

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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4   Running title: Zooplankton & fish in Sierra Nevada lakes

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18    **Summary**

19

- 20    1. We estimated the lake-wide biomass and vertical distribution of zooplankton and fish in four  
21    peri-alpine lakes in the Sierra Nevada Mountains of California, USA (Independence Lake, Lake  
22    Tahoe, Cherry Lake, and Lake Eleanor) using a dual-frequency echosounder. For zooplankton,  
23    we also quantified trends and patchiness in their horizontal distribution. In two of the lakes,  
24    Cherry and Eleanor, surveys were repeated four times at seasonal intervals between fall 2013  
25    and fall 2014.
- 26    2. Zooplankton were most abundant in these lakes in the spring and summer of 2014, with peak  
27    wet-weight biomasses estimated at 51 t in Lake Eleanor in April, and 110 t in Cherry Lake in  
28    June. The biomass and vertical distribution of fish also varied, increasing and moving  
29    shallower in the water column in June in both Cherry Lake and Lake Eleanor.
- 30    3. Zooplankton density was not horizontally homogeneous, displaying gradients at the lake basin  
31    scale (5-6 km), and nested patchiness at a range of smaller scales (0-2 km). This small-scale  
32    spatial variability is probably generated biologically, not physically. While it is well-known that  
33    the distribution of zooplankton is often patchy, this aspect of their ecology has not been  
34    quantified in most lakes, especially in remote montane locations.
- 35    4. These results illustrate how acoustic sampling can rapidly measure the biomass and spatial  
36    distribution of multiple trophic levels in small lakes. This capability provides unique  
37    opportunities to study the processes which generate and maintain gradients and patchiness in  
38    these components of the ecosystem.

39 **Introduction**

40 Zooplankton play a number of important roles in lake ecosystems. They influence water clarity  
41 and nutrient cycling through grazing on primary production. They are also the conduit through which  
42 primary production reaches larger predators such as fish, which often have commercial, recreational,  
43 and cultural importance for humans. In lakes at high elevations, the biomass of middle and upper  
44 trophic levels has been measured only rarely (McNaught *et al.*, 1999), in contrast with more common  
45 measurements of lower trophic level biomass (Pugnetti and Bettinetti, 1999; Higley *et al.*, 2001). The  
46 spatial distribution of that biomass within high-elevation lakes has been measured even more rarely  
47 (Masson *et al.*, 2001). Alpine and sub-alpine lakes differ in several important ways from low-elevation  
48 lakes. They typically have lower inputs of sediment and nutrients than lowland lakes, and are clearer  
49 and more oligotrophic. As a consequence, different environmental factors, such as ultraviolet radiation,  
50 may be more important in structuring their pelagic ecosystems (Rose *et al.* 2009). On average, lake  
51 size decreases with elevation, as does the duration of the effective growing season. These factors  
52 increase the potential for interactions between different habitats, and tend to increase food-related  
53 competition (Guisande *et al.*, 2003). Alpine and sub-alpine lakes may also be more sensitive to human  
54 disturbance, including eutrophication, pH changes, deforestation, and introductions of non-native plant  
55 and animal species (Bradford *et al.*, 1998; Knapp *et al.*, 2001; Schabetsberger *et al.*, 2009).

56 For the sake of simplicity, most models of food webs assume, explicitly or implicitly, that the  
57 spatial distributions of their component species can be ignored (Grünbaum, 2012). However, this is not  
58 always a valid assumption, since patchiness is common in nature (Pinel-Alloul, 1995; Pinel-Alloul and  
59 Ghadouani, 2007), and large fractions of total predation can occur in small patches over short  
60 timespans (Tessier, 1983; Temming *et al.*, 2007). Aquatic environments often feature sharp vertical  
61 gradients, both physical and biological, which strongly affect interactions between predators and prey,  
62 for instance through diel vertical migration (DVM). Horizontal heterogeneity in the distribution of  
63 organisms is driven by a variety of processes and may also mediate ecological interactions. Physical  
64 processes such as mixing, advection, and upwelling tend to dominate at larger scales (e.g. 10s of km  
65 and up), while biological processes such as migration, swarming, and predation assume more  
66 importance at smaller scales (Pinel-Alloul, 1995; Folt and Burns, 1999; Mackas *et al.*, 2005). While  
67 the potential importance of patchy distributions of zooplankton in lakes has been recognized fairly  
68 widely, only a few studies (e.g. Masson *et al.* 2001; Hembre and Megard 2003) have measured these  
69 distributions at high temporal or spatial resolutions.

70       The lack of high-resolution measurements of zooplankton is largely a consequence of sampling  
71 techniques. The most common methods for sampling zooplankton are net tows and traps. Even when  
72 closing nets are used for vertically stratified tows, spatial resolution is limited, and all nets and traps  
73 involve a degree of spatial or temporal blurring. Automated optical techniques (Finlay *et al.*,  
74 2007) have better spatial resolution than traps or nets, though observations are still limited to the  
75 instrument's towed path through the water, have small sampling volumes, and they lose taxonomic  
76 resolution relative to direct samples.

77       In contrast, active acoustics (i.e., scientific echosounders) can measure the density of animals  
78 through the water column quickly and at high (sub-meter) resolution. Acoustics are regularly used in  
79 lakes to survey fish (e.g. Brandt *et al.* 1991, Rudstam *et al.* 2009, Simonin *et al.* 2012), but have rarely  
80 been used for freshwater zooplankton, despite their long use in the marine environment (e.g., Holliday  
81 & Pieper, 1995; Parks *et al.*, 2012). This is chiefly because most lake zooplankton scatter sound very  
82 weakly at the acoustic frequencies used for fish surveys, with the notable example of some larger  
83 genera such as *Mysis* (Rudstam *et al.*, 2008) and *Macrohectopus* (Melnik *et al.*, 1993), and gas-bearing  
84 larvae of midges in the genus *Chaoborus* (Northcote, 1964; Teraguchi and Northcote, 1966). Only a  
85 few studies have used high-frequency (i.e. > 200 kHz) acoustics to measure the vertical or horizontal  
86 distribution of small (< 2 mm) zooplankton (Roman *et al.*, 2001; Hembre and Megard, 2003; Parks *et*  
87 *al.*, 2012). Likewise, few studies in lakes have examined the joint distribution of zooplankton with  
88 their fish predators at the same fine spatial scale (Pinel-Alloul *et al.*, 1999; Masson *et al.*, 2001).  
89 Acoustic methods are uniquely suited to address these questions, though they do have limitations.  
90 Most importantly, echoes give limited information on the identity of scattering organisms, so direct  
91 sampling is still necessary for identification and as ground-truth for acoustic density estimates.  
92 Acoustical techniques are a powerful tool for measuring the distribution of zooplankton, especially  
93 when higher frequencies enable the detection of small size classes or abundances of organisms (Warren  
94 *et al.*, 2016).

95       We surveyed the zooplankton and fish in four lakes in the Sierra Nevada mountains of  
96 California, USA, between autumn 2013 and autumn 2014: Cherry Lake, Lake Eleanor, Independence  
97 Lake, and Lake Tahoe. Cherry and Eleanor are similar in size and shape, and are less than 2 km apart  
98 from each other. Lake Tahoe and Independence Lake are located more than 100 km to the north, and  
99 are larger (Tahoe) and smaller (Independence) than Cherry and Eleanor. Our primary tool was a two-  
100 frequency acoustic system which allowed us to measure the vertical and horizontal distribution of these

101 animals at high (meter-scale) resolution. Acoustic observations were augmented with net samples to  
102 identify the zooplankton scatterers, measure their sizes, and parameterize models of their acoustic  
103 target strengths (TS). Fish TS were measured in situ. Zooplankton TS and fish TS values were used to  
104 convert acoustic backscatter to biomass, yielding estimates of total biomass of two trophic levels. The  
105 high-resolution nature of the acoustic data also let us compare the vertical profiles and horizontal trends  
106 of zooplankton and fish density among lakes. Changes in the distributions of zooplankton and fish  
107 from one season to another were also examined. Finally, we quantified the zooplankton's spatial  
108 variability across scales using empirical variograms. Spatially structured variance indicates a patchy  
109 distribution, which in turn would imply that the dominant ecological processes are spatially  
110 inhomogenous. Because Cherry Lake and Lake Eleanor are so similar, we expected that the spatial  
111 distributions of fish and zooplankton would not vary between these lakes, and that these communities  
112 would experience similar seasonal changes. And because Independence, Cherry, and Eleanor are all  
113 relatively small (< 5 km maximum extent) and located at similar elevations in similar landscapes, we  
114 hypothesized that the population dynamics of zooplankton within each lake would be synchronous, and  
115 their horizontal distributions homogeneous.

116

## 117 **Methods**

### 118 *Study lakes*

119 Surveys were conducted in four lakes in the Sierra Nevada: Cherry Lake, Lake Eleanor,  
120 Independence Lake, and Lake Tahoe (Figure 1). Our main focus was on Cherry Lake and Lake  
121 Eleanor, located at the border of Yosemite National Park near 38° 0' N, 119° 52.6' W (Figure 1). Both  
122 are reservoirs of the San Francisco Public Utilities Commission. Cherry Lake is artificial, created by  
123 the damming of Cherry Creek in 1955 (Hennesey, 2012). Lake Eleanor was formed naturally, but  
124 enlarged and deepened by the construction of a dam in 1918 (Eckart, 1940). Both lakes are  
125 approximately 1,420 m above sea level, placing them in the upper montane forest zone (Kaufman *et al.*,  
126 2007), though their catchments extend up through the subalpine zone and include large areas of bare  
127 rock above the treeline. Cherry lake has an area of 6.3 km<sup>2</sup> and a maximum depth of approximately 80  
128 m, while Lake Eleanor is slightly smaller at 3.9 km<sup>2</sup> and 68 m.. Both lakes have been stocked with fish,  
129 including rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), and, in Cherry Lake, eastern  
130 brook trout (*Salvelinus fontinalis*) (Bingaman, 1961; United States Forest Service, 2016). Cherry and  
131 Eleanor were surveyed in October 2013, April 2014, June 2014, and September 2014 (Figure 1). In

addition to our repeated surveys of Cherry and Eleanor, we surveyed Independence Lake, located at 39° 26.4' N, 120° 18.6' W, and Lake Tahoe, at 39° 10' N, 120° 0' W once each in October 2013. Independence is a natural lake, 2,127 m above sea level, 2.6 km<sup>2</sup> in area, and 45 m in depth. It has never been stocked with fish, and is one of only two lakes in the world with a self-sustaining population of Lahontan cutthroat trout, *Oncorhynchus clarkii henshawi* (Nielsen and Sage, 2002). Lake Tahoe, at 1,897 m elevation, is much larger and deeper than the other three lakes, with a surface area of 490 km<sup>2</sup> and maximum depth of 501 m. It is also oligotrophic, in contrast to the three smaller lakes, which are mesotrophic. The watersheds of the three smaller lakes are undeveloped, although portions of the Cherry and Eleanor Creek watersheds were burned during the 2013 Rim Fire (National Wildfire Coordinating Group, 2013). Lake Tahoe is bordered by several towns, with a total permanent population of approximately 50,000. All four watersheds are on granitic substrate.

143

#### 144 *Acoustic data collection*

Surveys were run from outboard-powered boats trailered to each lake. Because of the recent Rim Fire, camping was not permitted near Cherry Lake or Lake Eleanor, and the survey boats had to be towed in and out over 60 km of mountain roads, restricting our sampling to daylight hours. Acoustic volume backscatter was recorded at two frequencies, 120 and 710 kHz. Volume backscatter can be expressed either in logarithmic form as “mean volume backscattering strength”  $S_V$ , or a linear form as “volume backscattering coefficient,”  $s_V$  (with units of m<sup>-1</sup>), related by the equation  $S_V = 10\log_{10}(s_V)$  (MacLennan *et al.*, 2002). For sound-scattering objects of a given type and size, the volume backscattering coefficient is proportional to their numerical density in the water. The 120 kHz echosounder was a Simrad ES60 with a split-beam transducer (7° beam width), which can accurately measure the target strength of individual targets in situ. The 710 kHz echosounder was a Simrad EK60 with a single-beam (2.8° beam width) transducer. This high-frequency system could detect small (<1 mm) zooplankton (Holliday and Pieper, 1995; Warren *et al.*, 2016), but its effective range was limited to approximately 30 m due to sound attenuation in water. Both transducers were deployed on a pole mount off the side of the survey boat at depths of approximately 30-50 cm depending on wave conditions. Vessel survey speeds were approximately 2.5 m s<sup>-1</sup>. The echosounders generally transmitted once per second at of 500 W (120 kHz) and 100 W (710 kHz), with a 0.064 ms pulse length, though these setting were modified in some circumstances. In Lake Tahoe, the pulse length and 120 kHz power were increased to 0.256 ms and 1000 W to increase the penetration depth. The ping

163 rate was also decreased to 0.5 s<sup>-1</sup> at several points in the smaller lakes to mitigate interference due to  
164 multipath echoes and reverberation from the rocky lake bottom.

165       The 120 kHz system was calibrated in Lake Tahoe on 21 October 2013 with a 38.1 mm  
166 tungsten carbide standard target sphere (Foote *et al.*, 1987). Because of the 710 kHz transducer's  
167 narrow beam width, we were unable to center the sphere in the beam while in the field, and so  
168 performed an additional, ex-situ calibration for this instrument in a tank on land. A 166 L barrel, 80 cm  
169 deep and 50 cm across (Rubbermaid, Atlanta GA), was filled with fresh water and the transducer  
170 mounted at the barrel's center just below the water's surface. The calibration sphere could then be  
171 suspended in the center of the beam beyond the transducer's 40 cm near field.

172       Independence Lake was sampled on 20 October 2013, and Lake Tahoe was sampled on 21  
173 October 2013. Cherry Lake and Lake Eleanor were each sampled four times. Cherry was sampled on  
174 29 October 2013, and on 2 April, 24 June, and 10 September 2014. Eleanor was sampled one day later,  
175 on 30 October 2013, and 3 April, 25 June, and 11 September 2014. In the three smaller lakes, we  
176 attempted to perform a lengthwise transect from one end of the lake to the other. In Independence  
177 Lake, we were also able to add a series of zig-zag transects across the main axis of the lake (Figure 1).  
178 The April 2014 transects in Cherry and Eleanor were shorter due to snowfall, which required slow  
179 travel on the mountain roads and reduced the time available for sampling.

180

#### 181 *Direct sampling and target strength models*

182       Temperature profiles were measured from 0-50 m using a conductivity-temperature-depth  
183 (CTD) sensor in each lake and on each sampling date. Temperature in Independence Lake was  
184 measured with a YSI EXO (YSI Inc., Yellow Springs OH, USA), while temperature in all other lakes  
185 were measured using Sea-Bird CTD (Sea-Bird Electronics, Bellevue, WA, USA). A Sea-Bird model 19  
186 was used in September 2014, and a model 25 was used on all other trips. We used only data from the  
187 down-cast. After inspection for irregular data the temperature values for each lake and date were  
188 averaged into 1 m vertical bins.

189       Zooplankton were collected on each sampling day near the center of the lake with a vertical tow  
190 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  
191 equipment problem with the ring net during the October 2013 trip to Cherry and Eleanor, we instead  
192 used an open Van Dorn bottle (10 cm diameter) with an elastic nylon mesh (~100 µm) over one end.  
193 This was hauled vertically through the water column with its uncovered end up, acting like a small-

194 diameter net. Filtered volume was calculated as the depth of the cast multiplied by the cross-sectional  
195 area of the net mouth. Samples were preserved in 10% buffered formalin for later analysis. In the lab,  
196 the total biovolume of each sample was measured after allowing it to settle in a graduated cylinder.  
197 Because of the small diameter of the Van Dorn sampler, the biovolumes of the samples from Cherry  
198 and Eleanor in October 2013 were smaller than the finest graduation on our cylinder, preventing a  
199 precise measurement. We estimated them at 0.1 mL; our analyses did not appear sensitive to these  
200 estimates when they were in the range of 0-1 mL. A subsample of 200-300 animals was split from each  
201 original sample and counted under a compound microscope. Animals were identified to the lowest  
202 possible taxonomic level. In addition, the lengths of the first 30 animals counted were measured to the  
203 nearest 0.1 mm.

204 To convert acoustic backscatter to animal densities it is necessary to know the backscattering  
205 cross-section,  $\sigma_{BS}$  (in  $m^2$ ), of the scattering organisms. The backscattering cross-section is also  
206 expressed in logarithmic form in dB re  $1 m^2$ , as the target strength,  $TS = 10 \log_{10}(\sigma_{BS})$  (MacLennan *et*  
207 *al.*, 2002). We calculated these values using the stochastic distorted-wave born approximation  
208 (DWBA, Stanton *et al.* 1998, McGehee *et al.* 1998), implemented as a package, SDWBA.jl (Urmey,  
209 2016) in the Julia language (Bezanson *et al.*, 2012). This package uses models for the body shapes of  
210 cladocerans and calanoid copepods from Warren *et al.* (2016), and we assumed density and sound-  
211 speed contrasts of 1.04 (Stanton and Chu, 2000). For each lake, sampling date, and taxonomic group  
212 (i.e., cladocerans and copepods), we calculated the mean body length and its standard deviation (s.d.).  
213 We then drew 1000 random lengths from a normal distribution with these parameters (i.e., a parametric  
214 bootstrapping procedure, Efron and Tibshirani 1993). The generic body shape was scaled to each length  
215 and its backscattering cross-section ( $\sigma_{BS}$ ) calculated using the DWBA. We also calculated each body  
216 shape's dry weight,  $W_d$ , using a published regression for either calanoid nauplii, the calanoid  
217 *Diaptomus oregonensis*, or *Daphnia galeata* (Culver *et al.*, 1985). Dry weights were converted to wet  
218 weights,  $W_w$ , using a relationship from Wiebe *et al.* (1975).

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

$$222 \quad \langle \sigma_{BS,tot} \rangle = \sum_{i=1}^m p_i \langle \sigma_{BS,i} \rangle$$

$$223 \quad \langle W_{w,tot} \rangle = \sum_{i=1}^m p_i \langle W_{w,i} \rangle$$

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

228

229 *Acoustic data processing and analysis*

230 Acoustic data were processed using Echoview Software version 7.0 (Myriax Pty Ltd, 2016).  
231 Background noise was estimated and subtracted following De Robertis and Higginbottom (2007), using  
232 a 20 × 5 pixel averaging window (horizontal × vertical) with noise and SNR thresholds of -110 dB and  
233 10 dB. Data were manually scrutinized to correct bottom detection lines, exclude echoes from net and  
234 other instrument casts, and eliminate intermittent interference, such as multipath and sidelobe echoes  
235 from the steep rocky sides of the lake when close to shore. Data within 2 m of the surface and bottom  
236 were excluded to avoid integrating the transducers' ringdown, surface bubbles, or the near-bottom  
237 "dead zone." Acoustic data were integrated in bins 1 m deep and 10 m wide along-track and exported  
238 for further analysis.

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

246 Acoustic integration cells were classified as fish if their backscatter was higher at 120 kHz than  
247 at 710 kHz, since resonant scattering from fishes' swim bladders makes them stronger targets at the  
248 lower frequency. Based on the small sizes of the zooplankton, and the fact that they were all fluid-like  
249 scatterers, as opposed to gas-bearing ones such as *Chaoborus* (which were not present) the difference  
250 in their TS between 120 and 710 kHz was expected to be a robust criterion for classification. Because  
251 only 710 kHz data were available in Independence Lake, we used a different approach to eliminate fish  
252 backscatter, applying a top threshold to eliminate areas with  $S_v > -75$  dB re m<sup>-1</sup>. This value was  
253 determined iteratively by inspecting the echogram and histogram of  $S_v$  values and adjusting the  
254 threshold until all fish-like targets were excluded. Zooplankton backscatter at 710 kHz in each lake on

255 each sampling date was apportioned to copepods, cladocerans, and nauplius larvae using the  
256 proportional abundances in the net samples, and converted to numerical and biomass densities based on  
257 the representative values for the overall zooplankton community, as described above.

258 Fish densities were calculated from the integrated 120 kHz backscatter, using the mean TS of  
259 the individual fish targets to convert backscatter to fish densities. To obtain approximate estimates of  
260 fish biomass, we first converted each fish target's TS to a length (in cm). Because no specific TS-  
261 length relationships are available at 120 kHz for the salmonid species in these lakes, we used a generic  
262 relationship  $TS = 20 \log_{10}(L) - 67.4$  for physoclist fishes from Foote (1987). These lengths were  
263 then converted to approximate wet weights using published scaling relationships. Length-weight  
264 relationships for fish are usually assumed to follow a power law of the form  $\log_{10} W = a + b \log_{10} L$ ,  
265 where  $a$  and  $b$  are fitted empirically for a particular species or population. Because we could not  
266 identify fish targets to species, we averaged the parameters for rainbow trout ( $a = -4.898$ ,  $b = 2.99$ ,  
267 Simpkins and Hubert 1996), brook trout ( $a = -5.186$ ,  $b = 3.103$ , Hyatt and Hubert 2001), and brown  
268 trout ( $a = -4.867$ ,  $b = 2.96$ , Milewski and Brown 1994) to get a single length-weight equation with  $a =$   
269  $-4.98$  and  $b = 3.02$ . These lengths and weights were averaged into mean values for each lake and  
270 survey. All biomasses reported in this study are wet-weight.

271 Zooplankton and fish biomass densities were averaged across the survey track to create depth  
272 profiles of zooplankton and fish density. Additionally, they were integrated through the water column  
273 and multiplied by each lake's area to give estimates of the total biomass of fish and zooplankton in each  
274 lake and survey. This was not done in Lake Tahoe, since we felt such an extrapolation was suspect  
275 given the patchiness of the fish and the small extent of the survey relative to the lake. We also  
276 calculated the ratio of zooplankton biomass to fish biomass in each lake and survey.  
277

#### 278 *Comparison of net and acoustic biomass*

279 To test the agreement between acoustic estimates of zooplankton biomass and the direct net  
280 sampling, we regressed average acoustic biomass density within 25 m or 10 minutes of each net cast  
281 (whichever was less) on the biovolume from the net. These limits ensured the acoustic data used in the  
282 regression were close both in space and time to the net haul. Net biovolumes were normalized by the  
283 total volume of water filtered to give a biovolume density, in  $\text{mL m}^{-3}$ . The intercept in the linear  
284 regression was fixed at the origin, since a preliminary model showed it was not significantly different  
285 from zero (at the  $p=0.05$  level), and because it is physically reasonable. Fitting the model without an

intercept also added a degree of freedom, increasing power and precision for the slope estimate, which was advantageous given the small sample size ( $n=9$ ). When examining preliminary results, one data point (from Lake Eleanor in April 2014) appeared to be an outlier exerting undue influence on the slope, so we also fit the model without this point for comparison. The significance of the slopes was assessed at the  $p=0.05$  level. Several assumptions of the significance test are questionable in this case. The errors may not be homoskedastic, so the resulting  $p$ -values must be interpreted with caution. In addition, the independent variable, acoustic biomass, is itself measured with (unknown) error. To address the latter concern, we also conducted a geometric mean regression (Ricker, 1973). These analyses were run using R (R Development Core Team, 2016).

295

#### 296 *Distribution of zooplankton and fish*

Vertical profiles of fish and zooplankton density were constructed for each lake and date by averaging values horizontally within each depth bin. We also investigated horizontal spatial trends and patchiness of zooplankton by averaging their densities vertically through the water column. The densities in this horizontal dataset were  $\log_{10}$ -transformed, then regressed on their distances from the shoreline and from each lake's main stream inlet. This was done to test whether there were any spatial trends in the density of zooplankton. Spatial autocorrelation was assessed by calculating empirical variograms for the residuals of each regression. Two key features of a variogram are its *sill* and *range*. The sill is the variogram's maximum value, indicating the expected absolute differences between biomass densities at widely separated locations. The range is the spatial lag at which the variogram reaches its sill, and characterizes the decorrelation distance. Because we calculated the variograms for  $\log_{10}$ -transformed units, they imply multiplicative differences ( $\times/\div$ ) in zooplankton density in the linear domain. Variograms were calculated at spatial lags from zero to half the distance spanned by the transect in each lake, in bins 0.25 km wide. Lake Tahoe was omitted from these spatial analyses, because it is much larger and fed by many small streams at inlets around its perimeter, and because the sampling schedule did not permit extended transects.

312

### 313 **Results**

The zooplankton communities of the four lakes differed, both among lakes and, in the case of the repeated samples at Cherry and Eleanor, through time. Lake Tahoe's zooplankton were numerically dominated by the calanoid copepods *Leptodiaptomus tyrelli* (56%) and *Epischura nevadensis* (22%),

317 with another 20% made up by unidentified copepods and copepodites (Table 1). The zooplankton in  
318 Independence Lake were split more evenly between the cyclopoid copepod *Diacyclops thomasi* (48%)  
319 and the cladoceran *Daphnia middendorffiana* (46%), with the remainder composed of *Bosmina*  
320 *longirostris* (6%).

321 Over the four sampling dates, more zooplankton species were recorded in Cherry Lake and  
322 Lake Eleanor than in the single surveys in Independence and Tahoe (Table 1). In October 2013, the  
323 communities in both lakes were 50-60% cladocerans in the genera *Daphnia* and *Diplostraca*, with the  
324 remainder mostly composed of cyclopoid copepods in the genus *Euryyclops*. The following April,  
325 the community in Cherry Lake had similar proportions of cladocerans and copepods (though the former  
326 shifted from mostly *Diplostraca* to *Holopedium*), but in Lake Eleanor it had shifted to 59% Copepods,  
327 mostly *Epischura nevadensis*. During the final two surveys, in June and September 2014, the  
328 communities in both lakes were between 70 and 85% copepods, a large proportion of which were  
329 copepodites of unknown calanoid species. The cladocerans, which composed 15-32% of the  
330 communities in June and September 2014, were again a mix of *Daphnia*, *Pseudorida*, and unidentified  
331 species (Table 1). Biovolumes of zooplankton estimated from the nets ranged from 0.1 mL m<sup>-3</sup> in Lake  
332 Tahoe to 2.5 mL m<sup>-3</sup> in Lake Eleanor in June 2014 (Figure 2). Biovolumes in both Cherry Lake and  
333 Lake Eleanor were highest in June 2014 and lower in the other months.

334 Target strengths for the different classes of zooplankton scatterers calculated using the DWBA  
335 varied widely (Table 2). The strongest scatterers were copepods in Cherry Lake in April 2014, with an  
336 average TS of -111 dB. The weakest were nauplius larvae in Cherry Lake in October 2013, with a  
337 mean TS of -148 dB. Cladoceran target strengths fell between -113 and -127 dB. Adult copepod target  
338 strengths fell in the same broad range, from -104 to -128 dB. Nauplii, due to their much smaller size,  
339 were predicted to scatter much less sound, with their mean TS falling between -120 and -148 dB (Table  
340 2). After averaging across all scattering classes, overall mean TS ranged from -125 dB, in Cherry Lake  
341 in September 2014, to -105 dB, in Lake Tahoe in October 2013 (Table 2). There were no systematic  
342 trends in TS between the lakes, or through time.

343 Mean fish target strengths, measured in situ, ranged between -40 and -36 dB re m<sup>2</sup>,  
344 corresponding to mean lengths from 21 to 31 cm, and mean weights from 200 to 720 g (Table 3). In  
345 October 2013, the mean TS (and the mean lengths and weights derived from them) were roughly equal  
346 in Lake Eleanor and Lake Tahoe and slightly higher in Cherry Lake. In the following three surveys,  
347 however, mean TS was 1-3 dB higher in Lake Eleanor, with corresponding length and weight

348 differences of 20-80 mm and 140-380 g.

349 Water column stratification varied between lakes and over the four sampling dates. In October  
350 2013, all four lakes had surface mixed layers between 10 and 15 °C, with Cherry Lake the warmest and  
351 Independence lake the coolest (Figure 4). The mixed layer was shallowest in Lake Eleanor  
352 (approximately 8 m) and deepest in Lake Tahoe (27 m). In April 2014, both Cherry and Eleanor were  
353 vertically mixed with temperatures between 5 and 10 °C. By June, thermoclines had been reestablished  
354 in both lakes, starting around 6 m depth, though the thermocline in Lake Eleanor was sharper and the  
355 water was 2-3 °C cooler at depth than in Cherry Lake. At the end of the summer in September 2014,  
356 the temperature profile in Eleanor was similar to that in June, while in Cherry Lake the surface mixed  
357 layer was 3 m deeper and the thermocline was better defined.

358 The 710 kHz echosounder was able to detect small zooplankton in the lakes, and the frequency-  
359 differencing procedure could clearly separate them from fish echoes (Figure 3). Mean zooplankton  
360 wet-weight biomass densities measured acoustically were relatively low (< 10 g m<sup>-3</sup>) in all lakes, and  
361 varied seasonally (Figure 2). In October 2013, the mean zooplankton numerical density in all four  
362 lakes was low, with less than 5 g of zooplankton wet-weight biomass m<sup>-3</sup> (Figure 2). Lake Eleanor had  
363 a weak scattering layer extending from the surface to 15 m, corresponding to an estimated peak  
364 zooplankton biomass density of just over 4 g m<sup>-3</sup> (Figure 5). In April 2014, Cherry Lake contained  
365 zooplankton at similarly low densities, but Lake Eleanor had a denser zooplankton layer near the  
366 surface, increasing from near-zero density at 10 m depth to a maximum of 125 g m<sup>-3</sup> at 2 m depth, the  
367 bottom of the echosounder's blind zone (Figure 5). Two months later in June, this layer was still  
368 present, though not quite as deep as in April. During this time, a similar layer had also appeared in  
369 Cherry Lake, with a maximum density of 200 g m<sup>-3</sup> at 2 m depth (Figure 5). By September, the surface  
370 zooplankton layer in Lake Eleanor had mostly disappeared. The layer in Cherry Lake was much less  
371 dense (maximum 4 g m<sup>-3</sup>, Figure 5).

372 Peak fish densities in the lakes ranged between 0.007 and 1.6 fish per 1000 m<sup>-3</sup>, corresponding  
373 to biomass densities of 0.04 to 0.7 g m<sup>-3</sup> (Figure 5). These fish were mostly found below the  
374 zooplankton layers (Figure 5). In the first surveys in October 2013, fish in Cherry Lake were  
375 concentrated in a layer centered at 35 m depth, with much higher densities than the other three lakes  
376 (Figure 5). The overall mean fish density in October in Cherry Lake was 1.6 per 1000 m<sup>-3</sup>, compared to  
377 0.007 in Lake Eleanor. The next April, the depth distribution of fish in both lakes was bimodal,  
378 grouped in two layers at depths of 10 and 25 m in Cherry Lake, and deeper at 20 and 40 m in Lake

379 Eleanor (Figure 5). In June, fish in both lakes were concentrated in the upper 10-15 m and were more  
380 abundant overall than in April, with mean densities of 0.3 (Cherry) and 0.5 (Eleanor) fish per 1000 m<sup>-3</sup>,  
381 corresponding to biomass densities of 0.014 and 0.015 g m<sup>-3</sup>. In September, the fish in each lake were  
382 in one broad layer, between 5 to 20 m depth in Lake Eleanor and from 10 to 30 m in Cherry Lake.  
383 Overall densities were lower than in June, at 0.2 fish per 1000 m<sup>-3</sup> in Cherry Lake and 0.1 fish per 1000  
384 m<sup>-3</sup> in Lake Eleanor, giving biomass densities of 0.043 and 0.054 g m<sup>-3</sup>.

385 When depth-integrated and scaled by their respective lake areas, these densities yielded a wide  
386 range of estimates for the total biomasses of these trophic levels in the different lakes. In October  
387 2013, Lake Tahoe contained an estimated 7,500 kg of small zooplankton. Zooplankton in the three  
388 smaller lakes were 60-240 times denser than in Tahoe, but their much smaller areas led to total biomass  
389 estimates on the same order of magnitude as Tahoe's (Table 4). In April 2014, the zooplankton wet-  
390 weight biomass density in Lake Eleanor had increased to 13 g m<sup>-3</sup>, raising its total biomass estimate to  
391 over 51,000 kg, higher than that of Lake Tahoe in October 2013. Total zooplankton biomass in Cherry  
392 Lake in April was 3,300 kg, 14% of its level in the October survey. By June, however, it had increased  
393 to 110,000 kg, while the zooplankton biomass in Eleanor dropped to 31,000 kg. During the September  
394 2014 survey, zooplankton populations in both lakes had dropped back to lower levels (Table 4).

395 Estimates for total fish biomass were much lower than those for zooplankton. The highest  
396 estimate was 1,700 kg in Cherry Lake, in October 2013. Fish biomass in Cherry Lake and Lake  
397 Eleanor was lowest the following April, increasing somewhat in the following two surveys in June and  
398 September. Fish biomass did not vary as widely as zooplankton biomass. In all surveys, zooplankton  
399 outweighed fish by a factor between 3 and 850.

400 Net and acoustic estimates of zooplankton density were positively related (Figure 6). The  
401 regression of net-caught zooplankton biovolume on acoustically-estimated biomass was not statistically  
402 significant when all data points were included ( $p=0.1$ ,  $R^2=0.19$ ), though the fitted slope was positive.  
403 When the outlying measurement from Lake Eleanor in April 2014 was excluded, the fitted slope was  
404 significantly different from zero, with a fitted value of 0.85 mL g<sup>-1</sup>, and a 95% confidence interval from  
405 0.46 to 1.2 mL g<sup>-1</sup>. This model fit the data fairly well, with an adjusted  $R^2$  of 0.76. The slope from the  
406 geometric mean regression, 0.96 mL g<sup>-1</sup>, was not significantly different from that obtained with the  
407 standard regression.

408 Zooplankton biomass density displayed significant trends with respect to distance from the inlet  
409 and shore in most surveys, though the directions of these trends were variable (Table 5). The most

410 pronounced trend was in Cherry Lake in June 2014, where zooplankton biomass density was an order  
411 of magnitude higher near the lake's inlet than near the dam at the other end. In eight out of the nine  
412 surveys, the signs of the coefficients for distance from shore and distance from the inlet were the same.  
413 The single survey in Independence Lake was the exception, with biomass density increasing closer to  
414 the inlet and decreasing closer to shore. In three of the four surveys in Cherry Lake, zooplankton  
415 density increased towards the shore and inlet. In Lake Eleanor, the reverse was true: three out of four  
416 surveys showed zooplankton density higher away from shore and the inlet (Table 5). These spatial  
417 regressions explained a low-to-moderate amount of the variability in the data, with  $R^2$  values ranging  
418 from approximately zero in Lake Eleanor in October 2013, to 0.73 in Cherry Lake in June 2014 (Table  
419 5).

420 The residuals from these regressions were spatially autocorrelated in some, but not all, lakes  
421 and surveys. In October 2013, when biomass densities in all lakes were low, Lake Eleanor's variogram  
422 reached its sill of 0.1 at a range of about 2 km. Independence Lake's variogram was flat, showing little  
423 evidence for spatial autocorrelation, and in Cherry Lake, the variogram was higher at shorter lags,  
424 suggesting short-range anticorrelation (Figure 7). In April, Lake Eleanor's variogram was similar,  
425 with a sill of around 0.1 at a range of 1.5 km. Back-transformed to linear units, this implies an  
426 expected difference in biomass on the order of 25% across distances of 500 m or greater. The short  
427 transect in Cherry Lake in April limited the spatial information available for that variogram.

428 In June, the sill of the variogram in Lake Eleanor had increased to 0.15 at a range of 2 km  
429 (Figure 7), implying an expected difference in biomass on the order of 50% when transformed back to  
430 linear units. In Cherry Lake, the variogram was relatively flat (Figure 7), showing little evidence for  
431 spatial structure other than the lakewide trends described above. Spatial variability in Lake Eleanor  
432 decreased somewhat between June and September 2014. However, the variogram for Cherry Lake in  
433 the final survey showed higher overall variability, peaking at 0.37 at a lag of 1 km and a sill near 0.2  
434 beyond 1.5 km. Overall, the variogram sill values ranged from approximately 0.1 to 0.2. These  
435 values, in  $\log_{10}$ -transformed units, imply multiplicative differences ( $\times/\div$ ) in zooplankton density from  
436 0.25 to 1.6 at long ranges, where "long ranges," as defined by the variograms, are between 1 and 2 km.  
437

### 438 **Discussion**

439 Our acoustic measurements produced estimates of the total biomass of zooplankton and fish in  
440 four peri-alpine lakes in the Sierra Nevada Mountains. To our knowledge, these are the first biomass

441 estimates (for any trophic level) ever made in Independence Lake, Cherry Lake, and Lake Eleanor. In  
442 Lake Tahoe, our estimate of the mean density of small zooplankton (approximately 2,200 individuals  
443  $\text{m}^{-3}$ ) fell within the range of prior estimates (e.g. 0-23,000 individuals  $\text{m}^{-3}$ , Goldman et al. 1979). The  
444 measurements in Independence Lake and Lake Tahoe represent only a single snapshot of the  
445 zooplankton and fish in each lake, and should not be over-interpreted. The repeated sampling in  
446 Cherry Lake and Lake Eleanor did allow us to capture some of their seasonal variability.

447 A spring bloom of zooplankton occurred in both Cherry Lake and Lake Eleanor, with peak  
448 biomass densities of 4-6 g  $\text{m}^{-3}$ . In spring and summer, the zooplankton were concentrated in the upper  
449 5-10 m of the water column, closely associated with the stratified surface layer. In 2014, the bloom  
450 appeared to begin earlier in Lake Eleanor than in Cherry Lake, since a near-surface zooplankton layer  
451 was present in Eleanor, but not Cherry, during the early April survey. In fact, the surface zooplankton  
452 layer in Lake Eleanor was present before the lake's surface waters warmed and stratified. By June, both  
453 lakes had similar zooplankton densities, and by September, zooplankton populations in both lakes had  
454 declined by an order of magnitude. At this point there were still more zooplankton in Cherry Lake,  
455 however, suggesting that the bloom there, which started later, also took longer to collapse in the fall.  
456 This pattern, of a spring and summer increase in zooplankton as they respond to blooming  
457 phytoplankton, is consistent with standard models of seasonal cycles in lake ecosystems (Sommer *et*  
458 *al.*, 1986, 2012). While the seasonal changes in Cherry Lake and Lake Eleanor were similar there were  
459 also distinct differences, both in the vertical distribution of fish and zooplankton, and the timing of  
460 seasonal blooms. These differences were greater than expected given the apparent similarities between  
461 the sizes, depths, and catchments of the two lakes. Though both lakes had near-identical surface  
462 temperatures, Lake Eleanor was cooler at depth and more strongly stratified. This difference may have  
463 affected primary and secondary production, perhaps accounting for some of the differences seen in  
464 zooplankton biomass and distribution.

465 Fish biomass did not vary nearly as widely as zooplankton biomass, which is expected given  
466 their much longer life spans and generation times. At the height of the zooplankton blooms,  
467 zooplankton biomass was several hundred times that of fish, indicating that the former were effectively  
468 released from predatory control at those times. In both autumns, the zooplankton:fish ratios were much  
469 lower, suggesting a closer match between rates of zooplankton reproduction and fish predation. While  
470 fish were scarce in Lake Eleanor in October 2013, our estimate of total biomass (7 kg, Table 4) is  
471 probably extreme, reflecting error due to the patchy distribution of fish and our limited survey time as

472 much as the true biomass. While zooplankton were found mostly in the surface mixed layer, the fish  
473 (at least during our daytime sampling) were found in and below the thermocline, reflecting either light-  
474 driven DVM or a preferred thermal niche.

475 Our seasonal sampling interval may have caused us to miss shorter-scale variability in  
476 zooplankton populations, due either to sub-seasonal population dynamics, or responses to  
477 environmental forcings such as runoff from rainstorms or mixing of the water column by wind. This  
478 study also only covers one year, leaving longer-term trends unknown. Two longer-term environmental  
479 changes under way during this study deserve mention, though their effects are unclear. The first was  
480 the Rim Wildfire, which started approximately 20 km southwest of Cherry Lake and Lake Eleanor on  
481 17 August 2013, burned portions of both lakes' watersheds, and was not fully contained until several  
482 days after the first surveys in October 2013 (National Wildfire Coordinating Group, 2013). The second  
483 was a five-year drought (2012-2017) in the western United States. Fires can have a number of effects  
484 on lakes and the animals in them, for instance by increasing runoff from burned watersheds, depositing  
485 ash from the air, or altering the characteristics of incident solar radiation via drifting smoke plumes  
486 (Urmy *et al.*, 2016; Williamson *et al.*, 2016), though their effects on a lake's zooplankton are not  
487 necessarily large (Patoine *et al.*, 2002). While the drought probably contributed to the fire's severity, it  
488 may have actually mitigated some of the fire's effects on Cherry and Eleanor: precipitation during the  
489 winter of 2013-2014 was well below normal (California Department of Water Resources, 2014),  
490 meaning that runoff and erosion in the burned areas were much less than they might have been in a  
491 more normal year. The drought also led the San Francisco Public Utilities Commission to draw down  
492 water levels in Cherry and Eleanor nearly 8 m between October 2013 and September 2014. Both the  
493 drought and fire are likely to have affected the lakes, but the limited sampling schedule makes it  
494 impossible to separate these effects from the expected seasonal cycle for a temperate lake.  
495

496 Fish target strengths, and the corresponding estimated lengths, were in the expected range for  
497 lake salmonids. The vertical distribution of fish in Cherry Lake and Lake Eleanor was qualitatively  
498 similar in every survey but the first, suggesting similar dynamics in the fish community of both lakes.  
499 These dynamics cannot be determined from the limited information available in this study, but the  
500 similar vertical patterns of fish density, offset in some cases by up to 10 m, suggest that Cherry Lake  
501 and Lake Eleanor could be an interesting setting for further comparative studies of fish behavior. The  
502 vertical distributions of fish and zooplankton did not coincide except in June 2014, though this is not

503 particularly surprising, since our surveys occurred during the daytime and many fish migrate vertically.  
504 The lack of overlap emphasizes that interactions between predators and prey are not evenly distributed,  
505 and may be restricted to certain locations or times of day (Beauchamp *et al.*, 1999; Temming *et al.*,  
506 2007; Lørke *et al.*, 2008).

507 There was good agreement between the acoustic and net-based estimates of zooplankton  
508 biomass. However, the data from Lake Eleanor in April 2014 formed a notable outlier, with the net-  
509 based biovolume much lower relative to the acoustic biomass than expected, based on the other  
510 samples. That day, a relatively strong scattering layer was visible near the surface along the entire  
511 survey track. This layer, along with weaker-than-average zooplankton TS (Table 2), accounted for the  
512 high acoustic biomass estimate. The small biovolume estimate is accurate, at least based on the net  
513 sample (0.5 mL of zooplankton from a total filtered volume of 15 m<sup>3</sup>). The discrepancy between these  
514 two measures is probably due to some combination of random variability in the net sample and  
515 uncertainty in our TS estimates. Regardless, regressions with and without this outlier produced  
516 positive slopes. Without it, the slope was significantly different from zero with a value of 0.85 mL g<sup>-1</sup>.  
517 Wiebe *et al.* (1975) found that displacement biovolume *DV* and wet weight *WW* of marine zooplankton  
518 were related by the equation  $\log_{10}(DV) = 0.078 + 1.026 \log_{10}(WW)$  which, in linear terms, implies a  
519 slope of approximately 1.2 mL g<sup>-1</sup>, within the 95% confidence limits of our estimate. The spatial extent  
520 of our net sampling was quite limited compared with that of the acoustics, so these results should thus  
521 be interpreted with some caution. However, our procedures do produce realistic biomass values, with  
522 agreement between nets and acoustics, increasing our confidence that the patterns observed are  
523 biologically meaningful.

524 We did not calculate confidence intervals on our acoustic biomass estimates because the  
525 conversion process from acoustic backscatter to biovolume includes multiple sources of uncertainty,  
526 from the material properties of the scatterers to geostatistical error. Assessing their (nonlinear)  
527 cumulative effect would entail additional assumptions and conditional simulations, which we felt went  
528 beyond the scope of this paper. Previous studies of uncertainty in acoustic surveys have found that  
529 measurement errors (i.e., due to calibration, target strength uncertainty, length-weight conversion, etc.)  
530 are typically minor compared with errors due to limited sampling of heterogeneously distributed  
531 animals. In these studies total error, expressed as a coefficient of variation with respect to the estimated  
532 biomass, ranged from ~10-170% (Demer, 2004; Rose, Gauthier, & Lawson, 2000). If confidence  
533 intervals are required (e.g., if biomass estimates are to be used in management decisions), procedures

534 exist to calculate them (Demer, 2004; Simmonds and MacLennan, 2005).

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

546 Even after subtracting the lake-scale trend in zooplankton density, spatial autocorrelation was  
547 evident in the residuals, as illustrated by the empirical variograms (Figure 7). These should be  
548 interpreted with caution, since they were based in most cases on single reciprocal transects down the  
549 main axis of each lake which may not have captured any spatial anisotropy present. In particular, the  
550 restricted time available to survey Cherry Lake on 2 April 2013 meant that the transect was only about  
551 1 km long, limiting our ability to draw conclusions about the spatial distribution of zooplankton.  
552 Regardless, most of the variograms in Cherry Lake and Lake Eleanor did show evidence of spatial  
553 patchiness in the distribution of zooplankton, with approximate spatial scales, based on the variogram  
554 ranges, between 500 and 2000 m. These ranges are well below the sizes of the lake basins, suggesting  
555 that ecological processes in these lakes are not spatially uniform.

556 This result was somewhat unexpected given the relatively small sizes of Independence, Cherry,  
557 and Eleanor. It is unknown what processes generate and maintain patchiness in these lakes. In the  
558 ocean, patchiness in zooplankton appears to be driven mostly by bottom-up processes, with scales of  
559 biological variability mirroring scales of physical variability (Denman *et al.*, 1977; Mackas *et al.*, 1985;  
560 Urmy *et al.*, 2012). At smaller scales, animal behavior and ecological interactions become more  
561 important in generating spatial variability (Pinel-Alloul, 1995; Folt and Burns, 1999), though these  
562 scales and processes are harder to observe and have been studied less in the field. It seems unlikely  
563 that these lakes (with the possible exception of Tahoe) are large enough to support horizontal physical  
564 structures larger than internal waves or wind-driven Langmuir circulations on the scale of 10s of m, so

565 the km-scale patchiness in the zooplankton is probably due to other processes, such as aggregation  
566 (e.g., Byron et al. 1983) or local predation by schooling fish. In this interpretation, the lake's finite  
567 boundaries act like a high-pass filter, preventing large-scale physical processes (e.g. fronts, gyres,  
568 nutrient upwelling) from creating spatial variability that masks patchiness due to smaller-scale,  
569 biological processes (swarming, predator-prey interactions, etc.). If this interpretation is correct, future  
570 studies could use appropriately-sized lakes as model systems to study biogenic patchiness free of  
571 interference from larger-scale processes.

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

587 Despite these uncertainties, acoustic methods for surveying zooplankton have several  
588 compelling advantages. Acoustic methods provide high-resolution vertical profiles of fish and  
589 zooplankton densities, offering insights into the biotic and abiotic processes structuring lake  
590 ecosystems (Beauchamp *et al.*, 1999; Urmey *et al.*, 2016). Acoustics are also an excellent method for  
591 recording the diel vertical migration of lake zooplankton (Warren *et al.*, 2016). Although DVM was  
592 not part of this study, it would be a worthwhile topic for further investigation in these lakes. Acoustics  
593 can also reveal trends in the distribution of zooplankton that would be missed by traditional sampling  
594 methods (Pinel-Alloul *et al.*, 1999; Hembre and Megard, 2003). In this case, these included trends in  
595 zooplankton biomass density with distance from shore or from the stream inlet. Accounting for spatial

596 trends and patchiness in turn reduces uncertainty in the biomass estimates.

597       Perhaps most importantly, multi-frequency echosounders allow the biomass of multiple trophic  
598 levels to be measured efficiently, and at the same spatial resolution, providing valuable data for  
599 ecosystem based management decisions (Slocombe, 1985; Allan and Johnson, 1997; Link, 2002). In a  
600 relatively small lake such as Cherry, Eleanor, or Independence, the ability to survey large volumes of  
601 water quickly means that a virtual census of the lake's fauna is feasible. The time available for our  
602 acoustic surveys was somewhat constrained by the need to collect other optical, chemical, and  
603 biological data not reported in this study, as well as the time required to trailer the boat to each lake.  
604 However, we were still able to run full-length transects of the lakes in most of the surveys, and with  
605 just a few more hours it would be possible to survey the lakes quite thoroughly, producing detailed  
606 three-dimensional maps of the distribution of fish and zooplankton as well as accurate estimates of  
607 their numbers and biomass. As this study demonstrates, such a goal is achievable and offers an  
608 exciting prospect for studies of predator-prey interactions and lake food webs.

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840 **Table 1.** Numerical composition (%) of the crustacean zooplankton community in Cherry Lake, Lake  
 841 Eleanor, Independence Lake, and Lake Tahoe varied seasonally and between the lakes.  
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 843  
 844

Lake	Group	Genus	% Composition			
			2013-10	2014-04	2014-06	2014-09
Cherry	Cladocerans	<i>Bosmina</i>	10.9	0	0	0
		<i>Daphnia</i>	4.9	15.7	17.7	29.7
		<i>Diaphansoma</i>	0	2.2	0	0
		<i>Diplostraca</i>	42.9	0	0	0
		<i>Holopedium</i>	0	33.6	0	0
		<i>Pseudororida</i>	0	0	0	0
		Unk. Cladoceran	0	7.5	12.2	2
	Copepods	<i>Epischura</i>	1.6	1.5	57.5	3.4
		<i>Euryclops</i>	22.8	14.9	0	4.1
		<i>Eurytemora</i>	2.2	0	0	4.1
		<i>Leptodiaptomus</i>	0	0	0	3.4
		<i>Orthocyclops</i>	0	2.2	0	5.4
		Unk. Copepodite	14.7	22.4	12.6	48
Eleanor	Cladocerans	<i>Bosmina</i>	4.4	0	0	0
		<i>Daphnia</i>	41.6	31.9	11.1	11.8
		<i>Diaphonsoma</i>	0	0	0	0
		<i>Diplostraca</i>	17.6	0	0	0
		<i>Holopedium</i>	0	0	0	0
		<i>Pseudororida</i>	0	0	11.6	3.4
		Unk. Cladoceran	0	8.8	0	0
	Copepods	<i>Epischura</i>	0.4	38.5	3.7	6.5
		<i>Euryclops</i>	27.7	0	1.1	2.8
		<i>Eurytamora</i>	1.7	0	0	0
		<i>Leptodiaptomus</i>	1.7	0	2.6	1.6
		<i>Orthocyclops</i>	0	0	2.6	0
		Unk. Copepodite	4.8	20.9	67.4	73.8
Independence	Cladocerans	<i>Bosmina</i>	6.3			
		<i>Daphnia</i>	45.8			
	Copepods	<i>Diacyclops</i>	47.9			
Tahoe	Cladocerans	<i>Bosmina</i>	1.2			
		<i>Daphnia</i>	0.3			
	Copepods	<i>Epischura</i>	21.9			
		<i>Leptodiaptomus</i>	55.9			

845 **Table 2.** Acoustic properties of crustacean zooplankton. For each class of scatterers (Cladocerans,  
 846 Copepods, and Nauplii larvae), the mean acoustic target strength (dB re m<sup>2</sup>) and individual wet weight  
 847 ( $\mu\text{g}$ ) are displayed, along with the percentage by biomass of the net catch made up of that class of  
 848 scatterers.

Date	Lake	Cladocerans			Copepods			Nauplii			Weighted Avg.	
		TS (dB)	W ( $\mu\text{g}$ )	%	TS (dB)	W ( $\mu\text{g}$ )	%	TS (dB)	W ( $\mu\text{g}$ )	%	TS (dB)	W ( $\mu\text{g}$ )
2013-10	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
2014-04	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
2014-06	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
2014-09	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

849

850   **Table 3.** Average fish target strength (TS), with estimated lengths and wet weights, plus or minus  
 851 standard deviations. The final column gives the number of fish targets detected in each survey. Target  
 852 strengths were measured in-situ in each lake with a 120 kHz split-beam echosounder and converted to  
 853 lengths and weights using published empirical TS-length and length-weight scaling relations (see  
 854 Methods for details). The 120 kHz echosounder was not operated in Independence Lake, so no fish TS  
 855 values were recorded.

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

856

857 **Table 4.** Acoustic estimates of wet-weight biomass density (in g m<sup>-3</sup>) and total biomass (in kg) of  
 858 zooplankton and fish in each lake show seasonal changes in different trophic levels as well as inter-lake  
 859 differences. These values (as well as the ratio of lower to higher trophic level biomasses) may provide  
 860 useful data for investigations of various ecosystem-level processes in these habitats. Fish biomass was  
 861 not estimated in Independence Lake due to the lack of reliable target strength estimates, and was not  
 862 estimated in Lake Tahoe due to the small extent of the survey relative to the lake's size.

Date	Lake	Area (km <sup>2</sup> )	Zooplankton		Fish		Ratio
			Density (g m <sup>-2</sup> )	Biomass (kg)	Density (g m <sup>-2</sup> )	Biomass (kg)	
2013-10	Cherry	6.3	3.7	23,000	0.27	1,700	14
	Eleanor	3.9	0.92	3,600	0.0018	7	530
	Independence	2.6	1.4	3,600	—	—	—
	Tahoe	490	0.015	7,500	—	—	—
2014-04	Cherry	6.3	0.52	3,300	0.015	94	35
	Eleanor	3.9	13	51,000	0.015	60	850
2014-06	Cherry	6.3	17	110,000	0.044	280	400
	Eleanor	3.9	7.9	31,000	0.16	640	48
2014-09	Cherry	6.3	0.25	1,600	0.044	280	5.9
	Eleanor	3.9	0.24	930	0.054	210	4.5

863

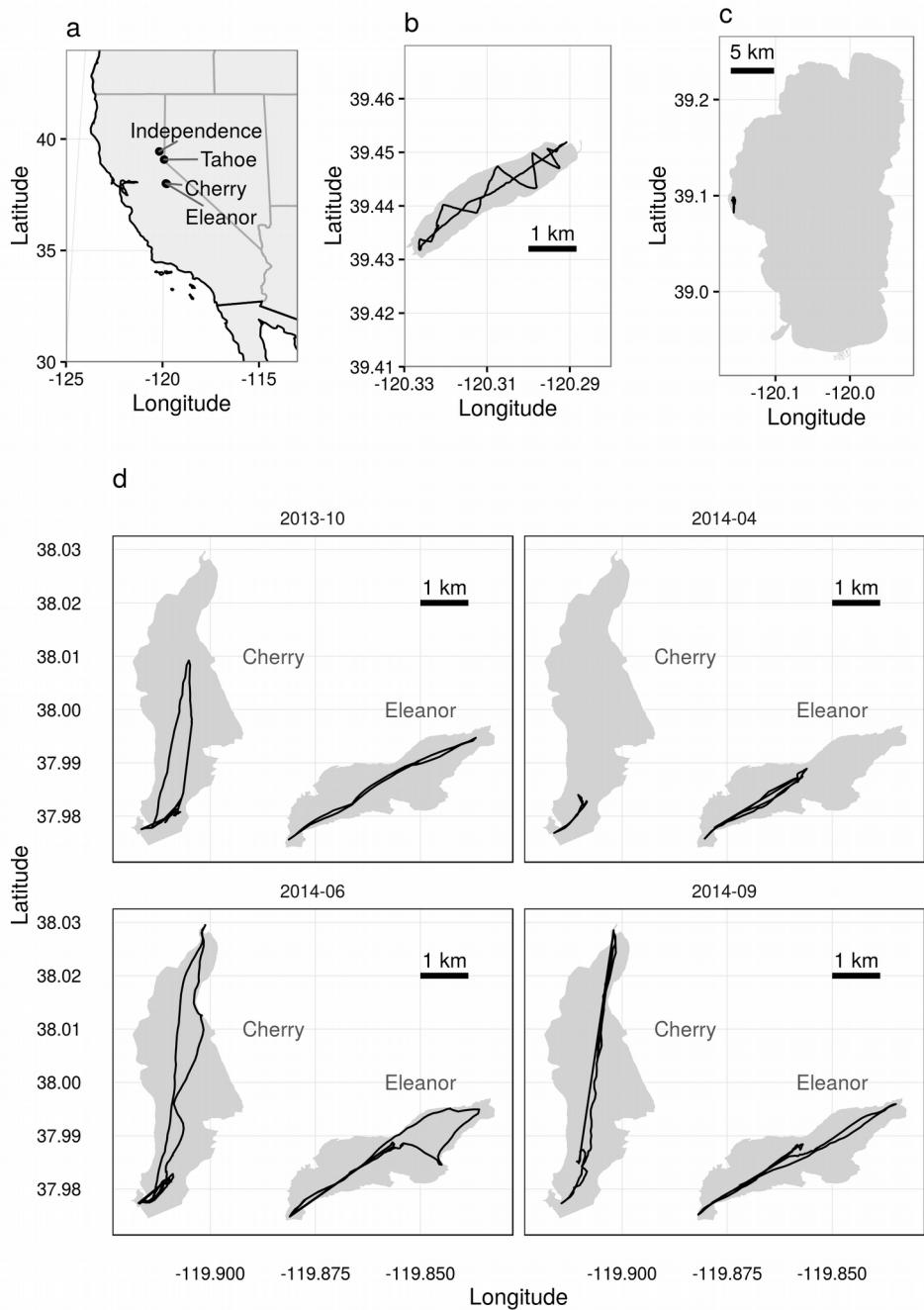
864 **Table 5.** Summary of regression models for spatial trends in the density of zooplankton, by lake and  
 865 survey. The average wet-weight biomass density of zooplankton (in g m<sup>-3</sup>), was averaged through the  
 866 water column, log<sub>10</sub>-transformed, and modeled as a linear function of distance (in km) from the lake's  
 867 inlet and from the shore. The columns "Intercept", "Inlet distance", and "Shore distance" give the  
 868 regression intercept and coefficients associated with each covariate. Their respective *p*-values are in  
 869 the columns to their right. These trends were not estimated in Lake Tahoe because only a small  
 870 proportion of the lake's area was surveyed (Figure 1).

871

Date	Lake	Intercept	<i>p</i>	Inlet	Shore	<i>p</i>	<i>R</i> <sup>2</sup>
				distance	distance		
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

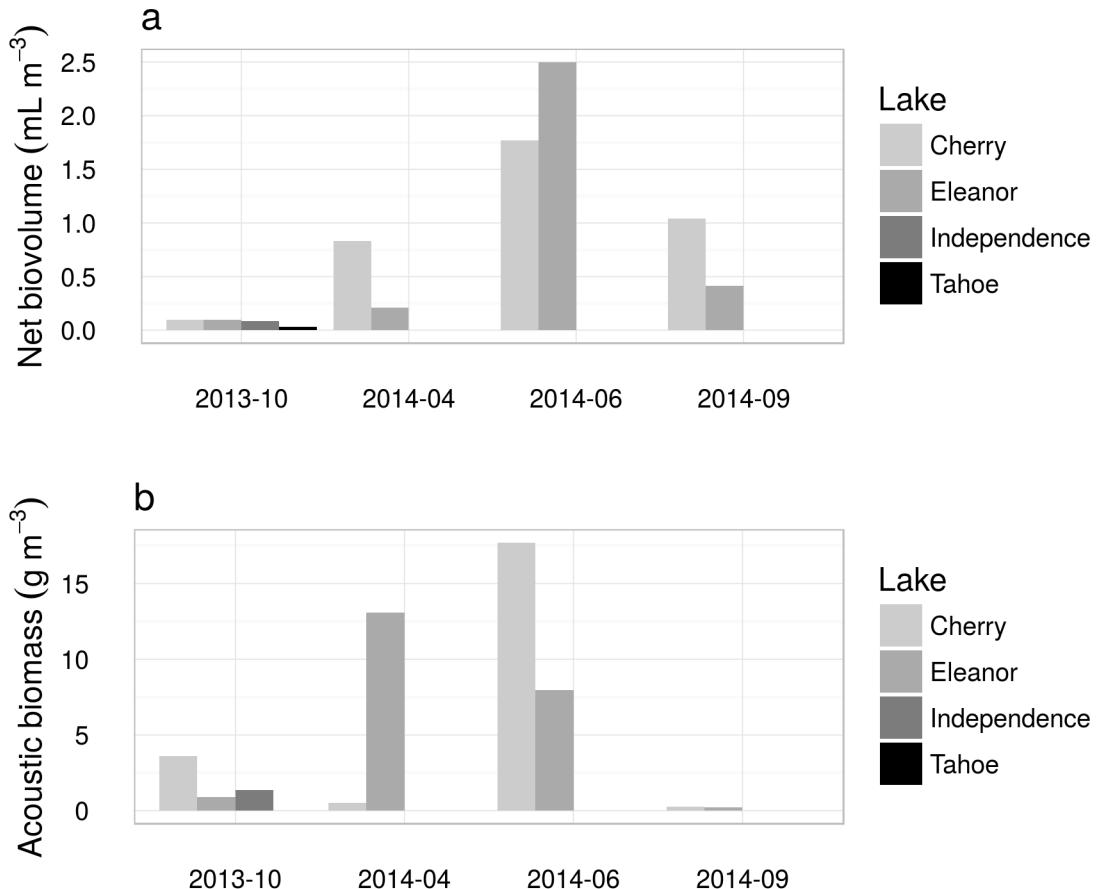
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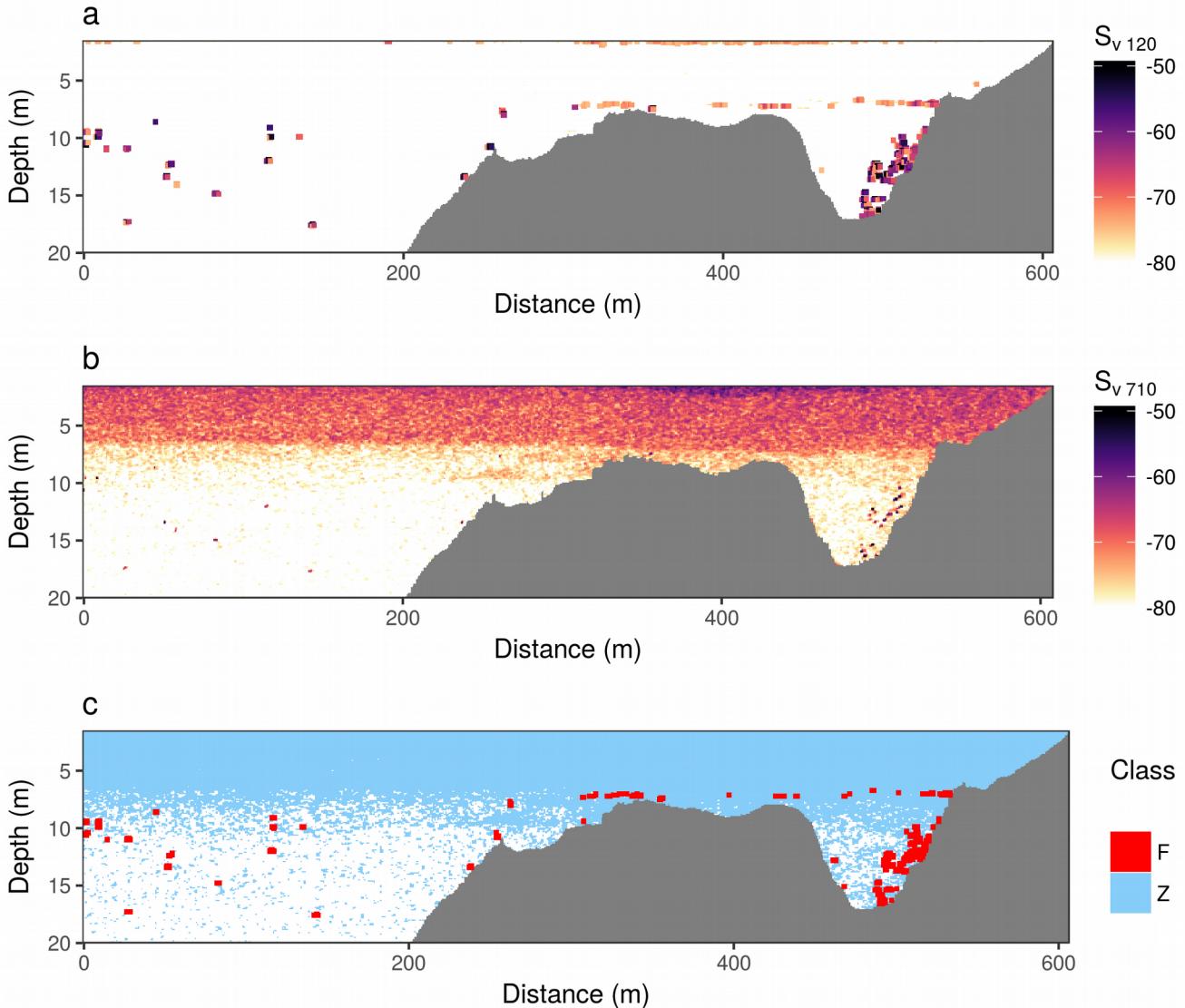
875

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



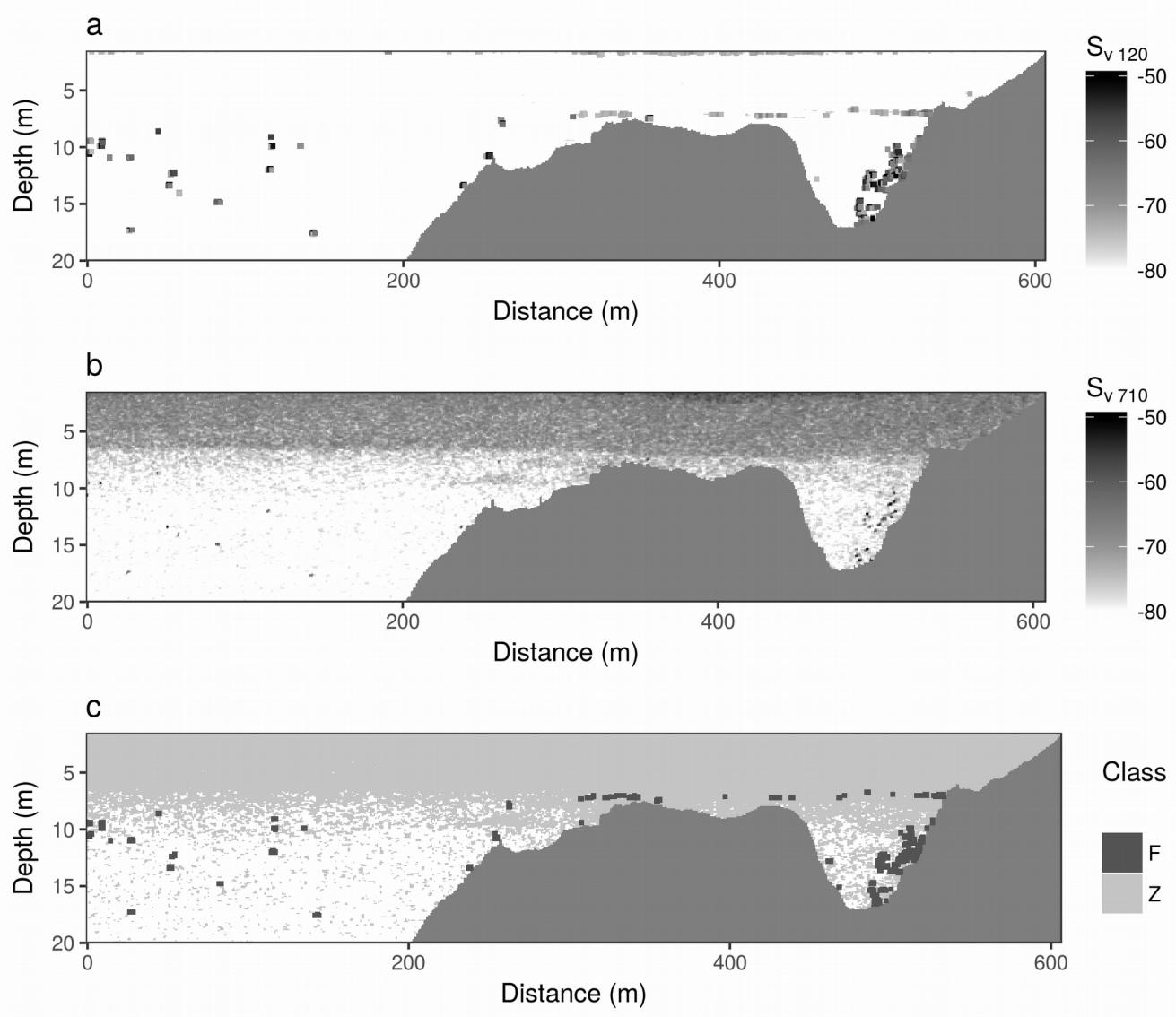
880

881 **Figure 2.** Zooplankton abundance measured by nets and acoustics in each of four seasonal surveys.  
882 The color of each bar indicates the lake; note that Independence and Tahoe were only sampled in  
883 October 2013, and that the acoustic biomass density in Tahoe was too low to be visible on the graph.  
884 (a) Biovolume of zooplankton caught in vertical net tows. These values are normalized by the volume  
885 of water filtered, giving units of mL of biovolume per cubic meter of lake water. (b) Wet-weight  
886 biomass of zooplankton per cubic meter, estimated from acoustic surveys, using measured zooplankton  
887 lengths and species identities to parameterize target strengths and length-weight relationships.



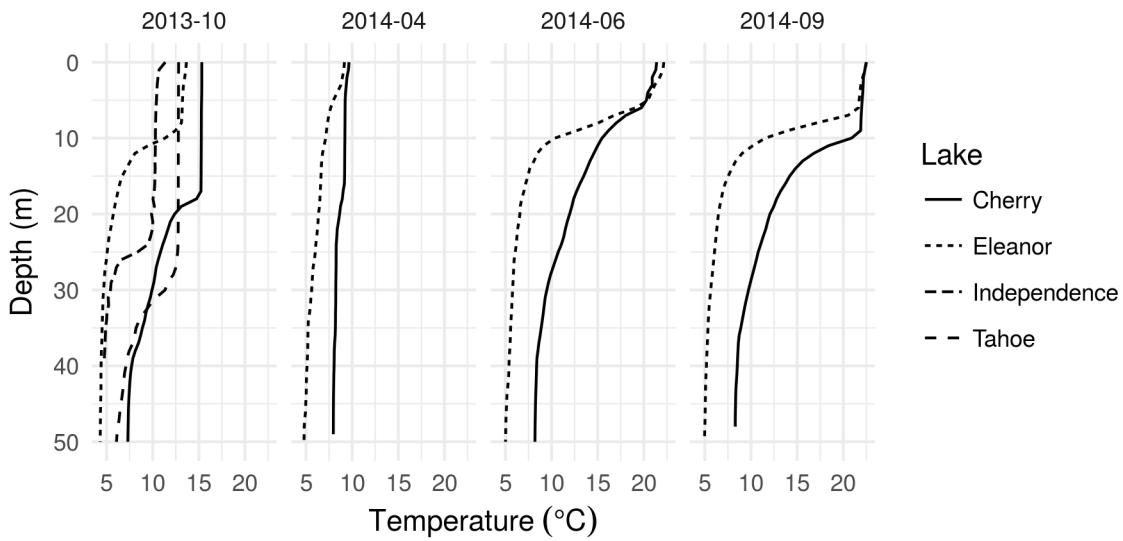
888

889 **Figure 3.** Acoustic profile through part of Cherry Lake on 24 June 2014, showing acoustic backscatter  
 890 at (a) 120 kHz and (b) 710 kHz. Isolated dots are echoes from individual fish, while the zone of  
 891 scattering between ~7 m and the surface represents echoes from zooplankton, which are only detectable  
 892 at 710 kHz. (c) Classification of backscatter as fish ("F") or zooplankton ("Z") based on frequency  
 893 differencing. Red areas are fish, scattering more strongly at 120 kHz, while blue area are zooplankton,  
 894 scattering more strongly at 710 kHz. Pixels classified as fish have been dilated slightly in (a) and (c)  
 895 for better visibility. White shows areas of empty water (volume backscatter < -80 dB at 710 kHz).



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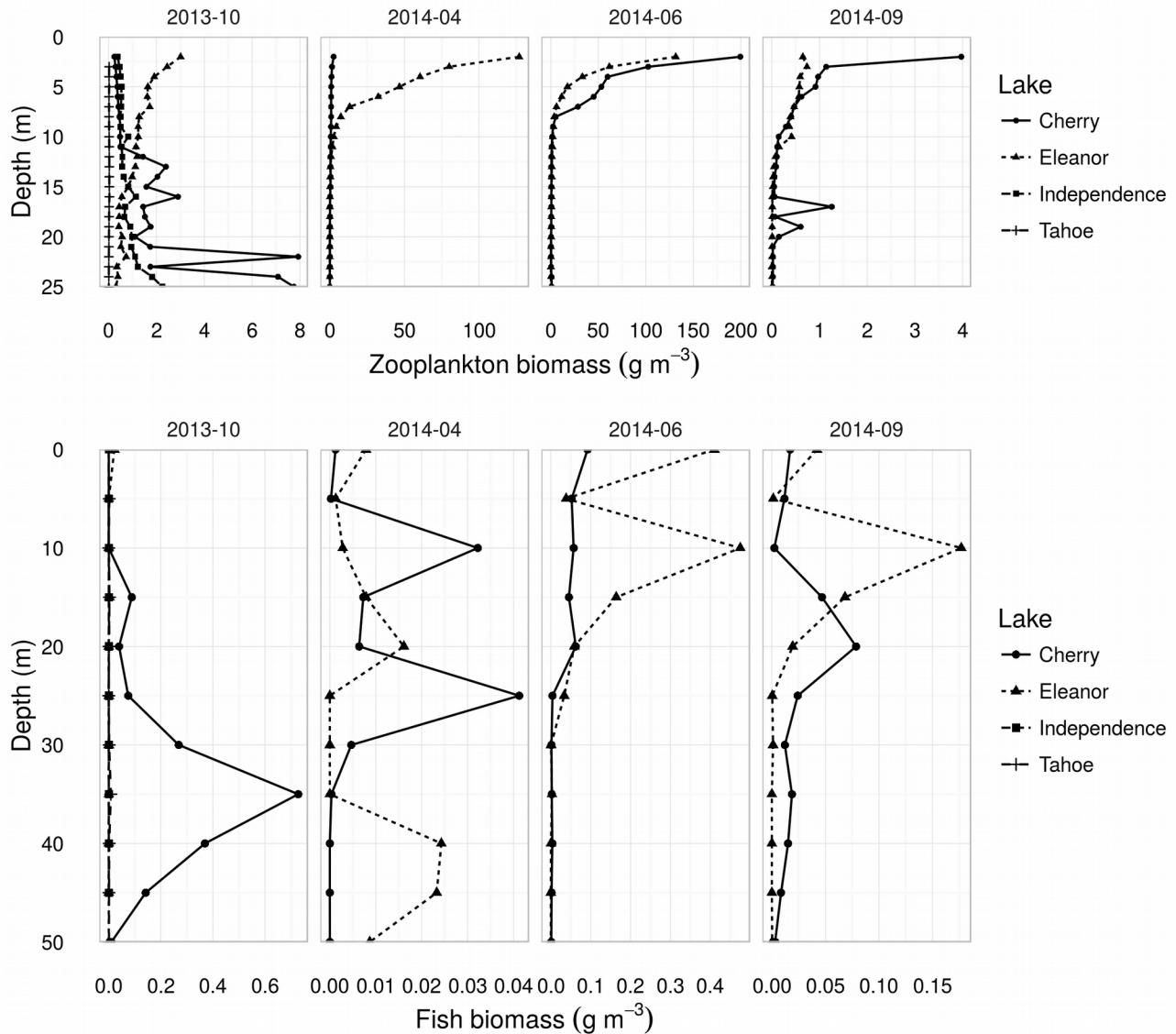
898 **Figure 3 (Grayscale rendering for print publication)**



899

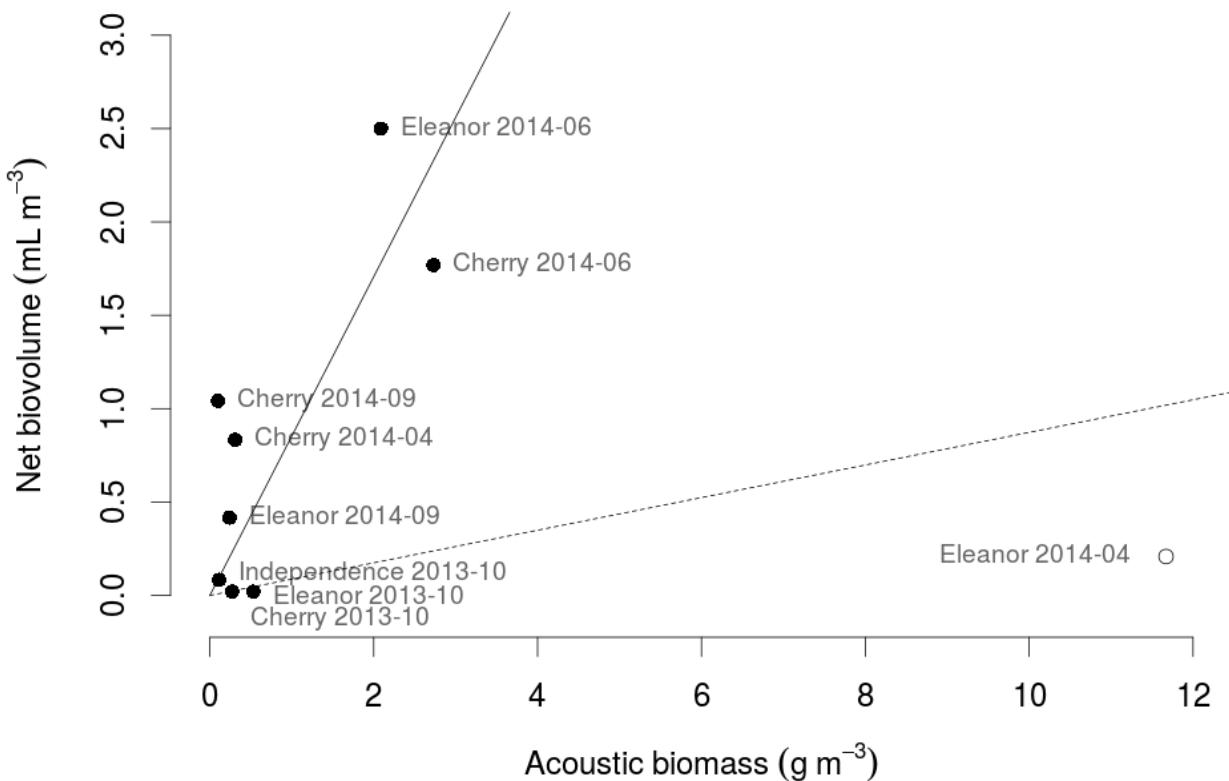
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901 **Figure 4:** Temperature profiles measured in the lakes during four seasonal surveys. (Lake Tahoe and  
 902 Independence Lake were only sampled in October 2013.) All four lakes had mixed layers between 30  
 903 m (Tahoe) and 10 m (Eleanor) in October 2013. Cherry and Eleanor were fully mixed in April 2014,  
 904 but thermoclines were reestablished around 10 m by June and had strengthened by the end of the  
 905 summer.



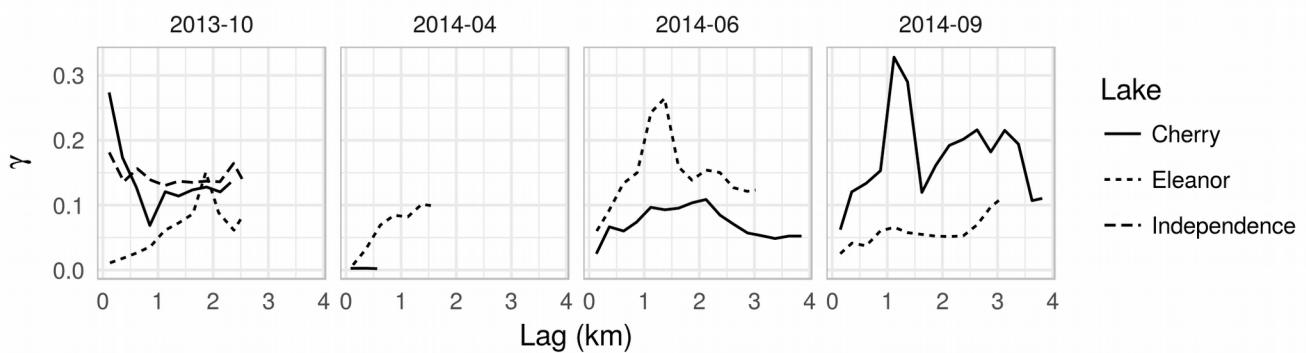
906

907 **Figure 5.** Depth profiles of zooplankton (top row) and fish (bottom row) wet weight biomass density  
 908 measured acoustically in the lakes sampled during each of four seasonal surveys. (Lake Tahoe and  
 909 Independence Lake were only sampled in October 2013). Lines show approximate biomass density of  
 910 all zooplankton as a function of depth,. The target strengths used to calculate numerical densities from  
 911 acoustic backscatter measurements were estimated using the distorted-wave Born approximations for  
 912 the zooplankton communities, and measured in-situ for fish using a split-beam echosounder. Note  
 913 differing x-axis scales in each plot.



914

915 **Figure 6.** Regression of biovolumes estimated from vertical net tows with acoustic estimates of wet  
 916 weight biomass density. Data points are labeled with their lake and date. Two best-fit lines are plotted:  
 917 the dashed line was fit to all data points, while the solid line excluded Lake Eleanor in April 2014,  
 918 plotted as an empty point.  
 919



920

921 **Figure 7.** Empirical variograms of log-transformed zooplankton areal biomass density (i.e., mass of  
 922 zooplankton per  $\text{m}^2$  of lake surface) for each lake and survey.