplankton did not coincide except in June 2014, though this is not
419 particularly surprising, since our surveys occurred during the daytime and many fish migrate vertically.
420 The lack of overlap emphasizes that interactions between predators and prey are not evenly distributed,
421 and may be restricted to certain locations or times of day (Beauchamp et al. 1999; Temming et al. 2007;
422 Lorke et al. 2008).

423 There was fair agreement between the acoustic and net-based estimates of zooplankton
424 biomass. However, the data from Lake Eleanor in April 2014 formed a notable outlier, with the net-
425 based biovolume much lower relative to the acoustic biomass than expected, based on the other
426 samples. A relatively strong scattering layer was visible near the surface along the entire survey track.
427 This layer, along with weaker-than-average zooplankton TS (Table 1), accounted for the high acoustic
428 biomass. The small biovolume estimate is accurate, at least based on the net sample (0.5 mL of
429 zooplankton from a total filtered volume of 15 m³). The discrepancy between these two measures is
430 probably due to some combination of random variability in the net sample and uncertainty in our TS
431 estimates. Regardless, regressions with and without this outlier produced positive slopes. Without it,
432 the slope was significantly different from zero with a value of 0.34 mL mg⁻¹. Wiebe et al. (1975) found
433 that displacement biovolume *DV* and wet weight *WW* of marine zooplankton were related by the
434 equation

435 $\log_{10}(DV) = 0.078 + 1.026 \log_{10}(WW)$

436 which, in linear terms, implies a slope of approximately 1.2 mL mg^{-1} , 3.5 times higher than our
437 estimate. This difference is not totally unexpected: Wiebe et al.'s (1975) data came exclusively from
438 net samples in marine environments, and acoustic estimates of biomass are often several times higher
439 than those based on net catches, probably due to avoidance reactions by the animals (Warren and Wiebe
440 2008; Wiebe et al. 2013). If true, this implies that a regression of net-based biovolume on acoustically-
441 derived biomass would have a shallower slope than the same regression on net-based biomass. The
442 multi-step conversion process from acoustic backscatter to biovolume introduces a number of
443 uncertainties, and should be interpreted with some caution. However, it does produce reasonable
444 values, increasing our confidence that the patterns observed are biologically meaningful.

445 The variable spatial trends in zooplankton density in the three small lakes defy a single
446 explanation, given the short surveys and limited set of spatial covariates available. The clearest trend
447 was increasing zooplankton density close to the Cherry Lake's main stream inlet in June 2014. One
448 reasonable explanation for this trend is that the stream transports nutrients, detritus, or other exogenous
449 resources into the lake near its inlet, supporting higher primary production, and maintaining a higher
450 rate of zooplankton growth at the upstream end of the lake. Alternatively, the higher biomass estimates
451 near the inlets could be an artifact due to acoustic scattering from sediments introduced by the streams
452 (Thorne and Hanes 2002). This explanation is consistent with the fact that the steepest gradient was
453 observed in June, near the peak of the seasonal snow melt and runoff. While sediments might remain
454 suspended near the stream mouth, they would settle out rapidly farther into the lake basin, and we do
455 not expect the effect on our lakewide biomass estimates to be large.

456 Even after subtracting the lake-scale trend in zooplankton density, spatial autocorrelation was
457 evident in the residuals, as illustrated by the empirical variograms (Figure 8). These should be
458 interpreted with caution, since they were based in most cases on single reciprocal transects down the
459 main axis of each lake which may not have captured any spatial anisotropy present. In particular, the
460 restricted time available to survey Cherry Lake on 2 April 2013 meant that the transect was only about
461 1 km long, limiting our ability to draw conclusions about the spatial distribution of zooplankton.
462 Regardless, most of the variograms did show evidence of spatial patchiness in the distribution of
463 zooplankton, with approximate spatial scales, based on the variogram ranges, between 500 and 2000
464 km. It is unknown what processes generate and maintain patchiness in these lakes. In the ocean,
465 patchiness in zooplankton appears to be driven mostly by bottom-up processes, with scales of
466 biological variability mirroring scales of physical variability (Denman et al. 1977; Mackas et al. 1985;

467 Urmy et al. 2012). It seems unlikely that these lakes (with the possible exception of Tahoe) are large
468 enough to support much horizontal physical variability, so the patchiness in the zooplankton is
469 probably due to other processes, such as aggregation (Byron et al. 1983) or predation by schooling fish.

470 The acoustic methods used here offer a number of advantages over traditional direct sampling
471 methods, though they also come with their own uncertainties and caveats. Identification of scatterers is
472 often a challenge with acoustics. However, using a two (or more) frequency system, as in this study,
473 reliably separates areas of backscatter from zooplankton and fish. Furthermore, direct net sampling of
474 the zooplankton community, especially in relatively small lakes such as Independence, Cherry, and
475 Eleanor, lets us confidently identify the main classes of zooplankton scatterers. The main source of
476 uncertainty when interpreting acoustic backscatter as an estimate of biomass density is in the target
477 strengths assumed for the scattering organisms. The DWBA is an accurate and widely used method to
478 calculate zooplankton target strengths, but it depends, sensitively, on accurate values for the scatterers'
479 material properties—namely the density- and sound-speed-contrasts g and h . To our knowledge, these
480 values have never been measured for any freshwater zooplankton. In their absence, we used generic
481 values from the literature, based on marine zooplankton (Stanton and Chu 2000). These values are
482 reasonable defaults, but they may not be accurate for the species considered here, introducing a degree
483 of unknown error into the TS and hence biomass estimates. Measurements of the material properties of
484 freshwater zooplankton would be a worthwhile objective for future research.

485 Despite these uncertainties, acoustic methods for surveying zooplankton have several
486 compelling advantages. Acoustic methods provide high-resolution vertical profiles of fish and
487 zooplankton densities, offering insights into the biotic and abiotic processes structuring lake
488 ecosystems (Beauchamp et al. 1999; Urmy et al. 2016). Acoustics are also an excellent method for
489 recording the diel vertical migration of lake zooplankton (Warren et al. 2016). Although DVM was not
490 part of this study, it would be a worthwhile topic for further investigation in these lakes. Acoustics can
491 also reveal trends in the distribution of zooplankton that would be missed by traditional sampling
492 methods (Pinel-Alloul et al. 1999; Hembre and Megard 2003). In this case, these included trends in
493 zooplankton biomass density with distance from shore or from the stream inlet. Accounting for spatial
494 trends and patchiness in turn reduces uncertainty in the biomass estimates.

495 Perhaps most importantly, multi-frequency echosounders allow the biomass of multiple trophic
496 levels to be measured efficiently, and at the same spatial resolution, providing valuable data for
497 ecosystem based management decisions (Slocombe 1985; Allan and Johnson 1997; Link 2002). In a

498 relatively small lake such as Cherry, Eleanor, or Independence, the ability to survey large volumes of
499 water quickly means that a virtual census of the lake's fauna is feasible. The time available for our
500 acoustic surveys was somewhat constrained by the need to collect other optical, chemical, and
501 biological data not reported in this study, as well as the time required to trailer the boat to each lake.
502 However, we were still able to run full-length transects of the lakes in most of the surveys, and with
503 just a few more hours it would be possible to survey the lakes quite thoroughly, producing detailed
504 three-dimensional maps of the distribution of fish and zooplankton as well as accurate estimates of
505 their numbers and biomass. As this study demonstrates, such a goal is realizable and offers an exciting
506 prospect for studies of predator-prey interactions and lake food webs.

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671 Leach and Jennifer Brentrup assisted with field work in Independence Lake and Lake Tahoe and helped
672 process some of the zooplankton samples. Maria Anderson, Kayla Hartigan, Michaela Miller, and
673 Helena Nierer identified, counted and measured the zooplankton. Erin Overholt maintained her good
674 humor while dealing with reimbursements for a dozen cross-country flights, booked on short notice.
675 This project was funded by the National Science Foundation's Division of Environmental Biology
676 RAPID grant 13-60066, awarded to Craig E. Williamson and S. Geoffrey Schladow.

677 **Table 1.** Acoustic properties of crustacean zooplankton. For each class of scatterers (Cladocerans,
 678 Copepods, and Nauplii larvae), the mean acoustic target strength (dB re m²) and individual wet weight
 679 (μg) are displayed, along with the percentage by biomass of the net catch made up of that class of
 680 scatterers.

Lake	Cladocerans			Copepods			Nauplii			Weighted Avg.	
	TS (dB)	W (μg)	%	TS (dB)	W (μg)	%	TS (dB)	W (μg)	%	TS (dB)	W (μg)
Cherry	-118.1	82.5	59	-121.1	112.7	31	-148.4	2.3	10	-119.4	83.6
Eleanor	-112.8	197.6	64	-113.4	153.5	32	—	—	—	-113.2	174.1
Independence	-113.9	162.6	50	-117.2	138.9	46	—	—	—	-115.4	143.8
Tahoe	—	—	—	-104.4	325.1	86	-130.5	6.7	12	-105.1	279.2
Cherry	-113.3	172.8	43	-111.5	144.7	19	-120.3	12.7	38	-114.3	106.6
Eleanor	-127.0	53.1	18	-123.8	85.3	38	-127.5	5.9	44	-125.6	44.7
Cherry	-119.5	70.6	30	-122.9	87.0	58	-133.4	3.8	13	-122.0	71.6
Eleanor	-117.4	108.8	23	-128.1	59.4	11	-125.4	9.2	67	-122.0	37.0
Cherry	-123.9	66.8	32	-128.0	54.8	22	-125.4	9.2	46	-125.3	37.4
Eleanor	-117.9	124.6	15	-110.8	261.5	11	-118.6	12.8	73	-116.6	56.6

681

682 **Table 2.** Average fish target strength (TS), with estimated lengths and wet weights. Standard
683 deviations are given in parentheses. The final column gives the number of fish targets detected in each
684 survey. Target strengths were measured in-situ in each lake with a 120 kHz split-beam echosounder
685 and converted to lengths and weights using published empirical TS-length and length-weight scaling
686 relations (see Methods for details).

Date	Lake	TS (dB)	L (mm)	W (g)	n
2013-10	Cherry	-36 (5.4)	31 (17)	720 (990)	4218
	Eleanor	-39 (5.3)	23 (14)	340 (590)	90
	Tahoe	-39 (6.0)	22 (14)	330 (670)	867
2014-04	Cherry	-39 (5.2)	24 (14)	350 (510)	195
	Eleanor	-38 (5.4)	26 (16)	480 (770)	453
2014-06	Cherry	-40 (4.3)	21 (10)	200 (270)	2068
	Eleanor	-37 (5.1)	29 (15)	580 (780)	166
2014-09	Cherry	-39 (5.0)	23 (13)	300 (520)	1060
	Eleanor	-37 (5.2)	29 (16)	610 (920)	116

687

688 **Table 3.** Acoustic estimates of total wet-weight biomass of zooplankton and fish in each lake show
689 seasonal changes in different trophic levels as well as interlake differences. These values (as well as the
690 ratio of lower to higher trophic level biomasses) may provide useful data for investigations of various
691 ecosystem-level processes in these habitats.

Date	Lake	Zooplankton (kg)	Fish (kg)	Ratio
2013-10	Cherry	23,000	1,700	14
	Eleanor	3,600	7	530
	Tahoe	7,500	2,200	3.4
2014-04	Cherry	3,300	94	35
	Eleanor	51,000	60	850
2014-06	Cherry	110,000	280	400
	Eleanor	31,000	640	48
2014-09	Cherry	1,600	280	5.9
	Eleanor	930	210	4.5

692

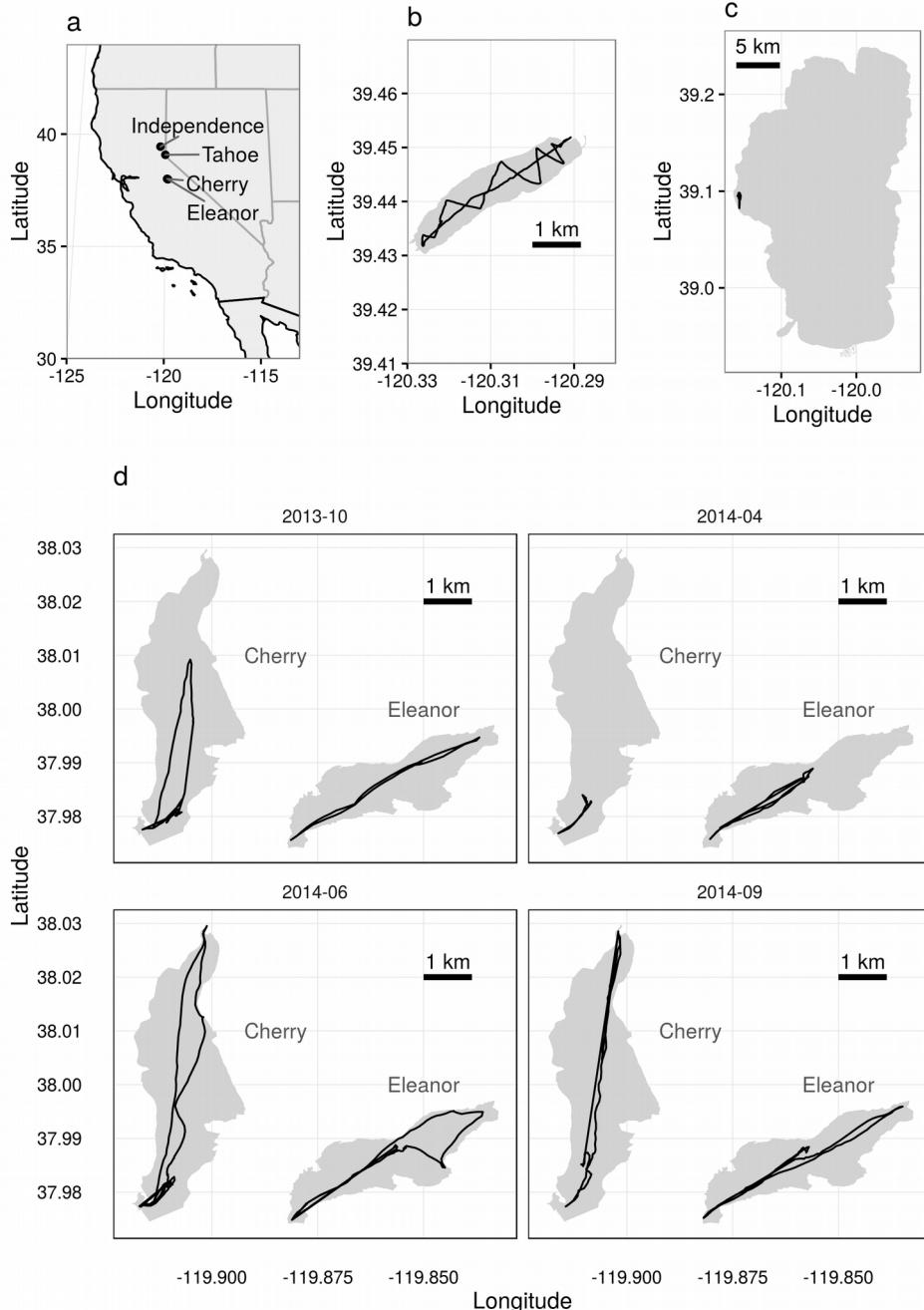
693 **Table 4.** Summary of regression models for spatial trends in the density of zooplankton, by lake and
694 survey. The average wet-weight biomass density of zooplankton (in g m⁻³), was averaged through the
695 water column, log₁₀-transformed, and modeled as a linear function of distance (in km) from the lake's
696 inlet and from the shore. The columns "Intercept", "Inlet distance", and "Shore distance" give the
697 regression intercept and coefficients associated with each covariate. Their respective *p*-values are in
698 the columns to their right.

699

Date	Lake	Intercept	<i>p</i>	Inlet		Shore		<i>R</i> ²
				distance	<i>p</i>	distance	<i>p</i>	
2013-10	Cherry	-1.37	0.002	0.231	< 0.001	0.0981	0.783	0.32
	Eleanor	0.269	0.044	-0.0112	0.679	-0.485	0.097	0.02
	Independence	-0.613	< 0.001	-0.0191	0.017	1.16	< 0.001	0.12
2014-04	Cherry	0.424	0.477	-0.0843	0.315	-0.419	0.063	0.17
	Eleanor	0.551	< 0.001	0.219	< 0.001	0.206	0.276	0.45
2014-06	Cherry	2.28	< 0.001	-0.184	< 0.001	-0.76	< 0.001	0.73
	Eleanor	0.725	< 0.001	0.0111	0.637	0.687	0.002	0.05
2014-09	Cherry	0.449	< 0.001	-0.109	< 0.001	-1.44	< 0.001	0.44
	Eleanor	0.126	0.103	0.0161	0.242	-1.68	< 0.001	0.55

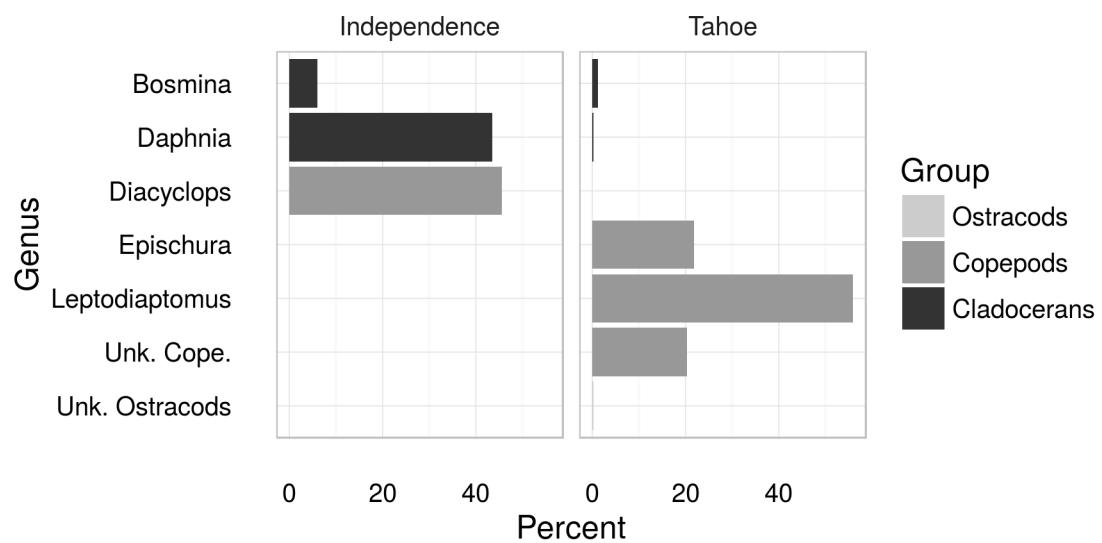
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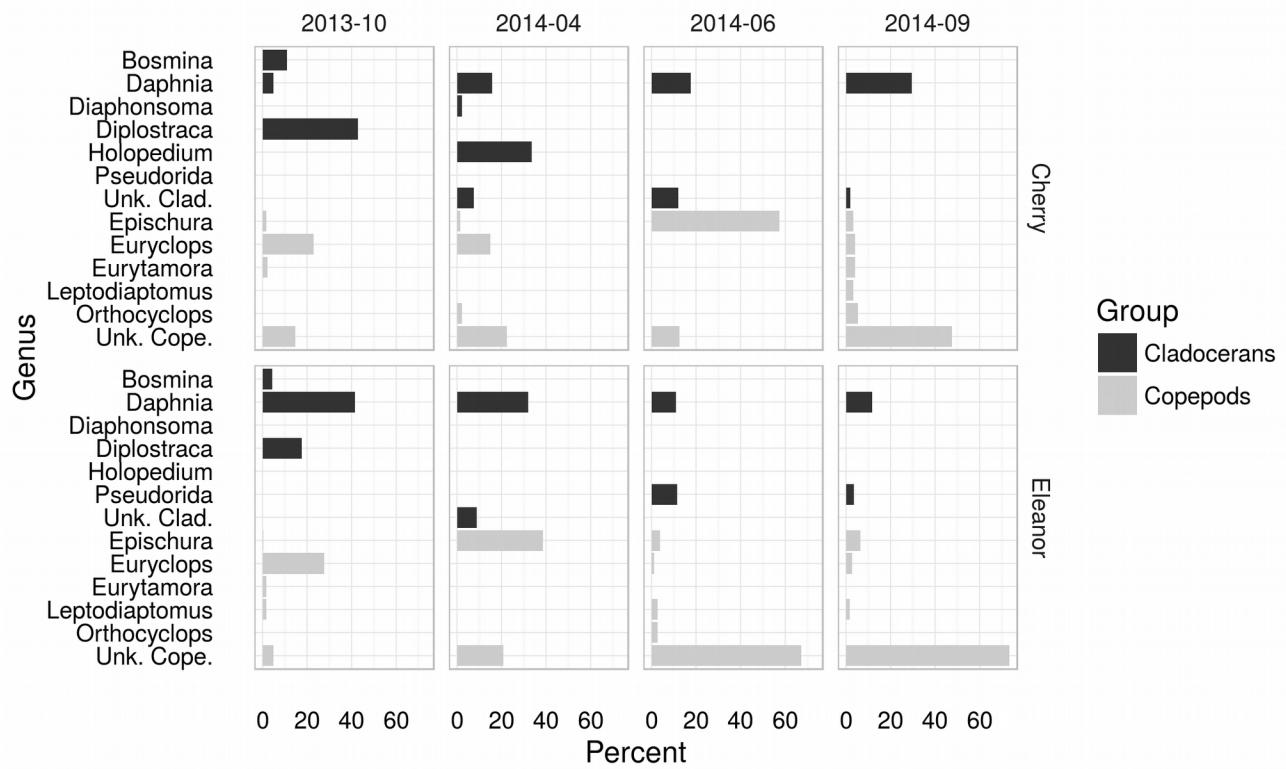
703

704 **Figure 1.** Maps of study lakes, showing (a) location of the four surveyed lakes in California in the
 705 western United States, survey tracks in October 2013 in (b) Independence Lake and (c) Lake Tahoe,
 706 and (d) repeated surveys in Cherry Lake and Lake Eleanor in October 2013, April 2014, June 2014, and
 707 September 2014.



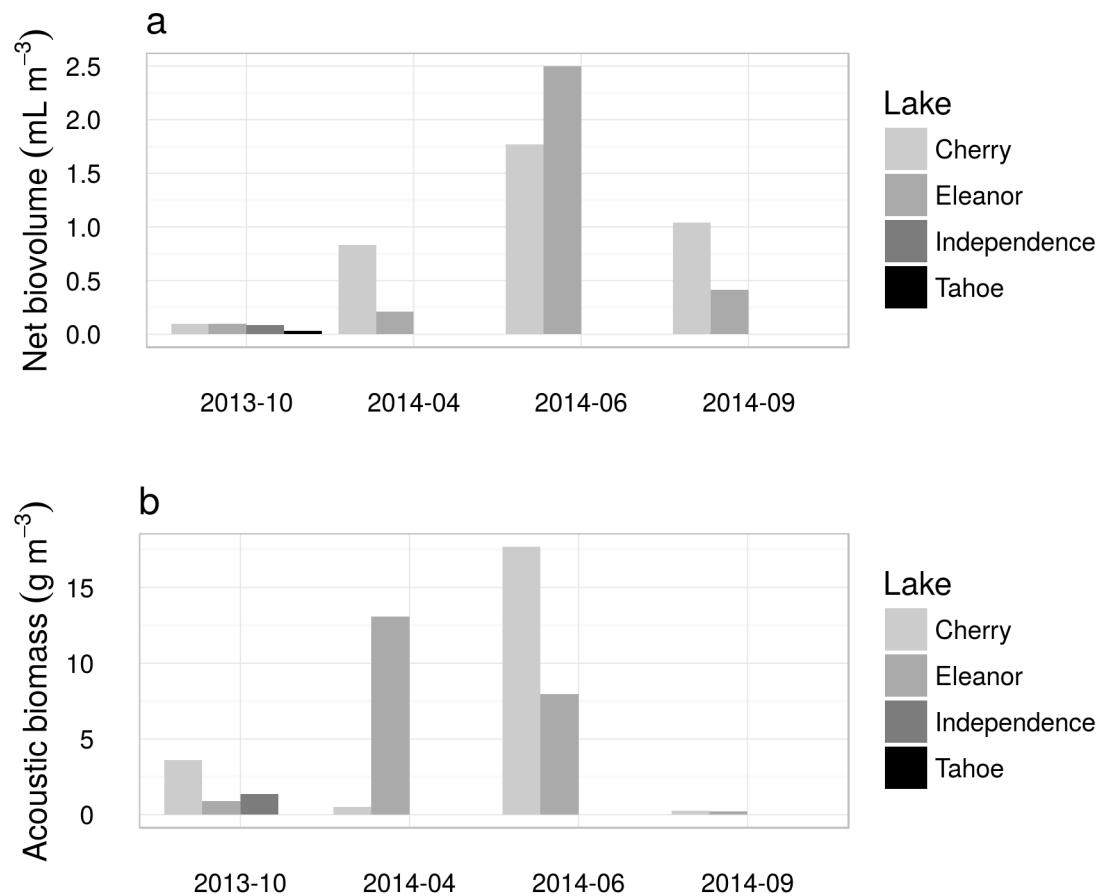
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709 **Figure 2.** Numerical composition of the crustacean zooplankton community in Independence Lake and
 710 Lake Tahoe in October 2013 was dominated by a few species.



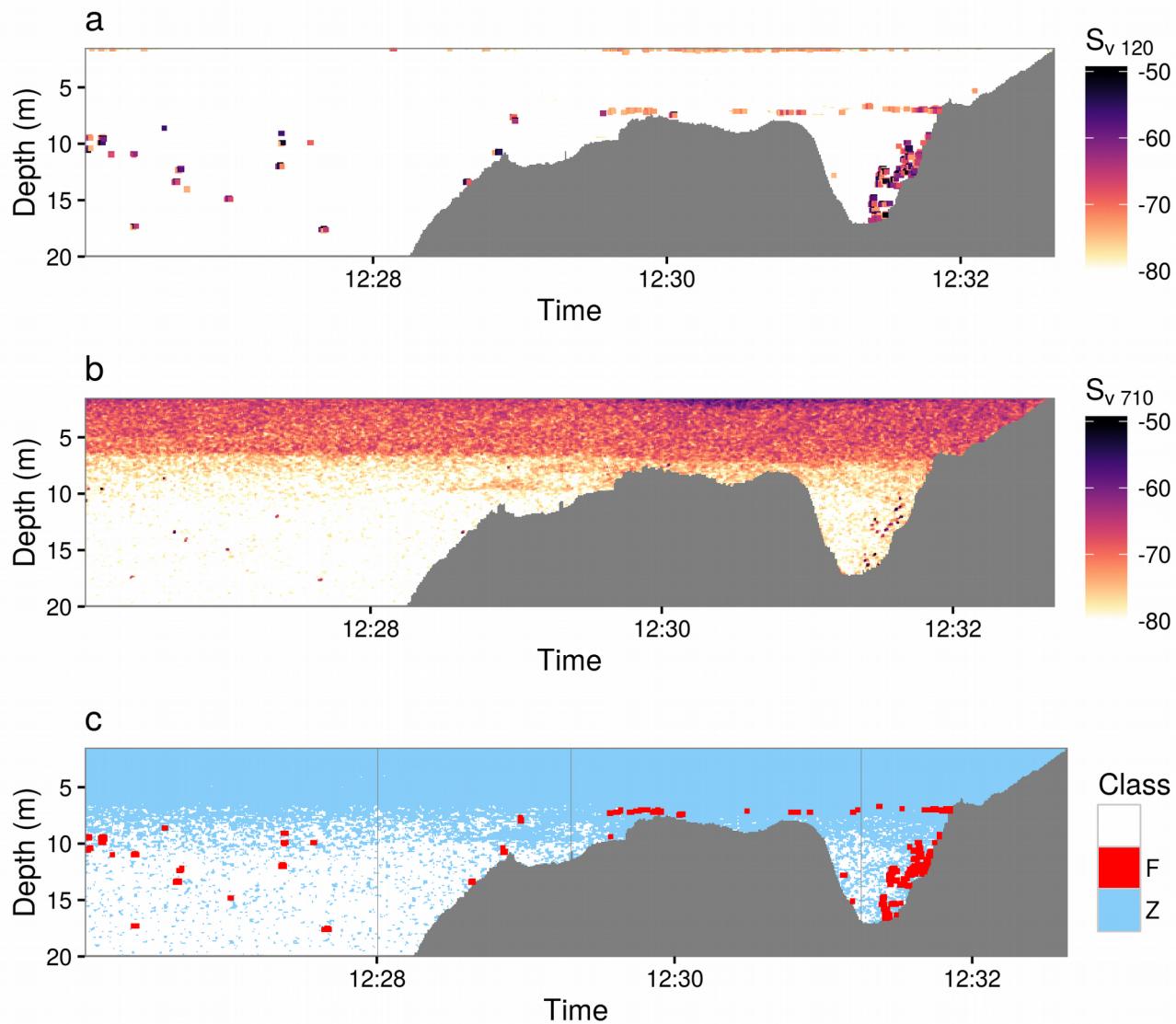
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712 **Figure 3.** Numerical composition of the crustacean zooplankton community in Cherry Lake and Lake
713 Eleanor in four seasonal surveys varied seasonally and between the two sites.



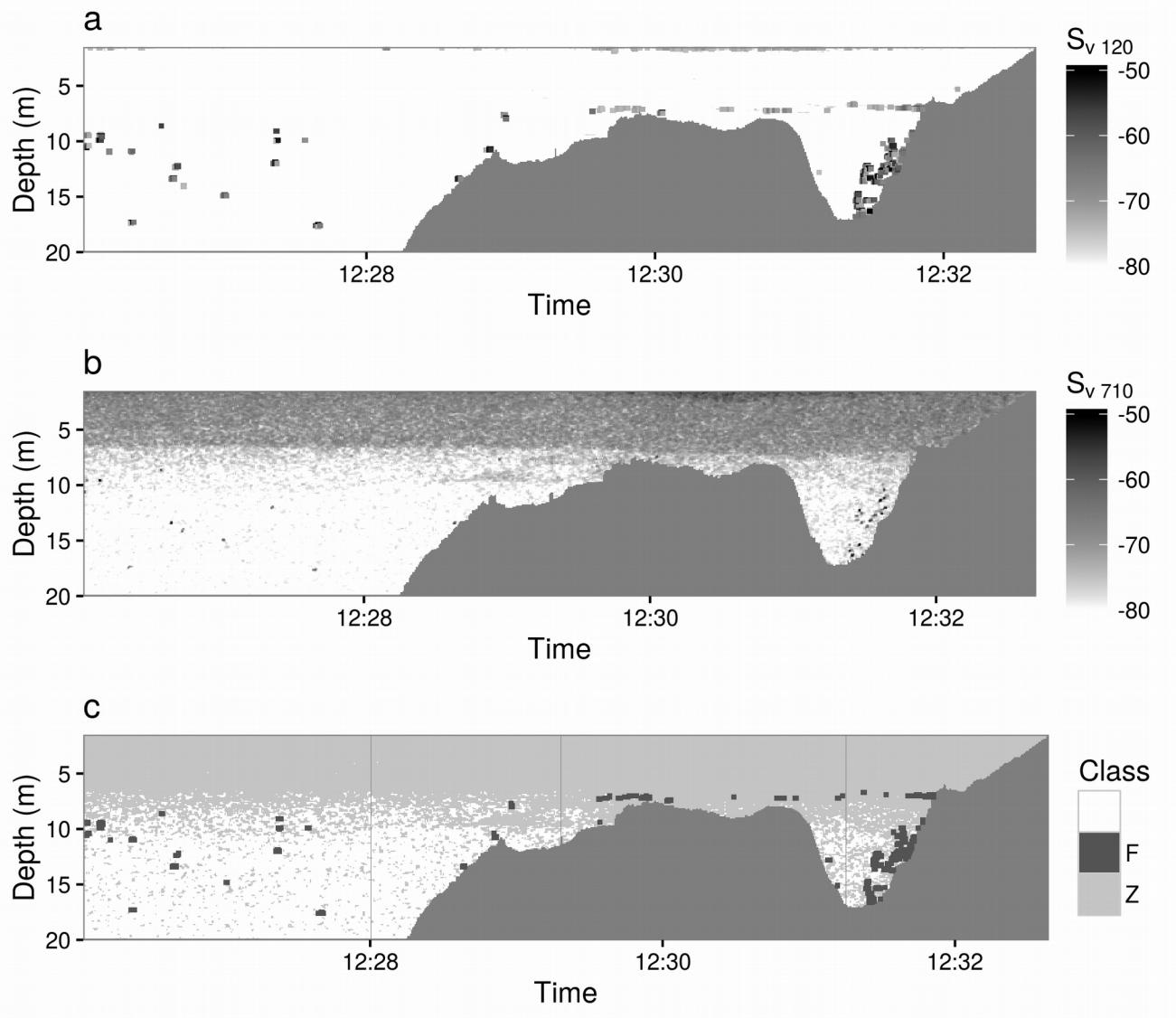
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715 **Figure 4.** Zooplankton abundance measured by nets and acoustics in each of four seasonal surveys.
 716 The color of each bar indicates the lake; note that Independence and Tahoe were only sampled in
 717 October 2013. (a) Biovolume of zooplankton caught in vertical net tows. These values are normalized
 718 by the volume of water filtered, giving units of mL of biovolume per cubic meter of lake water. (b)
 719 Wet-weight biomass of zooplankton per cubic meter, estimated from acoustic surveys, using measured
 720 zooplankton lengths and species identities to parameterize target strengths and length-weight
 721 relationships.



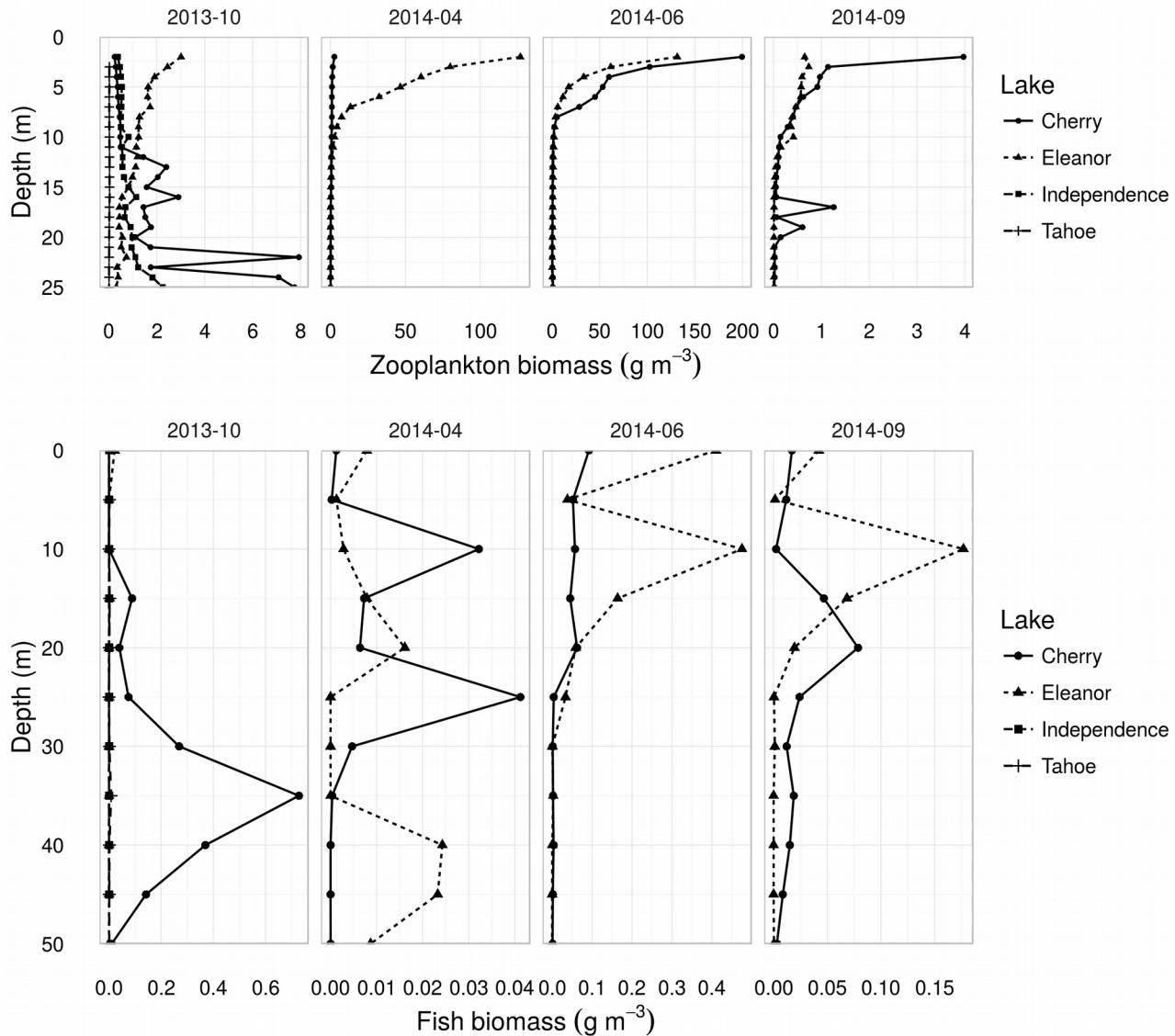
722

723 **Figure 5.** Acoustic profile through part of Cherry Lake on 24 June 2014, showing acoustic backscatter
 724 at (a) 120 kHz and (b) 710 kHz. Isolated dots are echoes from individual fish, while the layer of
 725 scattering between ~7 m and the surface represents echoes from zooplankton, which are only detectable
 726 at 710 kHz. (c) Classification of backscatter as fish (“F”) or zooplankton (“Z”) based on frequency
 727 differencing. Red areas are fish, scattering more strongly at 120 kHz, while blue area are zooplankton,
 728 scattering more strongly at 710 kHz. Pixels classified as fish have been dilated slightly in (a) and (c)
 729 for better visibility. White shows areas of empty water (volume backscatter < -80 dB at 710 kHz). The
 730 horizontal length of this section is approximately 700 m.



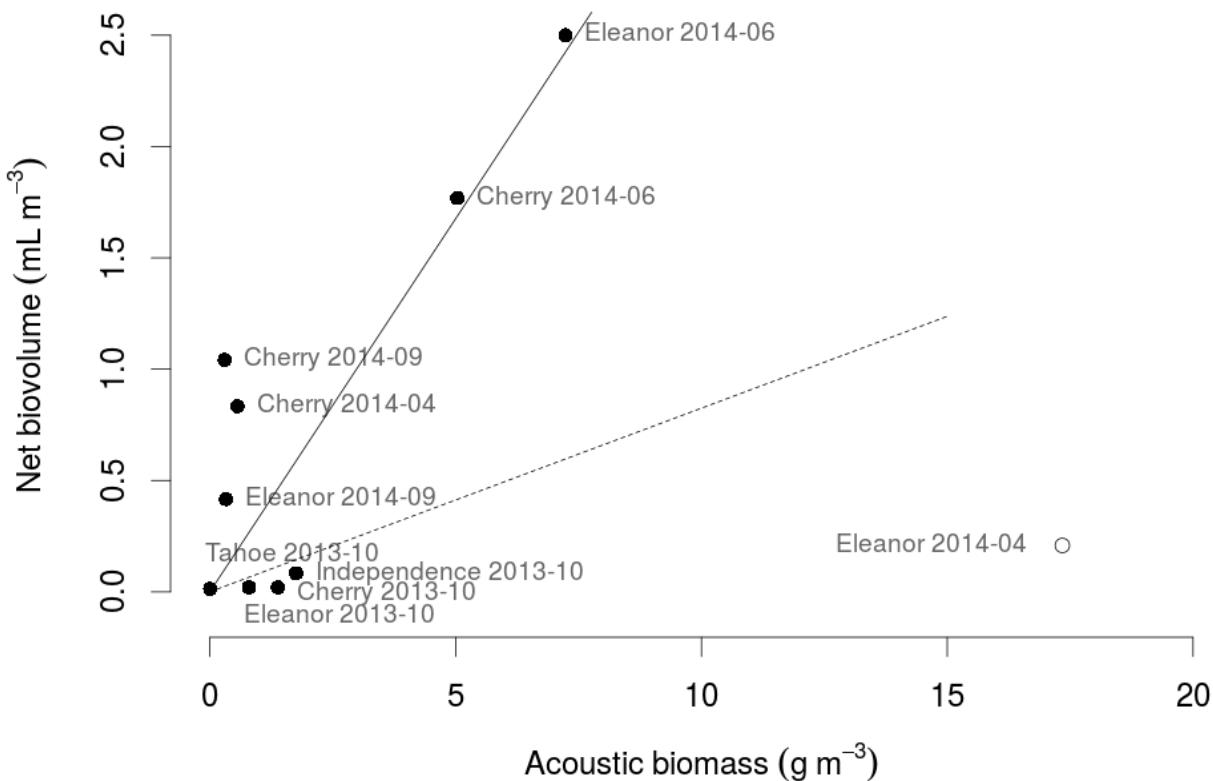
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732 **Figure 5 (Grayscale rendering for print publication)**



733

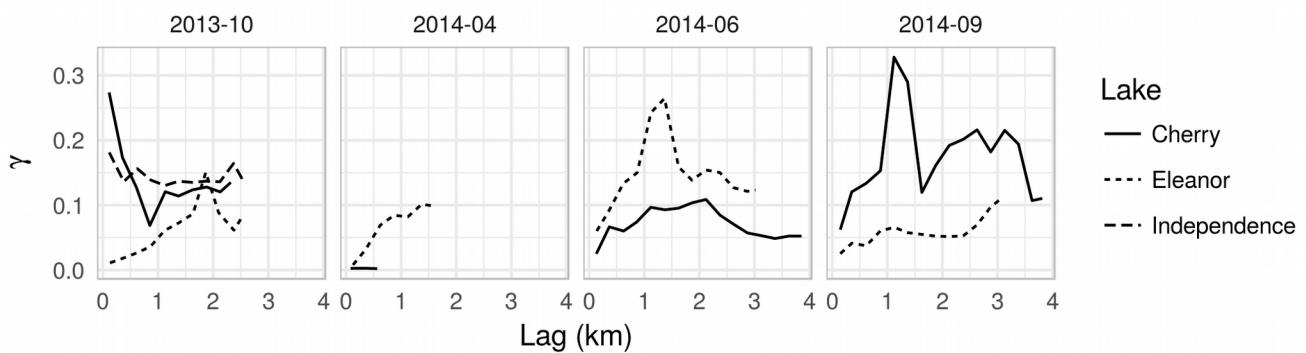
734 **Figure 6.** Depth profiles of zooplankton (top row) and fish (bottom row) wet weight biomass density
 735 measured acoustically in the lakes sampled during each of four seasonal surveys. (Lake Tahoe and
 736 Independence Lake were only sampled in October 2013). Lines show approximate biomass density of
 737 all zooplankton as a function of depth,. The target strengths used to calculate numerical densities from
 738 acoustic backscatter measurements were estimated using the distorted-wave Born approximations for
 739 the zooplankton communities, and measured in-situ for fish using a split-beam echosounder. Note
 740 differing x-axis scales in each plot.



741

742 **Figure 7.** Regression of biovolumes estimated from vertical net tows with acoustic estimates of wet
 743 weight biomass density. Data points are labeled with their lake and date. Two best-fit lines are plotted:
 744 the dashed line was fit to all data points, while the solid line excluded Lake Eleanor in April 2014,
 745 plotted as an empty point.

746



747

748 **Figure 8.** Empirical variograms of log-transformed zooplankton areal biomass density (i.e., mass of
 749 zooplankton per m^2 of lake surface) for each lake and survey.