

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 (Higley, Carrick, Brett, Luecke, & Goldman, 2001;
46 Pugnetti & Bettinetti, 1999). The spatial distribution of that biomass within high-elevation lakes has
47 been measured even more rarely (Masson, Angeli, Guillard, & Pinel-Alloul, 2001). Alpine and sub-
48 alpine lakes differ in several important ways from low-elevation lakes. They typically have lower
49 inputs of sediment and nutrients than lowland lakes, and are clearer and more oligotrophic. As a
50 consequence, different environmental factors, such as ultraviolet radiation, may be more important in
51 structuring their pelagic ecosystems (Rose, Williamson, Saros, Sommaruga, & Fischer, 2009;
52 Williamson et al., 2016). On average, lake size decreases with elevation, as does the duration of the
53 effective growing season. These factors increase the potential for interactions between different
54 habitats, and tend to increase food-related competition (Guisande, Bartumeus, Ventura, & Catalan,
55 2003). Alpine and sub-alpine lakes may also be more sensitive to human disturbance, including
56 eutrophication, pH changes, deforestation, and introductions of non-native plant and animal species
57 (Bradford et al., 1998; Knapp, Matthews, & Sarnelle, 2001; Schabetsberger, Luger, Drozdowski, &
58 Jagsch, 2009).

59 For the sake of simplicity, most models of food webs assume, explicitly or implicitly, that the
60 spatial distributions of their component species can be ignored (Grünbaum, 2012). However, this is not
61 always a valid assumption, since patchiness is common in nature (B. Pinel-Alloul, 1995; Bernadette
62 Pinel-Alloul & Ghadouani, 2007), and large fractions of total predation can occur in small patches over
63 short timespans (Temming, Floeter, & Ehrich, 2007; Tessier, 1983). Aquatic environments often
64 feature sharp vertical gradients, both physical and biological, which strongly affect interactions
65 between predators and prey, for instance through diel vertical migration (DVM). Horizontal
66 heterogeneity in the distribution of organisms is driven by a variety of processes and may also mediate
67 ecological interactions. Physical processes such as mixing, advection, and upwelling tend to dominate
68 at larger scales (e.g. 10s of km and up), while biological processes such as migration, swarming, and
69 predation assume more importance at smaller scales (Folt & Burns, 1999; Mackas, Tsurumi, Galbraith,

70 & Yelland, 2005; B. Pinel-Alloul, 1995). While the potential importance of patchy distributions of
71 zooplankton in lakes has been recognized fairly widely, only a few studies (e.g. Masson et al. 2001;
72 Hembre and Megard 2003) have measured these distributions at high temporal or spatial resolutions.

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

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

98 We surveyed the zooplankton and fish in four lakes in the Sierra Nevada mountains of
99 California, USA, between autumn 2013 and autumn 2014: Cherry Lake, Lake Eleanor, Independence
100 Lake, and Lake Tahoe. Cherry and Eleanor are similar in size and shape, and are less than 2 km apart

101 from each other. Lake Tahoe and Independence Lake are located more than 100 km to the north, and
102 are larger (Tahoe) and smaller (Independence) than Cherry and Eleanor. Our primary tool was a two-
103 frequency acoustic system which allowed us to measure the vertical and horizontal distribution of these
104 animals at high (meter-scale) resolution. Acoustic observations were augmented with net samples to
105 identify the zooplankton scatterers and measure their sizes, to parameterize models of their acoustic
106 target strengths (TS). Fish TS were measured in situ. Zooplankton TS and fish TS values were used to
107 convert acoustic backscatter to biomass, yielding estimates of total biomass at two trophic levels. The
108 high-resolution nature of the acoustic data also let us compare the vertical profiles and horizontal trends
109 of zooplankton and fish density among lakes. Changes in the distributions of zooplankton and fish
110 from one season to another were also examined. Finally, we quantified the zooplankton's spatial
111 variability across scales using empirical variograms. Spatially structured variance indicates a patchy
112 distribution, which in turn would imply that the dominant ecological processes are spatially
113 inhomogenous. Because Cherry Lake and Lake Eleanor are so similar, we hypothesized that the spatial
114 distributions of fish and zooplankton would not vary between these lakes, and that these communities
115 would experience similar seasonal changes.

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,
126 Rundel, Stephenson, & Weixelman, 2007), though their catchments extend up through the subalpine
127 zone and include large areas of bare rock above the treeline. Their areas are 6.3 km² (Cherry) and 3.9
128 km² (Eleanor). Both lakes have been stocked with fish, including rainbow trout (*Onchoryncus mykiss*),
129 brown trout (*Salmo trutta*), and, in Cherry Lake, eastern brook trout (*Salvelinus fontinalis*) (Bingaman,
130 1961; United States Forest Service, 2016). Cherry and Eleanor were surveyed in October 2013, April
131 2014, June 2014, and September 2014 (Figure 1). In addition to our repeated surveys of Cherry and

132 Eleanor, we surveyed Independence Lake, located at 39° 26.4' N, 120° 18.6' W, and Lake Tahoe, at 39°
133 10' N, 120° 0' W once each in October 2013. Independence is a natural lake, 2,127 m above sea level
134 and 2.6 km² in area. It has never been stocked with fish, and is one of only two lakes in the world with
135 a self-sustaining population of Lahontan cutthroat trout, *Oncorhynchus clarkii henshawi* (Nielsen &
136 Sage, 2002). Lake Tahoe, at 1,897 m elevation, is much larger and deeper than the other three lakes,
137 with a surface area of 490 km² and maximum depth of 501 m. It is also oligotrophic, in contrast to the
138 three smaller lakes, which are mesotrophic. The watersheds of the three smaller lakes are undeveloped,
139 although portions of the Cherry and Eleanor Creek watersheds were burned during the 2013 Rim Fire
140 (National Wildfire Coordinating Group, 2013). Lake Tahoe is bordered by several towns, with a total
141 permanent population of approximately 50,000. All four watersheds are on granitic substrate.

142

143 *Acoustic data collection*

144 Surveys were run from outboard-powered boats trailered to each lake. Because of the recent
145 Rim Fire, camping was not permitted near Cherry Lake or Lake Eleanor, and the survey boats had to be
146 towed in and out over 60 km of mountain roads, restricting our sampling to daylight hours. Acoustic
147 volume backscatter was recorded at two frequencies, 120 and 710 kHz. Volume backscatter can be
148 expressed either in logarithmic form as “mean volume backscattering strength,” S_V , or a linear form as
149 “volume backscattering coefficient,” s_V , related by the equation $s_V = 10\log_{10}(S_V)$ (MacLennan et al.,
150 2002). The volume backscattering coefficient is proportional to the numerical density of sound-
151 scattering objects in the water. The 120 kHz echosounder was a Simrad ES60 with a split-beam
152 transducer (7° beam width), which can accurately measure the target strength of individual fish in situ.
153 The 710 kHz echosounder was a Simrad EK60 with a single-beam (2.8° beam width) transducer. This
154 high-frequency system could detect small (<1 mm) zooplankton (Holliday & Pieper, 1995; Warren et
155 al., 2016), but its effective range was limited to approximately 30 m due to sound attenuation in water.
156 Both transducers were deployed on a pole mount off the side of the survey boat at depths of
157 approximately 30-50 cm depending on wave conditions.

158 The 120 kHz system was calibrated in Lake Tahoe on 21 October 2013 with a 38.1 mm
159 tungsten carbide standard target sphere (K.G. Foote, Knudsen, Vestnes, MacLennan, & Simmonds,
160 1987). Because of the 710 kHz transducer’s narrow beam width, we were unable to center the sphere
161 in the beam while in the field, and so performed an additional, ex-situ calibration for this instrument in
162 a tank on land. A 166 L barrel, 80 cm deep and 50 cm across (Rubbermaid, Atlanta GA), was filled

163 with fresh water and the transducer mounted at the barrel's center just below the water's surface. The
164 calibration sphere could then be suspended in the center of the beam beyond the transducer's 40 cm
165 near field.

166 Independence Lake was sampled on 20 October 2013, and Lake Tahoe was sampled on 21
167 October 2013. Cherry Lake and Lake Eleanor were each sampled four times. Cherry was sampled on
168 29 October 2013, and on 2 April, 24 June, and 10 September 2014. Eleanor was sampled one day later,
169 on 30 October 2013, and 3 April, 25 June, and 11 September 2014. In the three smaller lakes, we
170 attempted to perform a lengthwise transect from one end of the lake to the other. In Independence
171 Lake, we were also able to add a series of zig-zag transects across the main axis of the lake (Figure 1).
172 The April 2014 transects in Cherry and Eleanor were shorter due to snowfall, which required slow
173 travel on the mountain roads and reduced the time available for sampling.

174

175 *Zooplankton sampling and target strength models*

176 Zooplankton were collected on each sampling day near the center of the lake with a vertical tow
177 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
178 equipment problem with the ring net during the October 2013 trip to Cherry and Eleanor, we instead
179 used an open Van Dorn bottle (10 cm diameter) with an elastic nylon mesh (\sim 100 μm) over one end.
180 This was hauled vertically through the water column with its uncovered end up, acting like a small-
181 diameter net. Samples were preserved for later analysis in 10% buffered formalin. In the lab, the total
182 biovolume of each sample was measured after allowing it to settle in a graduated cylinder. Because of
183 the small diameter of the Van Dorn sampler, the biovolumes of the samples from Cherry and Eleanor in
184 October 2013 were smaller than the finest graduation on our cylinder, preventing a precise
185 measurement. We estimated them at 0.1 mL; our analyses did not appear sensitive to these estimates
186 when they were in the range of 0-1 mL. A subsample of 200-300 animals was split from each original
187 sample and counted under a compound microscope. Animals were identified to the lowest possible
188 taxonomic level. In addition, the lengths of the first 30 animals counted were measured to the nearest
189 0.1 mm.

190 To convert acoustic backscatter to animal densities it is necessary to know the backscattering
191 cross-section, σ_{BS} , of the scattering organisms. The backscattering cross-section is also expressed in its
192 logarithmic form, the target strength, $\text{TS} = 10 \log_{10}(\sigma_{\text{BS}})$ (MacLennan et al., 2002). We calculated these
193 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, Karpinski, Shah, & Edelman, 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 & 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 each body shape's dry weight, W_d , using a published regression for either calanoid nauplii, the calanoid *Diaptomus oregonensis*, or *Daphnia galeata* (Culver, Boucherle, Bean, & Fletcher, 1985). Dry weights were converted to wet weights, 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 $b_{tot} = n_{tot} \langle W_{w,tot} \rangle$.

214

215 *Acoustic data processing and analysis*

216 Acoustic data were processed using Echoview Software version 7.0 (Myriax Pty Ltd, 2016).
217 Background noise was estimated and subtracted following De Robertis and Higginbottom (2007). Data
218 were manually scrutinized to correct bottom detection lines, exclude echoes from net and other
219 instrument casts, and eliminate intermittent interference, such as multipath and sidelobe echoes from
220 the steep rocky sides of the lake when close to shore. Acoustic data were integrated in bins 1 m deep
221 and 10 m wide along-track and exported for further analysis.

222 Single fish targets were detected in the 120 kHz data using Echoview's individual-target-
223 detection operator (split-beam method 2), with an uncompensated TS threshold of -70 dB, pulse length

224 determination level of -6 dB, and minimum and maximum normalized pulse lengths of 0.5 and 2.0.
225 Targets were rejected if their beam-pattern compensation was greater than 6 dB or if their angular
226 standard deviation was greater than 0.5°. In Independence Lake, only the 710 kHz single-beam
227 echosounder was operated, so we did not measure fish TS in this lake. Fish target strengths were
228 averaged (in the linear domain) by lake and survey.

229 Acoustic integration cells were classified as fish if their backscatter was higher at 120 kHz than
230 at 710 kHz, since resonant scattering from fishes' swim bladders makes them stronger targets at the
231 lower frequency. Based on the small sizes of the zooplankton, the difference in their TS between 120
232 and 710 kHz was expected to be a robust criterion for classification. Zooplankton backscatter at 710
233 kHz in each lake on each sampling date was apportioned to copepods, cladocerans, and nauplius larvae
234 using the proportional abundances in the net samples, and converted to numerical and biomass
235 densities based on the representative values for the overall zooplankton community, as described
236 above.

237 Fish densities were calculated from the integrated 120 kHz backscatter, using the mean TS of
238 the individual fish targets to convert backscatter to fish densities. To obtain approximate estimates of
239 fish biomass, we first converted each fish target's TS to a length (in cm). Because no specific TS-
240 length relationships are available at 120 kHz for the salmonid species in these lakes, we used a generic
241 relationship $TS=20 \log_{10}(L)-67.4$ for physoclist fishes from Foote (1987). These lengths were
242 then converted to approximate wet weights using published scaling relationships. Length-weight
243 relationships for fish are usually assumed to follow a power law of the form $\log_{10} W=a+b \log_{10} L$,
244 where a and b are fitted empirically for a particular species or population. Because we could not
245 identify fish targets to species, we averaged the parameters for rainbow trout ($a = -4.898$, $b = 2.99$,
246 Simpkins and Hubert 1996), brook trout ($a = -5.186$, $b = 3.103$, Hyatt and Hubert 2001), and brown
247 trout ($a = -4.867$, $b = 2.96$, Milewski and Brown 1994) to get a single length-weight equation with $a =$
248 -4.98 and $b = 3.02$. These lengths and weights were averaged into mean values for each lake and
249 survey.

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

255

256 *Comparison of net and acoustic biomass*

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

268

269 *Distribution of zooplankton and fish*

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

285

286 **Results**

287 The zooplankton communities of the four lakes differed, both among lakes and, in the case of
288 the repeated samples at Cherry and Eleanor, through time. Lake Tahoe's zooplankton were numerically
289 dominated by the calanoid copepods *Leptodiaptomus tyrelli* (56%) and *Epischura nevadensis* (22%),
290 with another 20% made up by unidentified copepods and copepodites (Table 1). The zooplankton in
291 Independence Lake were split more evenly between the cyclopoid copepod *Diacyclops thomasi* (48%)
292 and the cladoceran *Daphnia middendorffiana* (46%), with the remainder composed of *Bosmina*
293 *longirostris* (6%).

294 Over the four sampling dates, more zooplankton species were recorded in Cherry Lake and
295 Lake Eleanor than in the single surveys in Independence and Tahoe (Table 2). In October 2013, the
296 communities in both lakes were 50-60% cladocerans in the genera *Daphnia* and *Diplostraca*, with the
297 remainder mostly composed of cyclopoid copepods in the genus *Euryyclops*. The following April,
298 the community in Cherry Lake remained similar, but in Lake Eleanor it had shifted to 59% Copepods,
299 mostly *Epischura nevadensis*. During the final two surveys, in June and September 2014, the
300 communities in both lakes were between 70 and 85% copepods, a large proportion of which were
301 copepodites of unknown calanoid species. The cladocerans, which composed 15-32% of the
302 communities in June and September 2014, were again a mix of *Daphnia* and *Diplostraca* (Table 2).
303 Biovolumes of zooplankton estimated from the nets ranged from 0.1 mL m⁻³ in Lake Tahoe to 2.5 mL
304 m⁻³ in Lake Eleanor in June 2014 (Figure 2). Biovolumes in both Cherry Lake and Lake Eleanor were
305 highest in June 2014 and lower in the other months.

306 Target strengths for the different classes of zooplankton scatterers calculated using the DWBA
307 varied widely (Table 3). The strongest scatterers were copepods in Cherry Lake in April 2014, with an
308 average TS of -111 dB. The weakest were nauplius larvae in Cherry Lake in October 2013, with a
309 mean TS of -148 dB. Cladoceran target strengths fell between -113 and -127 dB. Adult copepod target
310 strengths fell in the same broad range, from -104 to -128 dB. Nauplii, due to their much smaller size,
311 were predicted to scatter much less sound, with their mean TS falling between -120 and -148 dB (Table
312 3). After averaging across all scattering classes, overall mean TS ranged from -125 dB, in Cherry Lake
313 in September 2014, to -105 dB, in Lake Tahoe in October 2013 (Table 3). There were no systematic
314 trends in TS between the lakes, or through time.

315 Mean fish target strengths, measured in situ, ranged between -40 and -36 dB re m²,
316 corresponding to mean lengths from 21 to 31 cm, and mean weights from 200 to 720 g (Table 4). In

317 October 2013, the mean TS (and the mean lengths and weights derived from them) were roughly equal
318 in Lake Eleanor and Lake Tahoe and slightly higher in Cherry Lake. In the following three surveys,
319 however, mean TS was 1-3 dB higher in Lake Eleanor, with corresponding length and weight
320 differences of 2-8 cm and 140-380 g.

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

335 Peak fish densities in the lakes ranged between 0.007 and 1.6 fish per 1000 m⁻³, corresponding
336 to biomass densities of 0.04 to 0.7 g m⁻³ (Figure 4). These fish were mostly found below the
337 zooplankton layers (Figure 4). In the first surveys in October 2013, fish in Cherry Lake were
338 concentrated in a layer centered at 35 m depth, with much higher densities than the other three lakes
339 (Figure 4). The overall mean fish density in October in Cherry Lake was 1.6 per 1000 m⁻³, compared to
340 0.007 in Lake Eleanor. The next April, the fish in both lakes were grouped in two layers. These layers
341 were shallower in Cherry Lake, at depths of 10 and 25 m, than in Lake Eleanor, where they were at
342 depths of 20 and 40 m (Figure 4). In June, fish in both lakes were concentrated in the upper 10-15 m
343 and were more abundant overall than in April, with mean densities of 0.3 (Cherry) and 0.5 (Eleanor)
344 fish per 1000 m⁻³. In September, the fish in each lake were in one broad layer, between 5 to 20 m depth
345 in Lake Eleanor and from 10 to 30 m in Cherry Lake. Overall densities were lower than in June, at 0.2
346 fish per 1000 m⁻³ in Cherry Lake and 0.1 fish per 1000 m⁻³ in Lake Eleanor.

347 When depth-integrated and scaled by their respective lake areas, these densities yielded a wide

range of estimates for the total biomasses in the different lakes. In October 2013, Lake Tahoe contained an estimated 7,500 kg of small zooplankton. Zooplankton in the three smaller lakes were 60-240 times denser than in Tahoe, but their much smaller areas led to similar or smaller total biomass estimates (Table 5). In April 2014, the zooplankton wet-weight biomass density in Lake Eleanor had increased to 13 g m⁻³, raising its total biomass estimate to over 51,000 kg, higher than that of Lake Tahoe in October 2013. Total zooplankton biomass in Cherry Lake in April was 3,300 kg, 14% of its level in the October survey. By June, however, it had increased to 110,000 kg, while the zooplankton biomass in Eleanor dropped to 31,000 kg. During the September 2014 survey, zooplankton populations in both lakes had dropped back to lower levels (Table 5).

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

Net and acoustic estimates of zooplankton density were positively related (Figure 5). The regression of net-caught zooplankton biovolume on acoustically estimated biomass was not statistically significant when all data points were included ($p=0.1$, $R^2=0.19$), though the fitted slope was positive. When the outlying measurement from Lake Eleanor in April 2014 was excluded, the fitted slope was significantly different from zero, with a fitted value of 0.34 mL mg⁻¹, and a 95% confidence interval from 0.21 to 0.46 mL mg⁻¹. This model fit the data fairly well, with an adjusted R^2 of 0.81.

Zooplankton biomass density displayed significant trends with respect to distance from the inlet and shore in most surveys, though the directions of these trends were variable (Table 6). The most pronounced trend was in Cherry Lake in June 2014, where zooplankton biomass density was an order of magnitude higher near the lake's inlet than near the dam at the other end. In eight out of the nine surveys, the signs of the coefficients for distance from shore and distance from the inlet were the same. The single survey in Independence Lake was the exception, with biomass density increasing closer to the inlet and decreasing closer to shore. In three of the four surveys in Cherry Lake, zooplankton density increased towards the shore and inlet. In Lake Eleanor, the reverse was true: three out of four surveys showed zooplankton density higher away from shore and the inlet (Table 6). These spatial regressions explained a low-to-moderate amount of the variability in the data, with R^2 values ranging from approximately zero in Lake Eleanor in October 2013, to 0.73 in Cherry Lake in June 2014 (Table

379 6).

380 The residuals from these regressions were spatially autocorrelated in some, but not all, lakes
381 and surveys. In October 2013, when biomass densities in all lakes were low, Lake Eleanor's variogram
382 reached its sill of 0.1 at a range of about 2 km. Independence Lake's variogram was flat, showing little
383 evidence for spatial autocorrelation, and in Cherry Lake, the variogram was higher at shorter lags,
384 suggesting short-range antivariation (Figure 6). In April, Lake Eleanor's variogram was similar,
385 with a sill of around 0.1 at a range of 1.5 km. Back-transformed to linear units, this implies an
386 expected difference in biomass on the order of 25% across distances of 500 m or greater. The short
387 transect in Cherry Lake in April limited the spatial information available for that variogram.

388 In June, the sill of the variogram in Lake Eleanor had increased to 0.15 at a range of 2 km
389 (Figure 6), implying an expected difference in biomass on the order of 50% when transformed back to
390 linear units. In Cherry Lake, the variogram was relatively flat (Figure 6), showing little evidence for
391 spatial structure other than the lakewide trends described above. Spatial variability in Lake Eleanor
392 decreased somewhat between June and September 2014. However, the variogram for Cherry Lake in
393 the final survey showed higher overall variability, peaking at 0.37 at a lag of 1 km and a sill near 0.2
394 beyond 1.5 km. Overall, the variogram sill values ranged from approximately 0.1 to 0.2. These
395 values, in \log_{10} -transformed units, imply multiplicative differences (\times/\div) in zooplankton density from
396 0.25 to 1.6 at long ranges, where "long ranges," as defined by the variograms, are between 1 and 2 km.
397

398 **Discussion**

399 Our acoustic measurements produced estimates of the total biomass of zooplankton and fish in
400 four peri-alpine lakes in the Sierra Nevada Mountains. To our knowledge, these are the first biomass
401 estimates (for any trophic level) ever made in Independence Lake, Cherry Lake, and Lake Eleanor. In
402 Lake Tahoe, our estimate of the mean density of small zooplankton (approximately 2,200 individuals
403 m^{-3}) fell within the range of prior estimates (e.g. 0-23,000 individuals m^{-3} , Goldman et al. 1979). The
404 measurements in Independence Lake and Lake Tahoe represent only a single snapshot of the
405 zooplankton and fish in each lake, and should not be over-interpreted. The repeated sampling in
406 Cherry Lake and Lake Eleanor did allow us to capture some of their seasonal variability.

407 A spring bloom of zooplankton occurred in both Cherry Lake and Lake Eleanor, with peak
408 biomass densities of 4-6 g m^{-3} . In spring and summer, the zooplankton were concentrated in the upper
409 5-10 m of the water column, probably associated with a stratified surface layer. In 2014, the bloom

410 appeared to begin earlier in Lake Eleanor than in Cherry Lake, since a near-surface zooplankton layer
411 was present in Eleanor, but not Cherry, during the early April survey. By June, both lakes had similar
412 zooplankton densities, and by September, zooplankton populations in both lakes had declined by an
413 order of magnitude. At this point there were still more zooplankton in Cherry Lake, however,
414 suggesting that the bloom there, which started later, also took longer to collapse in the fall. This
415 pattern, of a spring and summer increase in zooplankton as they respond to blooming phytoplankton, is
416 consistent with standard models of seasonal cycles in lake ecosystems (Sommer et al., 2012; Sommer,
417 Gliwicz, Lampert, & Duncan, 1986). While the seasonal changes in Cherry Lake and Lake Eleanor
418 were similar there were also distinct differences, both in the vertical distribution of fish and
419 zooplankton, and the timing of seasonal blooms. These differences were greater than expected given
420 the apparent similarities between the sizes, depths, and catchments of the two lakes. Whether these
421 differences emerged endogenously or were driven by unobserved physical factors is unknown.

422 Fish biomass did not vary nearly as widely as zooplankton biomass, which is expected given
423 their much longer life spans and generation times. At the height of the zooplankton blooms,
424 zooplankton biomass was several hundred times that of fish, indicating that the former were effectively
425 released from predatory control at those times. In both autumns, the zooplankton:fish ratios were much
426 lower, suggesting a closer match between rates of zooplankton reproduction and fish predation. While
427 fish were scarce in Lake Eleanor in October 2013, our estimate of total biomass (7 kg, Table 5) is
428 probably extreme, reflecting error due to the patchy distribution of fish and our short surveys as much
429 as the true biomass. It should also be noted that our seasonal sampling interval may have caused us to
430 miss shorter-scale variability in zooplankton populations, due either to sub-seasonal population
431 dynamics, or responses to environmental forcings such as runoff from rainstorms or mixing of the
432 water column by wind. This study also only covers one year, leaving longer-term trends unknown.

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

441 al., 2016), though their effects on a lake's zooplankton are not necessarily large (Patoine, Pinel-Alloul,
442 & Prepas, 2002).

443 The second major environmental trend was a five-year drought (2012-2017) in the western
444 United States. One consequence of the drought was a decline in the water levels of Cherry Lake and
445 Lake Eleanor, which were nearly 8 m lower in the final survey in September 2014 than they were in the
446 first survey, in October 2013 (United States Geological Survey, 2017). Both lakes are reservoirs
447 supplying water and electricity to San Francisco, so their levels are managed by that city's Public
448 Utilities Commission. The drought probably also played a role in the spread of the Rim Fire: most of
449 California's largest wildfires, including the Rim Fire, have occurred during droughts (Williamson et al.,
450 2016). However, the drought may also have mitigated some of the fire's effects on Cherry and Eleanor:
451 precipitation during the winter of 2013-2014 was well below normal (California Department of Water
452 Resources, 2014), meaning that runoff and erosion in the burned areas were much less than they might
453 have been in a more normal year. Both the drought and fire are likely to have affected the lakes in
454 some way, but the limited sampling schedule makes it impossible to separate these effects from the
455 expected seasonal cycle for a temperate lake.

456 Fish target strengths, and the corresponding estimated lengths, were in the expected range for
457 lake salmonids. The vertical distribution of fish in Cherry Lake and Lake Eleanor was qualitatively
458 similar in every survey but the first, suggesting similar dynamics in the fish community of both lakes.
459 These dynamics cannot be determined from the limited information available in this study, but the
460 similar vertical patterns of fish density, offset in some cases by up to 10 m, suggest that Cherry Lake
461 and Lake Eleanor could be an interesting setting for further comparative studies of fish behavior. The
462 vertical distributions of fish and zooplankton did not coincide except in June 2014, though this is not
463 particularly surprising, since our surveys occurred during the daytime and many fish migrate vertically.
464 The lack of overlap emphasizes that interactions between predators and prey are not evenly distributed,
465 and may be restricted to certain locations or times of day (Beauchamp, Baldwin, Vogel, & Gubala,
466 1999; Lørke, Weber, Hofmann, & Peeters, 2008; Temming et al., 2007).

467 There was fair agreement between the acoustic and net-based estimates of zooplankton
468 biomass. However, the data from Lake Eleanor in April 2014 formed a notable outlier, with the net-
469 based biovolume much lower relative to the acoustic biomass than expected, based on the other
470 samples. A relatively strong scattering layer was visible near the surface along the entire survey track.
471 This layer, along with weaker-than-average zooplankton TS (Table 3), accounted for the high acoustic

472 biomass. The small biovolume estimate is accurate, at least based on the net sample (0.5 mL of
473 zooplankton from a total filtered volume of 15 m³). The discrepancy between these two measures is
474 probably due to some combination of random variability in the net sample and uncertainty in our TS
475 estimates. Regardless, regressions with and without this outlier produced positive slopes. Without it,
476 the slope was significantly different from zero with a value of 0.34 mL mg⁻¹. Wiebe et al. (1975) found
477 that displacement biovolume *DV* and wet weight *WW* of marine zooplankton were related by the
478 equation $\log_{10}(DV) = 0.078 + 1.026 \log_{10}(WW)$ which, in linear terms, implies a slope of
479 approximately 1.2 mL mg⁻¹, 3.5 times higher than our estimate. This difference is not totally
480 unexpected: Wiebe et al.'s (1975) data came exclusively from net samples in marine environments, and
481 acoustic estimates of biomass are often several times higher than those based on net catches, probably
482 due to avoidance reactions by the animals (Warren & Wiebe, 2008; Wiebe et al., 2013). If true, this
483 implies that a regression of net-based biovolume on acoustically-derived biomass would have a
484 shallower slope than the same regression on net-based biomass. The multi-step conversion process
485 from acoustic backscatter to biovolume introduces a number of uncertainties. In addition, the spatial
486 extent of our net sampling was quite limited compared with that of the acoustics. Our results should
487 thus be interpreted with some caution. However, our procedures do produce realistic biomass values,
488 with reasonable agreement between nets and acoustics, increasing our confidence that the patterns
489 observed are biologically meaningful.

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

501 Even after subtracting the lake-scale trend in zooplankton density, spatial autocorrelation was
502 evident in the residuals, as illustrated by the empirical variograms (Figure 6). These should be

503 interpreted with caution, since they were based in most cases on single reciprocal transects down the
504 main axis of each lake which may not have captured any spatial anisotropy present. In particular, the
505 restricted time available to survey Cherry Lake on 2 April 2013 meant that the transect was only about
506 1 km long, limiting our ability to draw conclusions about the spatial distribution of zooplankton.
507 Regardless, most of the variograms in Cherry Lake and Lake Eleanor did show evidence of spatial
508 patchiness in the distribution of zooplankton, with approximate spatial scales, based on the variogram
509 ranges, between 500 and 2000 m. These ranges are well below the sizes of the lake basins, suggesting
510 that ecological processes in these lakes are not spatially uniform.

511 It is unknown what processes generate and maintain patchiness in these lakes. In the ocean,
512 patchiness in zooplankton appears to be driven mostly by bottom-up processes, with scales of
513 biological variability mirroring scales of physical variability (Denman, Okubo, & Platt, 1977; Mackas,
514 Denman, & Abbott, 1985; Urmy, Horne, & Barbee, 2012). At smaller scales, animal behavior and
515 ecological interactions become more important in generating spatial variability (Folt & Burns, 1999; B.
516 Pinel-Alloul, 1995), though these scales and processes are harder to observe and have been studied less
517 in the field. It seems unlikely that these lakes (with the possible exception of Tahoe) are large enough
518 to support horizontal physical structures larger than internal waves or wind-driven Langmuir
519 circulations on the scale of 10s of m, so the km-scale patchiness in the zooplankton is probably due to
520 other processes, such as aggregation (e.g., Byron et al. 1983) or local predation by schooling fish. In
521 this interpretation, the lake's finite boundaries act like a high-pass filter, preventing large-scale physical
522 processes (e.g. fronts, gyres, nutrient upwelling) from creating spatial variability that masks patchiness
523 due to smaller-scale, biological processes (swarming, predator-prey interactions, etc.). If this
524 interpretation is correct, future studies could use appropriately-sized lakes as model systems to study
525 biogenic patchiness free of interference from larger-scale processes.

526 The acoustic methods used here offer a number of advantages over traditional direct sampling
527 methods, though they also come with their own uncertainties and caveats. Identification of scatterers is
528 often a challenge with acoustics. However, using a two (or more) frequency system, as in this study,
529 reliably separates areas of backscatter from zooplankton and fish. Furthermore, direct net sampling of
530 the zooplankton community, especially in relatively small lakes such as Independence, Cherry, and
531 Eleanor, lets us confidently identify the main classes of zooplankton scatterers. The main source of
532 uncertainty when interpreting acoustic backscatter as an estimate of biomass density is in the target
533 strengths assumed for the scattering organisms. The DWBA is an accurate and widely used method to

534 calculate zooplankton target strengths, but it depends, sensitively, on the values of the scatterers'
535 material properties—namely the density- and sound-speed-contrasts g and h . To our knowledge, these
536 values have never been measured for any freshwater zooplankton. In their absence, we used generic
537 values from the literature, based on marine zooplankton (Stanton & Chu, 2000). These are reasonable
538 defaults, but they may not be accurate for the species considered here, introducing a degree of unknown
539 error into the TS and hence biomass estimates. Measurements of the material properties of freshwater
540 zooplankton would be a worthwhile objective for future research.

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

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

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782 lakes and their ecosystem services. *Frontiers in Ecology and the Environment*, 14(2), 102–109.
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784 **Table 1.** Numerical composition (%) of the crustacean zooplankton community in Independence Lake
785 and Lake Tahoe in October 2013 was dominated by a few species.

786

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788

Lake	Group	Genus	% Composition
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
		Unk. Cope.	20.3

789 **Table 2.** Numerical composition (%) of the crustacean zooplankton community in Cherry Lake and
 790 Lake Eleanor in four seasonal surveys varied seasonally and between the two sites.
 791
 792

793

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>Diaphonisma</i>	0	2.2	0	0
		<i>Diplostraca</i>	42.9	0	0	0
		<i>Holopedium</i>	0	33.6	0	0
		<i>Pseudoridea</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
Eleanor	Cladocerans	<i>Eurytacops</i>	22.8	14.9	0	4.1
		<i>Eurytamora</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
		<i>Bosmina</i>	4.4	0	0	0
		<i>Daphnia</i>	41.6	31.9	11.1	11.8
	Copepods	<i>Diaphonisma</i>	0	0	0	0
		<i>Diplostraca</i>	17.6	0	0	0
		<i>Holopedium</i>	0	0	0	0
		<i>Pseudoridea</i>	0	0	11.6	3.4
		Unk. Cladoceran	0	8.8	0	0
		<i>Epischura</i>	0.4	38.5	3.7	6.5
		<i>Eurytacops</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

794 **Table 3.** Acoustic properties of crustacean zooplankton. For each class of scatterers (Cladocerans,
 795 Copepods, and Nauplii larvae), the mean acoustic target strength (dB re m²) and individual wet weight
 796 (μg) are displayed, along with the percentage by biomass of the net catch made up of that class of
 797 scatterers.

Date	Lake	Cladocerans			Copepods			Nauplii			Weighted Avg.	
		TS (dB)	W (μg)	%	TS (dB)	W (μg)	%	TS (dB)	W (μg)	%	TS (dB)	W (μg)
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

798

799 **Table 4.** Average fish target strength (TS), with estimated lengths and wet weights, plus or minus
 800 standard deviations. The final column gives the number of fish targets detected in each survey. Target
 801 strengths were measured in-situ in each lake with a 120 kHz split-beam echosounder and converted to
 802 lengths and weights using published empirical TS-length and length-weight scaling relations (see
 803 Methods for details). The 120 kHz echosounder was not operated in Independence Lake, so no fish TS
 804 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

805

806 **Table 5.** Acoustic estimates of wet-weight biomass density (in g m⁻²) and total biomass (in kg) of
 807 zooplankton and fish in each lake show seasonal changes in different trophic levels as well as interlake
 808 differences. These values (as well as the ratio of lower to higher trophic level biomasses) may provide
 809 useful data for investigations of various ecosystem-level processes in these habitats. Fish biomass was
 810 not estimated in Independence Lake due to the lack of reliable target strength estimates.

Date	Lake	Area (km ²)	Zooplankton		Fish		Ratio
			Density (g m ⁻²)	Biomass (kg)	Density (g m ⁻²)	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	0.0045	2,200	3.4
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
811 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

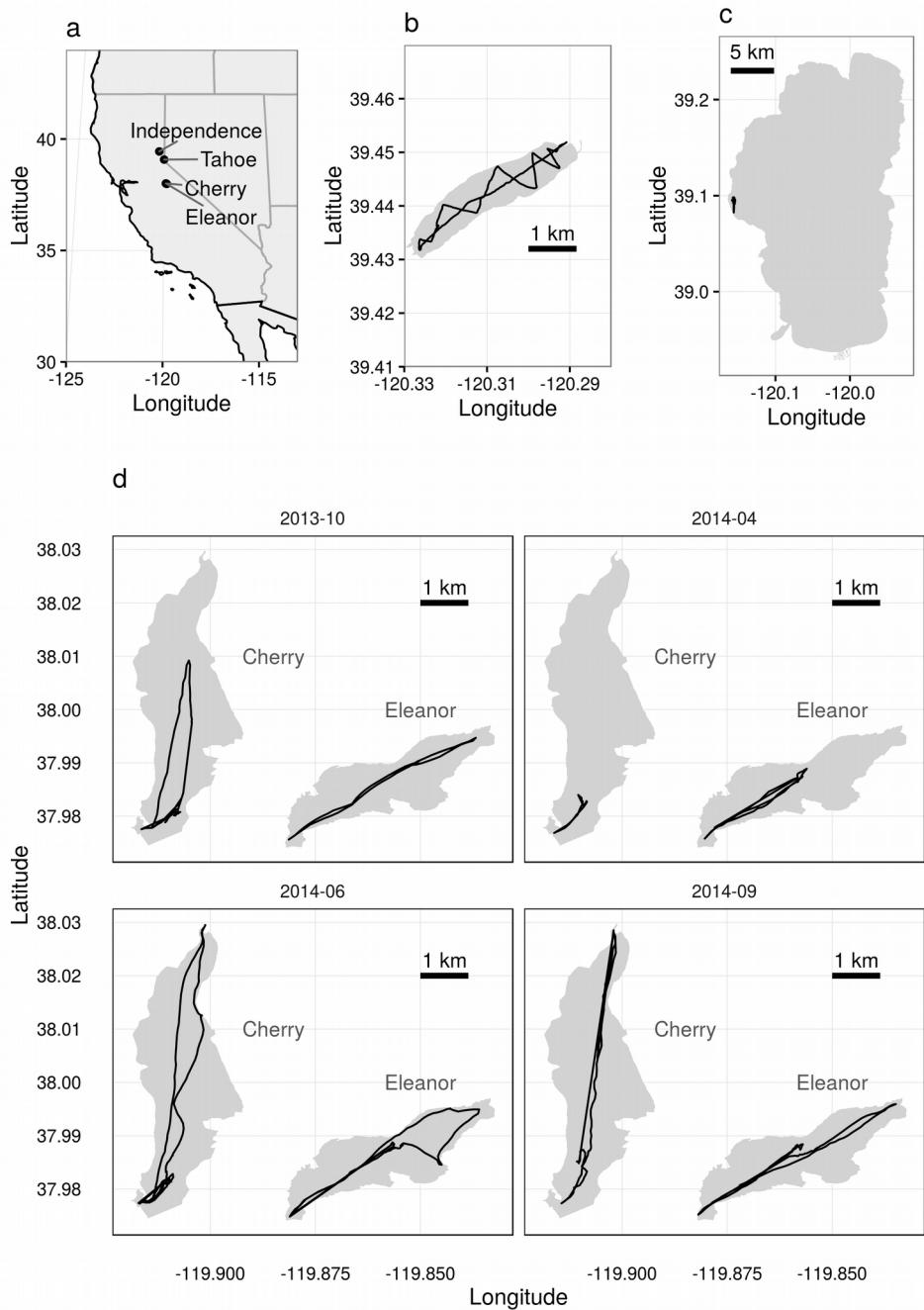
812 **Table 6.** Summary of regression models for spatial trends in the density of zooplankton, by lake and
 813 survey. The average wet-weight biomass density of zooplankton (in g m⁻³), was averaged through the
 814 water column, log₁₀-transformed, and modeled as a linear function of distance (in km) from the lake's
 815 inlet and from the shore. The columns "Intercept", "Inlet distance", and "Shore distance" give the
 816 regression intercept and coefficients associated with each covariate. Their respective *p*-values are in
 817 the columns to their right. These trends were not estimated in Lake Tahoe because only a small
 818 proportion of the lake's area was surveyed (Figure 1).

819

Date	Lake	Intercept	<i>p</i>	Inlet	Shore	<i>p</i>	<i>R</i> ²
				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
820	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

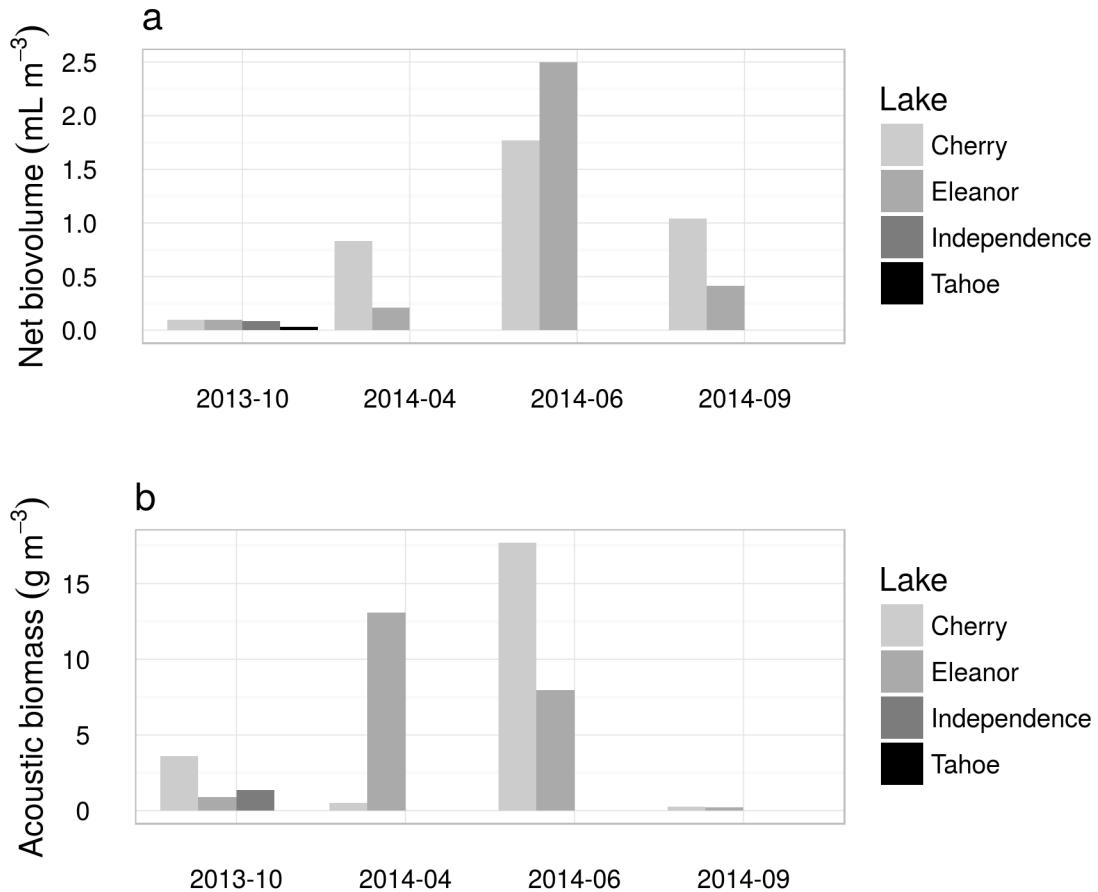
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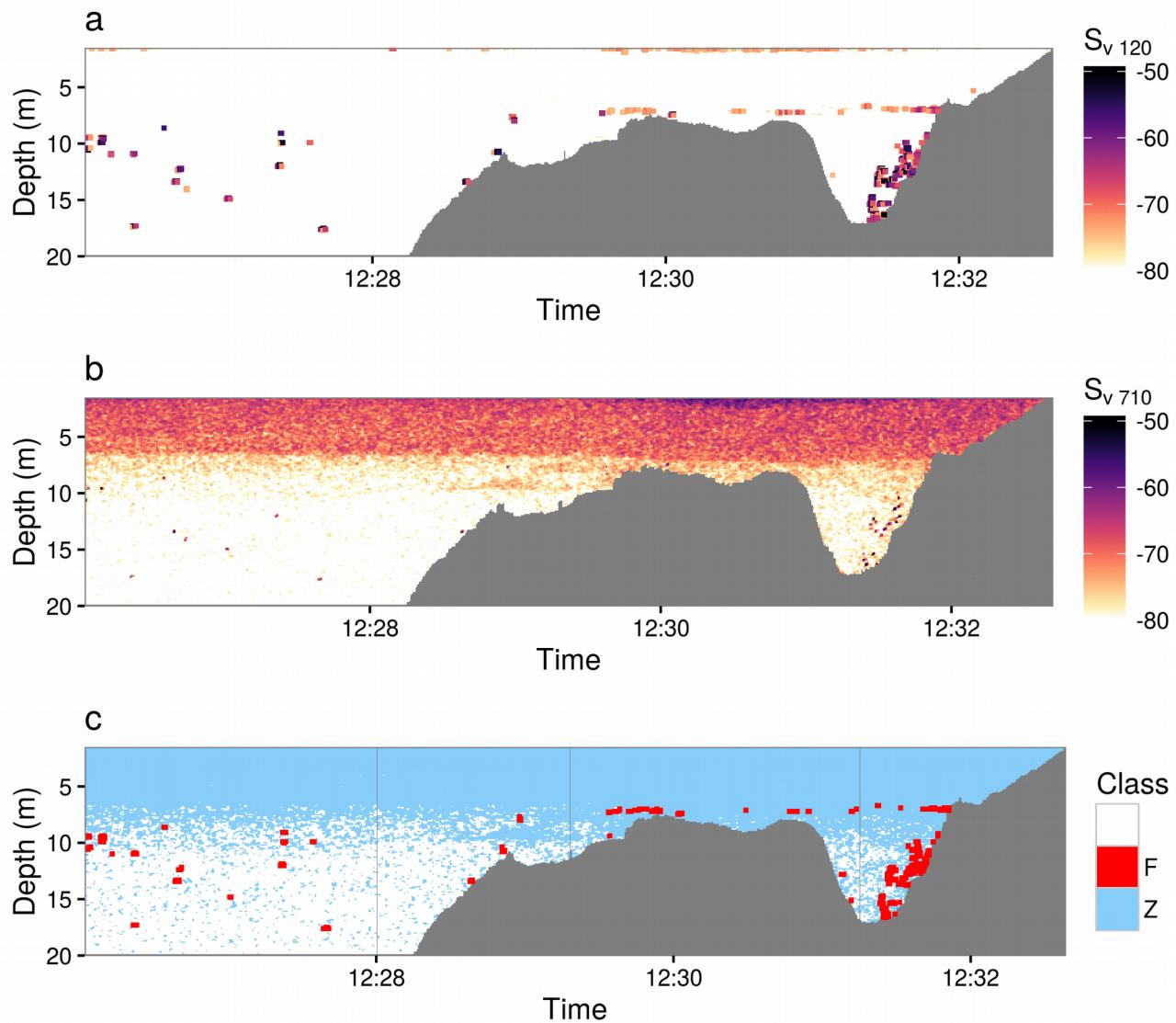
823

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



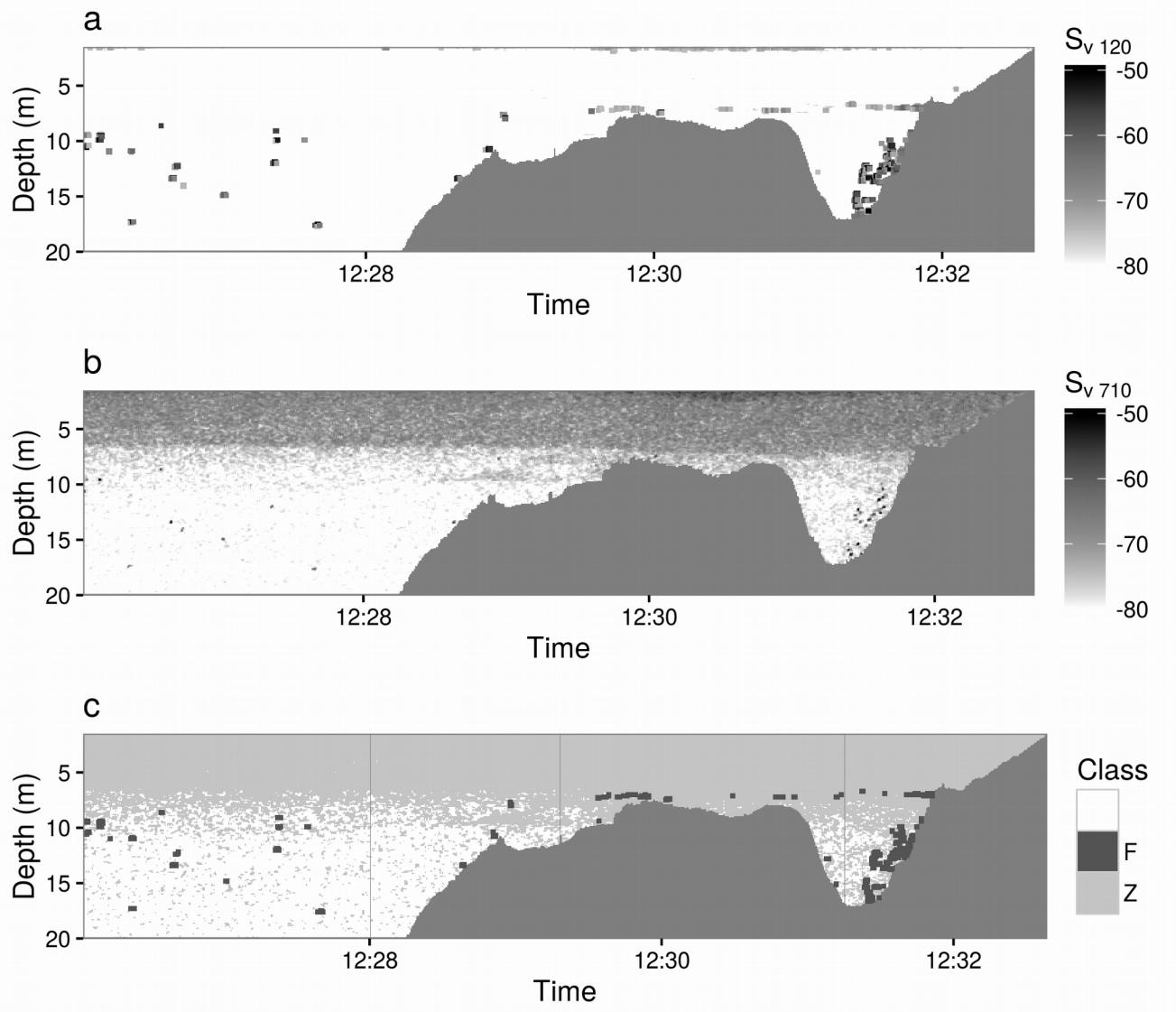
828

829 **Figure 2.** Zooplankton abundance measured by nets and acoustics in each of four seasonal surveys.
 830 The color of each bar indicates the lake; note that Independence and Tahoe were only sampled in
 831 October 2013. (a) Biovolume of zooplankton caught in vertical net tows. These values are normalized
 832 by the volume of water filtered, giving units of mL of biovolume per cubic meter of lake water. (b)
 833 Wet-weight biomass of zooplankton per cubic meter, estimated from acoustic surveys, using measured
 834 zooplankton lengths and species identities to parameterize target strengths and length-weight
 835 relationships.



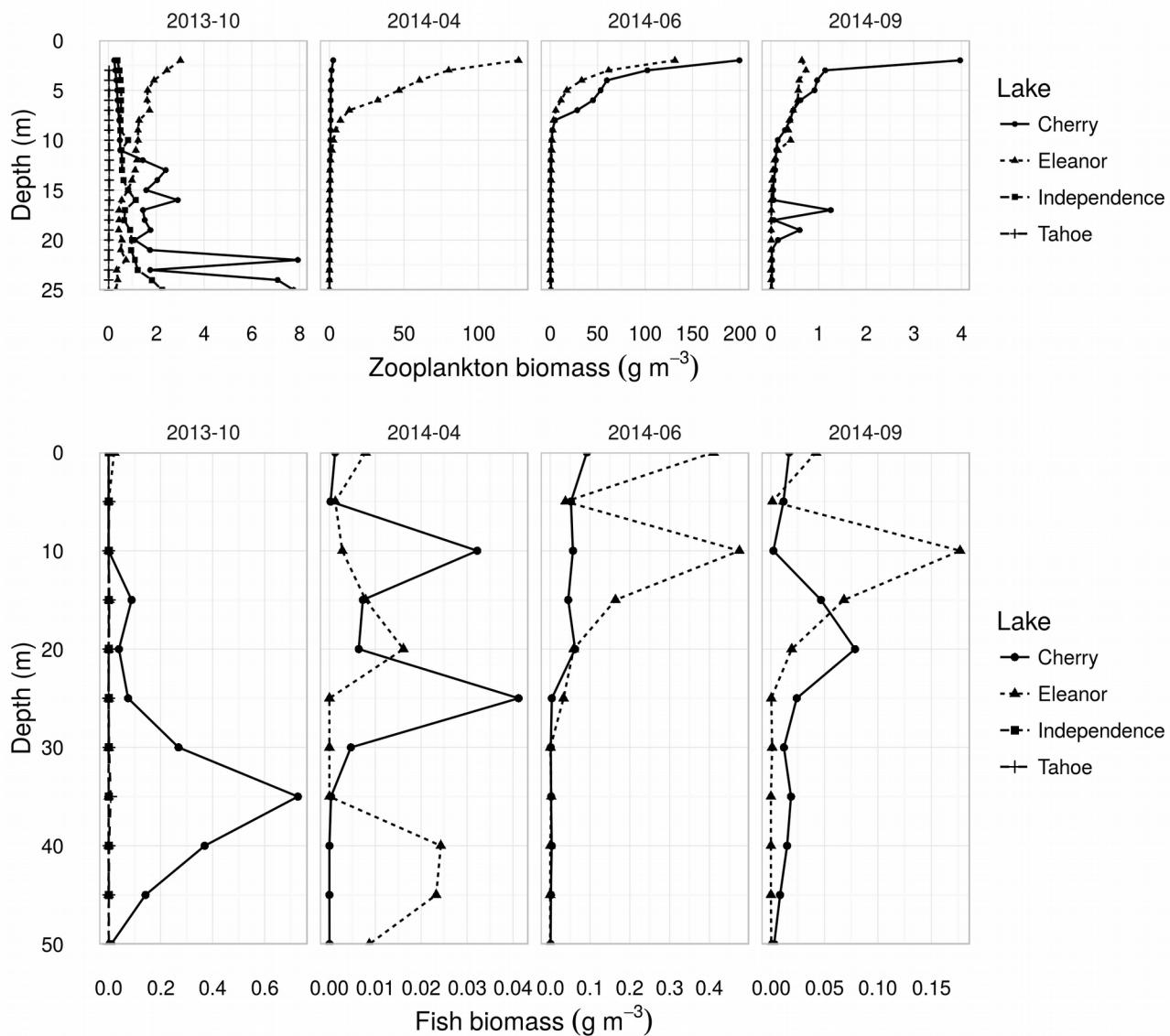
836

837 **Figure 3.** Acoustic profile through part of Cherry Lake on 24 June 2014, showing acoustic backscatter
 838 at (a) 120 kHz and (b) 710 kHz. Isolated dots are echoes from individual fish, while the layer of
 839 scattering between ~7 m and the surface represents echoes from zooplankton, which are only detectable
 840 at 710 kHz. (c) Classification of backscatter as fish (“F”) or zooplankton (“Z”) based on frequency
 841 differencing. Red areas are fish, scattering more strongly at 120 kHz, while blue area are zooplankton,
 842 scattering more strongly at 710 kHz. Pixels classified as fish have been dilated slightly in (a) and (c)
 843 for better visibility. White shows areas of empty water (volume backscatter < -80 dB at 710 kHz). The
 844 horizontal length of this section is approximately 700 m.



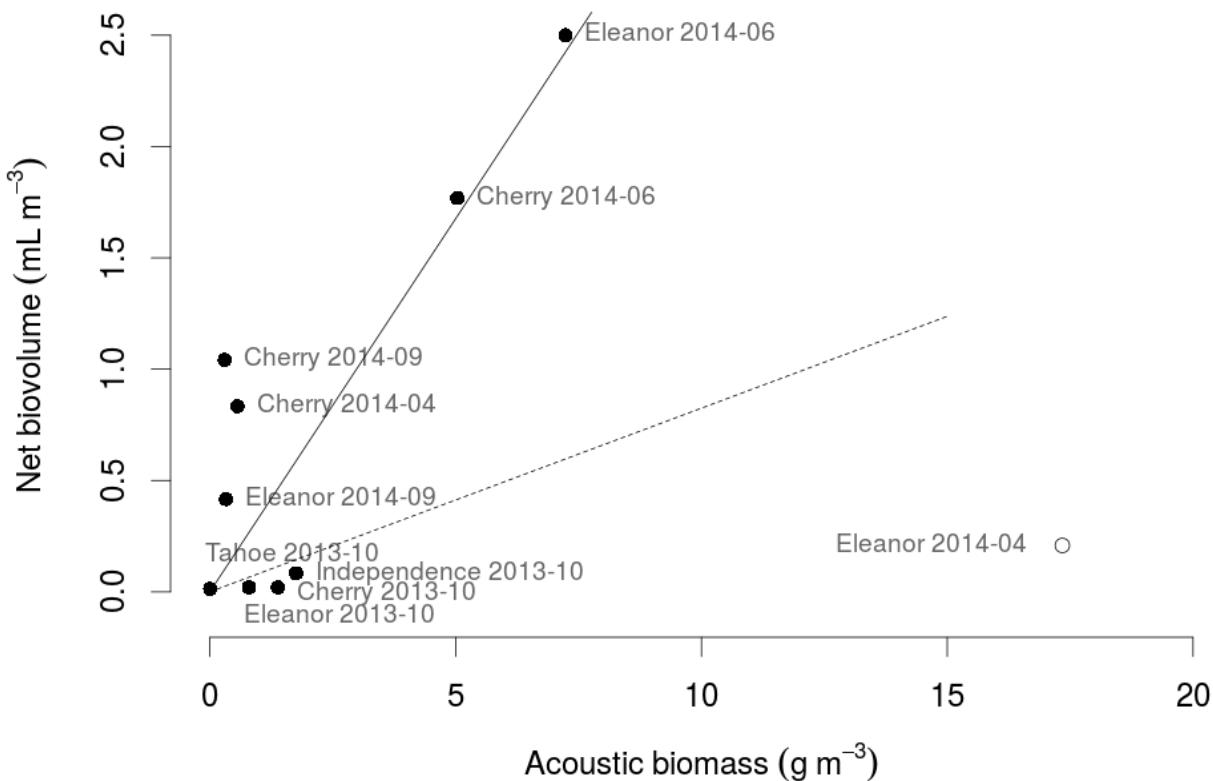
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846 **Figure 3 (Grayscale rendering for print publication)**



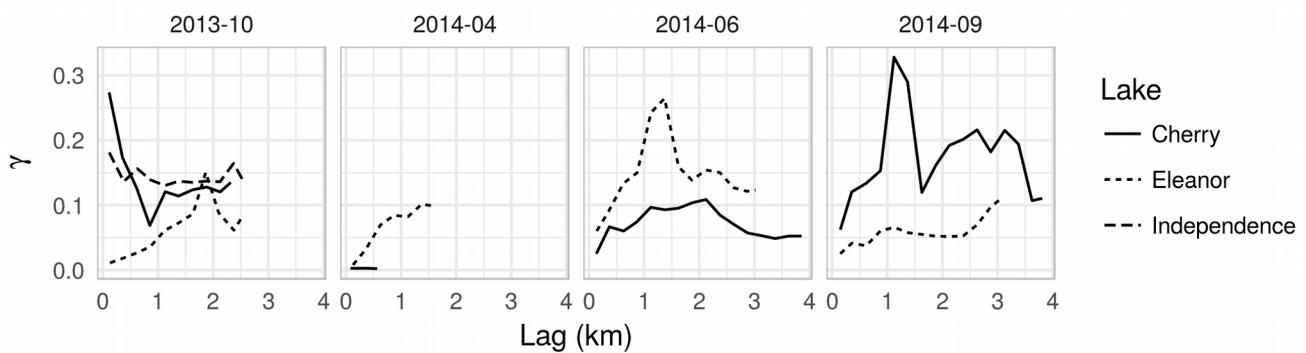
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848 **Figure 4.** Depth profiles of zooplankton (top row) and fish (bottom row) wet weight biomass density
849 measured acoustically in the lakes sampled during each of four seasonal surveys. (Lake Tahoe and
850 Independence Lake were only sampled in October 2013). Lines show approximate biomass density of
851 all zooplankton as a function of depth,. The target strengths used to calculate numerical densities from
852 acoustic backscatter measurements were estimated using the distorted-wave Born approximations for
853 the zooplankton communities, and measured in-situ for fish using a split-beam echosounder. Note
854 differing x-axis scales in each plot.



855

856 **Figure 5.** Regression of biovolumes estimated from vertical net tows with acoustic estimates of wet
 857 weight biomass density. Data points are labeled with their lake and date. Two best-fit lines are plotted:
 858 the dashed line was fit to all data points, while the solid line excluded Lake Eleanor in April 2014,
 859 plotted as an empty point.
 860



861

862 **Figure 6.** Empirical variograms of log-transformed zooplankton areal biomass density (i.e., mass of
 863 zooplankton per m^2 of lake surface) for each lake and survey.