

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

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12 Running head: Zooplankton and fish in Sierra Nevada Lakes

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14 Keywords: acoustics, biomass estimation, fish, patchiness, target strength, variograms, zooplankton.

15 **Abstract**

16

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

33 **Introduction**

34 Zooplankton play a number of important roles in lake ecosystems. They influence water clarity
35 and nutrient cycling through grazing on primary production. They are also the conduit through which
36 primary production reaches larger predators such as fish, which often have commercial, recreational,
37 and cultural importance for humans. In lakes at high elevations, the biomass of middle and upper
38 trophic levels has been measured infrequently (McNaught et al. 1999), in contrast with more common
39 measurements of lower trophic level biomass (Pugnetti and Bettinetti 1999; Higley et al. 2001). The
40 spatial distribution of that biomass within high-elevation lakes has been measured only rarely (Masson
41 et al. 2001). Alpine and sub-alpine lakes differ in several important ways from low-elevation lakes.
42 They typically have lower inputs of sediment and nutrients than lowland lakes, and are clearer and
43 more oligotrophic. As a consequence, different environmental factors, such as ultraviolet radiation,
44 may be more important in structuring their pelagic ecosystems (Rose et al. 2009; Williamson et al.
45 2016). On average, lake size decreases with elevation, as does the duration of the effective growing
46 season. These factors increase the potential for interactions between different habitats, and tend to
47 increase food-related competition (Guisande et al. 2003). Alpine and sub-alpine lakes may also be
48 more sensitive to human disturbance, including eutrophication, pH changes, deforestation, and
49 introductions of non-native plant and animal species (Bradford et al. 1998; Knapp et al. 2001;
50 Schabetsberger et al. 2009).

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

64 measured these distributions at high temporal or spatial resolutions.

65 The lack of high-resolution measurements of zooplankton is largely a consequence of sampling
66 techniques. The most common methods for sampling zooplankton are net tows and traps. Even when
67 closing nets are used for vertically stratified tows, spatial resolution is limited, and all nets and traps
68 involve a degree of spatial or temporal blurring. Automated optical techniques (Finlay et al.
69 2007) have better spatial resolution than traps or nets, though observations are still limited to the
70 instrument's towed path through the water, and they lose taxonomic resolution relative to direct
71 samples.

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

88 We surveyed the zooplankton and fish in four lakes in the Sierra Nevada mountains of
89 California, USA, between autumn 2013 and autumn 2014: Cherry Lake, Lake Eleanor, Independence
90 Lake, and Lake Tahoe. Cherry and Eleanor are similar in size and shape, and are less than 2 km apart
91 from each other. Lake Tahoe and Independence Lake are located more than 100 km to the north, and
92 are larger (Tahoe) and smaller (Independence) than Cherry and Eleanor. Our primary tool was a two-
93 frequency acoustic system which allowed us to measure the vertical and horizontal distribution of these
94 animals at high (meter-scale) resolution. Acoustic observations were augmented with net samples to

95 identify the zooplankton scatterers and measure their sizes, to parameterize models of their acoustic
96 target strengths (TS). Fish TS were measured in situ. Zooplankton TS and fish TS values were used to
97 convert acoustic backscatter to biomass, yielding estimates of total biomass at two trophic levels. The
98 high-resolution nature of the acoustic data also let us compare the vertical profiles and horizontal trends
99 of zooplankton and fish density among lakes. Changes in the distributions of zooplankton and fish
100 from one season to another were also examined. Finally, we quantified the zooplankton's spatial
101 variability across scales using empirical variograms. Spatially structured variance indicates a patchy
102 distribution, which in turn implies that the dominant ecological process or processes are spatially
103 inhomogenous. Because Cherry Lake and Lake Eleanor are so similar, we hypothesized that the spatial
104 distributions of fish and zooplankton would not vary between these lakes, and that these communities
105 would experience similar seasonal changes.

106

107 **Methods**

108 *Study lakes*

109 Surveys were conducted in four lakes in the Sierra Nevada: Cherry Lake, Lake Eleanor,
110 Independence Lake, and Lake Tahoe (Figure 1). Our main focus was on Cherry Lake and Lake
111 Eleanor, located at the border of Yosemite National Park near 38° 0' N, 119° 52.6' W (Figure 1). Both
112 are reservoirs of the San Francisco Public Utilities Commission. Cherry Lake is artificial, created by
113 the damming of Cherry Creek in 1955 (Hennesey 2012). Lake Eleanor formed naturally, but was
114 enlarged and deepened by the construction of a dam in 1918 (Eckart 1940). Both lakes are
115 approximately 1,420 m above sea level, placing them in the upper montane forest zone (Kaufman et al.
116 2007), though their catchments extend up through the subalpine zone and include large areas of bare
117 rock above the treeline. Their areas are 6.3 km² (Cherry) and 3.9 km² (Eleanor). Both lakes have been
118 stocked with fish, including rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), and, in
119 Cherry Lake, eastern brook trout (*Salvelinus fontinalis*) (Bingaman 1961; United States Forest Service
120 2016). Cherry and Eleanor were surveyed in October 2013, April 2014, June 2014, and September
121 2014 (Figure 1). In addition to our repeated surveys of Cherry and Eleanor, we surveyed Independence
122 Lake, located at 39° 26.4' N, 120° 18.6' W, and Lake Tahoe, at 39° 10' N, 120° 0' W once each in
123 October 2013. Independence is a natural lake, 2,127 m above sea level and 2.6 km² in area. It has
124 never been stocked with fish, and is one of only two lakes in the world with a self-sustaining
125 population of Lahontan cutthroat trout, *Oncorhynchus clarkii henshawi* (Nielsen and Sage 2002). Lake

126 Tahoe, at 1,897 m elevation, is much larger and deeper than the other three lakes, with a surface area of
127 490 km² and maximum depth of 501 m. It is also oligotrophic, in contrast to the three smaller lakes,
128 which are mesotrophic. The watersheds of the three smaller lakes are undeveloped, although portions
129 of the Cherry and Eleanor Creek watersheds were burned during the 2013 Rim Fire (National Wildfire
130 Coordinating Group 2013). Lake Tahoe is bordered by several towns, with a total permanent
131 population of approximately 50,000. All four watersheds are on granitic substrate.

132

133 *Acoustic data collection*

134 Surveys were run from outboard-powered boats trailered to each lake, and took place during
135 daytime. Acoustic volume backscatter was recorded at two frequencies, 120 and 710 kHz. Volume
136 backscatter can be expressed either in logarithmic form as “mean volume backscattering strength,” S_V ,
137 or a linear form as “volume backscattering coefficient,” s_V , related by the equation $s_V = 10\log_{10}(S_V)$
138 (MacLennan et al. 2002). The volume backscattering coefficient is proportional to the numerical
139 density of sound-scattering objects in the water. The 120 kHz echosounder was a Simrad ES60 with a
140 split-beam transducer (7° beam width), which can accurately measure the target strength of individual
141 fish in situ. The 710 kHz echosounder was a Simrad EK60 with a single-beam (2.8° beam width)
142 transducer. This high-frequency system could detect small (<1 mm) zooplankton (Holliday and Pieper
143 1995; Warren et al. 2016), but its effective range was limited to approximately 30 m due to sound
144 attenuation in water. Both transducers were deployed on a pole mount off the side of the survey boat at
145 depths of approximately 30-50 cm depending on wave conditions.

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

153 Independence Lake was sampled on 20 October 2013, and Lake Tahoe was sampled on 21
154 October 2013. Cherry Lake and Lake Eleanor were each sampled four times. Cherry was sampled on
155 29 October 2013, and on 2 April, 24 June, and 10 September 2014. Eleanor was sampled one day later,
156 on 30 October 2013, and 3 April, 25 June, and 11 September 2014. In the three smaller lakes, we

157 attempted to perform a lengthwise transect from one end of the lake to the other. In Independence
158 Lake, we were also able to add a series of zig-zag transects across the main axis of the lake (Figure 1).
159 The April 2014 transects in Cherry and Eleanor were shorter due to a snowstorm, which required slow
160 travel on the mountain roads and reduced the time available for sampling.

161

162 *Zooplankton sampling and target strength models*

163 Zooplankton were collected on each sampling day near the center of the lake with a vertical tow
164 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
165 equipment problem with the ring net during the October 2013 trip to Cherry and Eleanor, we instead
166 used an open Van Dorn bottle (10 cm diameter) with an elastic nylon mesh ($\sim 100 \mu\text{m}$) over one end.
167 This was hauled vertically through the water column with its uncovered end up, acting like a small-
168 diameter net. Samples were preserved for later analysis in 10% buffered formalin. In the lab, the total
169 biovolume of each sample was measured after allowing it to settle in a graduated cylinder. Because of
170 the small diameter of the Van Dorn sampler, the biovolumes of the samples from Cherry and Eleanor in
171 October 2013 were smaller than the finest graduation on our cylinder, preventing a precise
172 measurement. We estimated them at 0.1 mL; our analyses did not appear sensitive to these estimates
173 when they were in the range of 0-1 mL. A subsample of 200-300 animals was split from each original
174 sample and counted under a compound microscope. Animals were identified to the lowest possible
175 taxonomic level. In addition, the lengths of the first 30 animals counted were measured to the nearest
176 0.1 mm.

177 To convert acoustic backscatter to animal densities it is necessary to know the backscattering
178 cross-section, σ_{BS} , of the scattering organisms. The backscattering cross-section is also expressed in its
179 logarithmic form, the target strength, $\text{TS} = 10 \log_{10}(\sigma_{\text{BS}})$ (MacLennan et al. 2002). We calculated these
180 values using the distorted-wave born approximation (DWBA, Stanton et al. 1998, McGehee et al.
181 1998), implemented as a package, SDWBA.jl (Urmey 2016) in the Julia language (Bezanson et al.
182 2012). This package uses models for the body shapes of cladocerans and calanoid copepods from
183 Warren et al. (2016), and we assumed density and sound-speed contrasts of 1.04 (Stanton and Chu
184 2000). For each lake, sampling date, and taxonomic group (i.e., cladocerans and copepods), we
185 calculated the mean body length and its standard deviation (s.d.). We then drew 1000 random lengths
186 from a normal distribution with these parameters (i.e., a parametric bootstrapping procedure, Efron and
187 Tibshirani 1993). The generic body shape was scaled to each length and its backscattering cross-section

188 (σ_{BS}) calculated using the DWBA. We also calculated each body shape's dry weight, W_d , using a
189 published regression for either calanoid nauplii, the calanoid *Diaptomus oregonensis*, or *Daphnia*
190 *galeata* (Culver et al. 1985). Dry weights were converted to wet weights, W_w , using a relationship
191 from Wiebe et al. (1975).

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

195 $\langle \sigma_{BS,tot} \rangle = \sum_{i=1}^m p_i \langle \sigma_{BS,i} \rangle$

196 $\langle W_{w,tot} \rangle = \sum_{i=1}^m p_i \langle W_{w,i} \rangle$

197 where p_i is the proportional numerical abundance of scattering class i in the net sample and the angled
198 brackets denote an average or expected value. The total numerical density of all zooplankton (number
199 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 $b_{tot} = n_{tot}$
200 $\langle W_{w,tot} \rangle$.

201

202 *Acoustic data processing and analysis*

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

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

216 Acoustic integration cells were classified as fish if their backscatter was higher at 120 kHz than
217 at 710 kHz, since resonant scattering from fishes' swim bladders makes them stronger targets at the

lower frequency. Zooplankton backscatter at 710 kHz in each lake on each sampling date was apportioned to copepods, cladocerans, and nauplius larvae using the proportional abundances in the net samples and converted to numerical and biomass densities based on the representative values for the overall zooplankton community, as described above.

Fish densities were calculated from the integrated 120 kHz backscatter, using the mean TS of the individual fish targets to convert backscatter to fish densities. To obtain approximate estimates of fish biomass, we first converted each fish target's TS to a length (in cm) by solving the relationship

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

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

Comparison of net and acoustic biomass

To test the agreement between acoustic estimates of zooplankton biomass and the direct net sampling, we regressed the acoustic estimate of biomass density for each lake on the biovolume from the corresponding net sample. Net biovolumes were normalized by the total volume of water filtered to give a biovolume density, in mL m^{-3} . The intercept in the linear regression was fixed at the origin, since a preliminary model showed it was not significantly different 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 ($n=10$). 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

249 without this point for comparison. The significance of the slopes was assessed at the $p=0.05$ level.
250 These analyses were run using R (R Development Core Team 2016).

251

252 *Distribution of zooplankton and fish*

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

268

269 **Results**

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

277 Over the four sampling dates, more zooplankton species were recorded in Cherry Lake and
278 Lake Eleanor than in the single surveys in Independence and Tahoe (Table 2). In October 2013, the
279 communities in both lakes were 50-60% cladocerans in the genera *Daphnia* and *Diplostraca*, with the

280 remainder mostly composed of cyclopoid copepods in the genus *Euryyclops*,. The following April,
281 the community in Cherry Lake remained similar, but in Lake Eleanor it had shifted to 59% Copepods,
282 mostly *Epischura nevadensis*. During the final two surveys, in June and September 2014, the
283 communities in both lakes were between 70 and 85% copepods, a large proportion of which were
284 copepodites of unknown calanoid species. The cladocerans, which composed 15-32% of the
285 communities in June and September 2014, were again a mix of *Daphnia* and *Diplostraca* (Table 2).
286 Biovolumes of zooplankton estimated from the nets ranged from 0.1 mL m⁻³ in Lake Tahoe to 2.5 mL
287 m⁻³ in Lake Eleanor in June 2014 (Figure 2). Biovolumes in both Cherry Lake and Lake Eleanor were
288 highest in June 2014 and lower in the other months.

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

298 Mean fish target strengths, measured in situ, ranged between -40 and -36 dB re m²,
299 corresponding to mean lengths from 21 to 31 cm, and mean weights from 200 to 720 g (Table 4). In
300 October 2013, the mean TS (and the mean lengths and weights derived from them) were roughly equal
301 in Lake Eleanor and Lake Tahoe and slightly higher in Cherry Lake. In the following three surveys,
302 however, mean TS was 1-3 dB higher in Lake Eleanor, with corresponding length and weight
303 differences of 2-8 cm and 140-380 g.

304 The 710 kHz echosounder was able to detect small zooplankton in the lakes, and the frequency-
305 differencing procedure could clearly separate them from fish echoes (Figure 3). Mean zooplankton
306 wet-weight biomass densities measured acoustically were relatively low (< 20 g m⁻³) in all lakes, and
307 varied seasonally (Figure 2). In October 2013, the mean zooplankton numerical density in all four
308 lakes was low, with less than 5 g of zooplankton wet-weight biomass m⁻³ (Figure 2). Lake Eleanor had
309 a weak sound-scattering layer extending from the surface to 15 m, corresponding to an estimated peak
310 zooplankton biomass density of just over 4 g m⁻³ (Figure 4). In April 2014, Cherry Lake contained

zooplankton at similarly low densities, but Lake Eleanor had a denser zooplankton layer near the surface, increasing from near-zero density at 10 m depth to a maximum of 125 g m⁻³ at 2 m depth, the bottom of the echosounder's blind zone (Figure 4). Two months later in June, this layer was still present, though not quite as deep as in April. During this time, a similar layer had also appeared in Cherry Lake, with a maximum density of 200g m⁻³ at 2 m depth (Figure 4). By September, the surface zooplankton layer in Lake Eleanor had mostly disappeared, and the layer in Cherry Lake was much less dense (maximum 4 g m⁻³, Figure 4).

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

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.

342 Fish biomass in Cherry Lake and Lake Eleanor was lowest the following April, increasing somewhat in
343 the following two surveys in June and September. Fish biomass did not vary as widely as zooplankton
344 biomass. In all surveys, zooplankton outweighed fish by a factor between 3 and 850.

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

351 Zooplankton biomass density displayed significant trends with respect to distance from the inlet
352 and shore in most surveys, though the directions of these trends were variable (Table 6). The most
353 pronounced trend was in Cherry Lake in June 2014, where zooplankton biomass density was an order
354 of magnitude higher near the lake's inlet than near the dam at the other end. In eight out of the nine
355 surveys, the signs of the coefficients for distance from shore and distance from the inlet were the same.
356 The single survey in Independence Lake was the exception, with biomass density increasing closer to
357 the inlet and decreasing closer to shore. In three of the four surveys in Cherry Lake, zooplankton
358 density increased towards the shore and inlet. In Lake Eleanor, the reverse was true: three out of four
359 surveys showed zooplankton density higher away from shore and the inlet (Table 6). These spatial
360 regressions explained a low-to-moderate amount of the variability in the data, with R^2 values ranging
361 from approximately zero in Lake Eleanor in October 2013, to 0.73 in Cherry Lake in June 2014 (Table
362 6).

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

371 In June, the sill of the variogram in Lake Eleanor had increased to 0.15 at a range of 2 km
372 (Figure 6), implying an expected difference in biomass on the order of 50% when transformed back to

373 linear units. In Cherry Lake, the variogram was relatively flat (Figure 6), showing little evidence for
374 spatial structure other than the lakewide trends described above. Spatial variability in Lake Eleanor
375 decreased somewhat between June and September 2014. However, the variogram for Cherry Lake in
376 the final survey showed higher overall variability, peaking at 0.37 at a lag of 1 km and a sill near 0.2
377 beyond 1.5 km. Overall, the variogram sill values ranged from approximately 0.1 to 0.2. These
378 values, in \log_{10} -transformed units, imply multiplicative differences (\times/\div) in zooplankton density from
379 0.25 to 1.6 at long ranges, where “long ranges,” as defined by the variograms, are between 1 and 2 km.
380

381 Discussion

382 Our acoustic measurements produced estimates of the total biomass of zooplankton and fish in
383 four peri-alpine lakes in the Sierra Nevada Mountains. To our knowledge, these are the first biomass
384 estimates for any trophic level ever made in Independence Lake, Cherry Lake, and Lake Eleanor. In
385 Lake Tahoe, our estimate of the mean density of small zooplankton (approximately 2,200 individuals
386 m^{-3}) was in good agreement with prior estimates (e.g. 0-23,000 individuals m^{-3} , Goldman et al. 1979).
387 The measurements in Independence Lake and Lake Tahoe represent only a single snapshot of the
388 zooplankton and fish in each lake, and should not be over-interpreted. The repeated sampling in
389 Cherry Lake and Lake Eleanor did allow us to capture some of their seasonal variability.

390 A spring bloom of zooplankton occurred in both Cherry Lake and Lake Eleanor, with peak
391 biomass densities of 4-6 g m^{-3} . In spring and summer, the zooplankton were concentrated in the upper
392 5-10 m of the water column, probably associated with a stratified surface layer. In 2014, the bloom
393 appeared to begin earlier in Lake Eleanor than in Cherry Lake, since a near-surface zooplankton layer
394 was present in Eleanor, but not Cherry, during the early April survey. By June, both lakes had similar
395 zooplankton densities, and by September, zooplankton populations in both lakes had declined by an
396 order of magnitude. At this point there were still more zooplankton in Cherry Lake, however,
397 suggesting that the bloom there, which started later, also took longer to collapse in the fall. This
398 pattern, of a spring and summer increase in zooplankton as they respond to blooming phytoplankton, is
399 consistent with standard models of seasonal cycles in lake ecosystems (Sommer et al. 1986, 2012).
400 While the seasonal changes in Cherry Lake and Lake Eleanor were similar, there were also distinct
401 differences, both in the vertical distribution of fish and zooplankton, and the timing of seasonal blooms.
402 These differences were greater than expected given the apparent similarities between the sizes, depths,
403 and catchments of the two lakes. Whether these differences emerged endogenously or were driven by

404 unobserved physical factors is unknown.

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

416 Two longer-term environmental changes under way during this study deserve particular
417 mention. The first was the Rim Wildfire, which started approximately 20 km southwest of Cherry Lake
418 and Lake Eleanor on 17 August 2013. The fire spread rapidly, becoming the third-largest wildfire on
419 record in California, and burned portions of both lakes' watersheds. The fire was not fully contained
420 until several days after the first surveys in October 2013 (National Wildfire Coordinating Group 2013).
421 Fires may have a number of effects on lakes and the animals in them, for instance by increasing runoff
422 from burned watersheds, depositing ash from the air, or altering the characteristics of incident solar
423 radiation via drifting smoke plumes (Urmy et al. 2016; Williamson et al. 2016). On the other hand, the
424 effect of a burned catchment on a lake's zooplankton may be minimal (Patoine et al. 2002).

425 The second major environmental trend was a five-year drought (2012-2017) in the western
426 United States. One consequence of the drought was a decline in the water levels of Cherry Lake and
427 Lake Eleanor, which were nearly 8 m lower in the final survey in September 2014 than they were in the
428 first survey, in October 2013 (United States Geological Survey 2017). Both lakes are reservoirs
429 supplying water and electricity to San Francisco, so their levels are managed by that city's Public
430 Utilities Commission. The drought probably also played a role in the spread of the Rim Fire: most of
431 California's largest wildfires, including the Rim Fire, have occurred during droughts (Williamson et al.
432 2016). However, the drought may also have mitigated some of the fire's effects on Cherry and Eleanor:
433 precipitation during the winter of 2013-2014 was well below normal (California Department of Water
434 Resources 2014), meaning that runoff and erosion in the burned areas were much less than they might

435 have been in a more normal year. Both the drought and fire are likely to have affected the lakes in
436 some way, but the limited sampling schedule makes it impossible to separate these effects from the
437 expected seasonal cycle for a temperate lake.

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

449 There was fair agreement between the acoustic and net-based estimates of zooplankton
450 biomass. However, the data from Lake Eleanor in April 2014 formed a notable outlier, with the net-
451 based biovolume much lower relative to the acoustic biomass than expected, based on the other
452 samples. A relatively strong scattering layer was visible near the surface along the entire survey track.
453 This layer, along with weaker-than-average zooplankton TS (Table 3), accounted for the high acoustic
454 biomass. The small biovolume estimate is accurate, at least based on the net sample (0.5 mL of
455 zooplankton from a total filtered volume of 15 m³). The discrepancy between these two measures is
456 probably due to some combination of random variability in the net sample and uncertainty in our TS
457 estimates. Regardless, regressions with and without this outlier both produced positive slopes.
458 Without it, the slope was significantly different from zero with a value of 0.34 mL mg⁻¹. Wiebe et al.
459 (1975) found that displacement biovolume *DV* and wet weight *WW* of marine zooplankton were related
460 by the equation

$$461 \log_{10}(DV) = 0.078 + 1.026 \log_{10}(WW)$$

462 which, in linear terms, implies a slope of approximately 1.2 mL mg⁻¹, 3.5 times higher than our
463 estimate. This difference is not totally unexpected: Wiebe et al.'s (1975) data came exclusively from
464 net samples in marine environments, and acoustic estimates of biomass are often several times higher
465 than those based on net catches, probably due to avoidance reactions by the animals (Warren and Wiebe

466 2008; Wiebe et al. 2013). If true, this implies that a regression of net-based biovolume on acoustically-
467 derived biomass would have a shallower slope than the same regression on net-based biomass. The
468 multi-step conversion process from acoustic backscatter to biovolume introduces a number of
469 uncertainties. In addition, the spatial extent of our net sampling was quite limited compared with that
470 of the acoustics, and individual net samples may not be fully representative of the lake-wide
471 zooplankton community. Our results should thus be interpreted with some caution. However, our
472 procedures do produce realistic biomass values, with reasonable agreement between nets and acoustics,
473 increasing our confidence that the patterns observed are biologically meaningful.

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

485 Even after subtracting the lake-scale trend in zooplankton density, spatial autocorrelation was
486 evident in the residuals, as illustrated by the empirical variograms (Figure 6). These should be
487 interpreted with caution, since they were based in most cases on single reciprocal transects down the
488 main axis of each lake which may not have captured any spatial anisotropy present. In particular, the
489 restricted time available to survey Cherry Lake on 2 April 2013 meant that the transect was only about
490 1 km long, limiting our ability to draw conclusions about the spatial distribution of zooplankton.
491 Regardless, most of the variograms in Cherry Lake and Lake Eleanor did show evidence of spatial
492 patchiness in the distribution of zooplankton, with approximate spatial scales, based on the variogram
493 ranges, between 500 and 2000 km. These ranges are well below the sizes of the lake basins, suggesting
494 that ecological processes in these lakes are not spatially uniform.

495 It is unknown what processes generate and maintain patchiness in these lakes. In the ocean,
496 patchiness in zooplankton appears to be driven mostly by bottom-up processes, with scales of

497 biological variability mirroring scales of physical variability (Denman et al. 1977; Mackas et al. 1985;
498 Urmy et al. 2012). At smaller spatial scales, animal behavior and ecological interactions become more
499 important in generating spatial variability (Pinel-Alloul 1995; Folt and Burns 1999), though these
500 scales and processes are harder to observe and have been studied less in the field. It seems unlikely
501 that these lakes (with the possible exception of Tahoe) are large enough to support much horizontal
502 physical variability, so the patchiness in the zooplankton is probably due to other processes, such as
503 aggregation (e.g., Byron et al. 1983) or local predation by schooling fish. In this interpretation, the
504 lake's finite boundaries act like a high-pass filter, preventing large-scale physical processes (e.g. fronts,
505 gyres, nutrient upwelling) from creating spatial variability that masks patchiness due to smaller-scale,
506 biological processes (swarming, predator-prey interactions, etc.). If this interpretation is correct, future
507 studies could use appropriately-sized lakes as model systems to study biogenic patchiness free of
508 interference from larger-scale processes.

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

524 Despite these uncertainties, acoustic methods for surveying zooplankton have several
525 compelling advantages. Acoustic methods provide high-resolution vertical profiles of fish and
526 zooplankton densities, offering insights into the biotic and abiotic processes structuring lake
527 ecosystems (Beauchamp et al. 1999; Urmy et al. 2016). Acoustics are also an excellent method for

528 recording the diel vertical migration of lake zooplankton (Warren et al. 2016). Although DVM was not
529 part of this study, it would be worth investigating further in these lakes. Acoustics can also reveal
530 trends in the distribution of zooplankton that would be missed by traditional sampling methods (Pinel-
531 Alloul et al. 1999; Hembre and Megard 2003). In this case, these included trends in zooplankton
532 biomass density with distance from shore or from the stream inlet. Accounting for spatial trends and
533 patchiness in turn reduces uncertainty in the biomass estimates.

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

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727 **Acknowledgements**

728 Many of the logistical aspects of this project were planned and executed on short notice, and
729 could not have succeeded without help from a number of people. The staff of the UC Davis Tahoe
730 Environmental Research Center, in particular Raph Townsend, Katie Webb, and Brant Allen, got us in
731 and out of the lakes safely in conditions that were usually difficult and at times dangerous. Taylor
732 Leach and Jennifer Brentrup assisted with field work in Independence Lake and Lake Tahoe and helped
733 process some of the zooplankton samples. Maria Anderson, Kayla Hartigan, Michaela Miller, and
734 Helena Nierer identified, counted and measured the zooplankton. Erin Overholt maintained her good
735 humor while dealing with reimbursements for a dozen cross-country flights, booked on short notice.
736 An anonymous reviewer provided a number of very helpful comments. This project was funded by the
737 National Science Foundation's Division of Environmental Biology RAPID grant 13-60066, awarded to
738 Craig E. Williamson and S. Geoffrey Schladow.

738 **Table 1.** Numerical composition (%) of the crustacean zooplankton community in Independence Lake
739 and Lake Tahoe in October 2013 was dominated by a few species.

740

741

742

Lake	Group	Genus	2013-10
Independence	Cladocerans	Bosmina	6.3
		Daphnia	45.8
	Copepods	Diacyclops	47.9
Tahoe	Cladocerans	Bosmina	1.2
		Daphnia	0.3
	Copepods	Epischura	21.9
		Leptodiaptomus	55.9
		Unk. Cope.	20.3

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

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747

Lake	Group	Genus	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>Diaphonsoma</i>	0	2.2	0	0
		<i>Diplostraca</i>	42.9	0	0	0
		<i>Holopedium</i>	0	33.6	0	0
		<i>Pseudorida</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>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
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>Pseudorida</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

748 **Table 3.** Acoustic properties of crustacean zooplankton. For each class of scatterers (Cladocerans,
 749 Copepods, and Nauplii larvae), the mean acoustic target strength (dB re m²) and individual wet weight
 750 (μg) are displayed, along with the percentage by biomass of the net catch made up of that class of
 751 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

752

753 **Table 4.** Average fish target strength (TS), with estimated lengths and wet weights. Standard
 754 deviations are given in parentheses. The final column gives the number of fish targets detected in each
 755 survey. Target strengths were measured in-situ in each lake with a 120 kHz split-beam echosounder
 756 and converted to lengths and weights using published empirical TS-length and length-weight scaling
 757 relations (see Methods for details). The 120 kHz echosounder was not operated in Independence Lake,
 758 so no fish TS 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

759

760 **Table 5.** Acoustic estimates of total wet-weight biomass of zooplankton and fish in each lake show
 761 seasonal changes in different trophic levels as well as interlake differences. These values (as well as the
 762 ratio of lower to higher trophic level biomasses) may provide useful data for investigations of various
 763 ecosystem-level processes in these habitats. Fish biomass was not estimated in Independence Lake due
 764 to the lack of reliable target strength estimates.

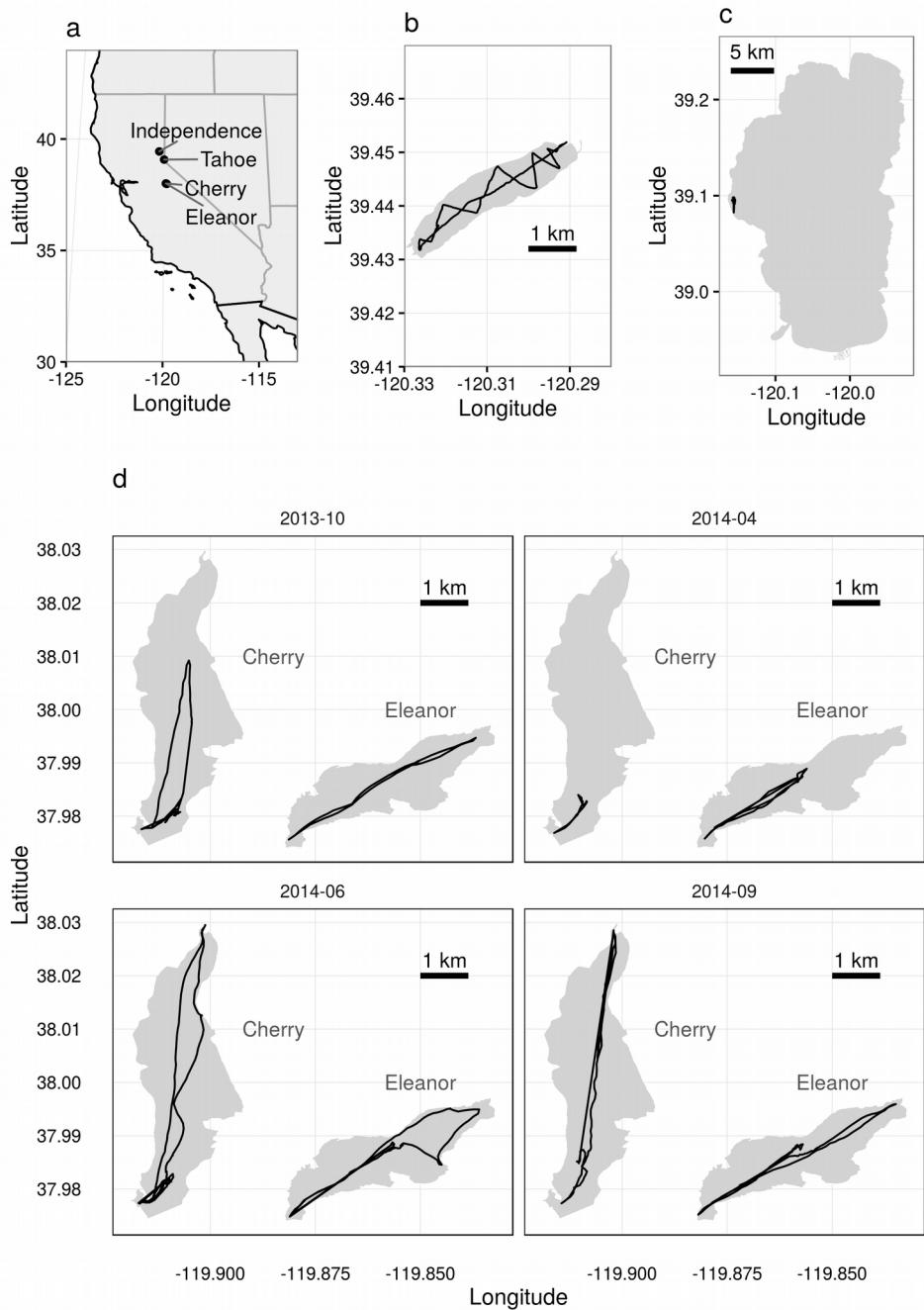
Date	Lake	Zooplankton (kg)	Fish (kg)	Ratio
2013-10	Cherry	23,000	1,700	14
	Eleanor	3,600	7	530
	Independence	3,600	—	—
	Tahoe	7,500	2,200	3.4
2014-04	Cherry	3,300	94	35
	Eleanor	51,000	60	850
2014-06	Cherry	110,000	280	400
	Eleanor	31,000	640	48
765 2014-09	Cherry	1,600	280	5.9
	Eleanor	930	210	4.5

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

773

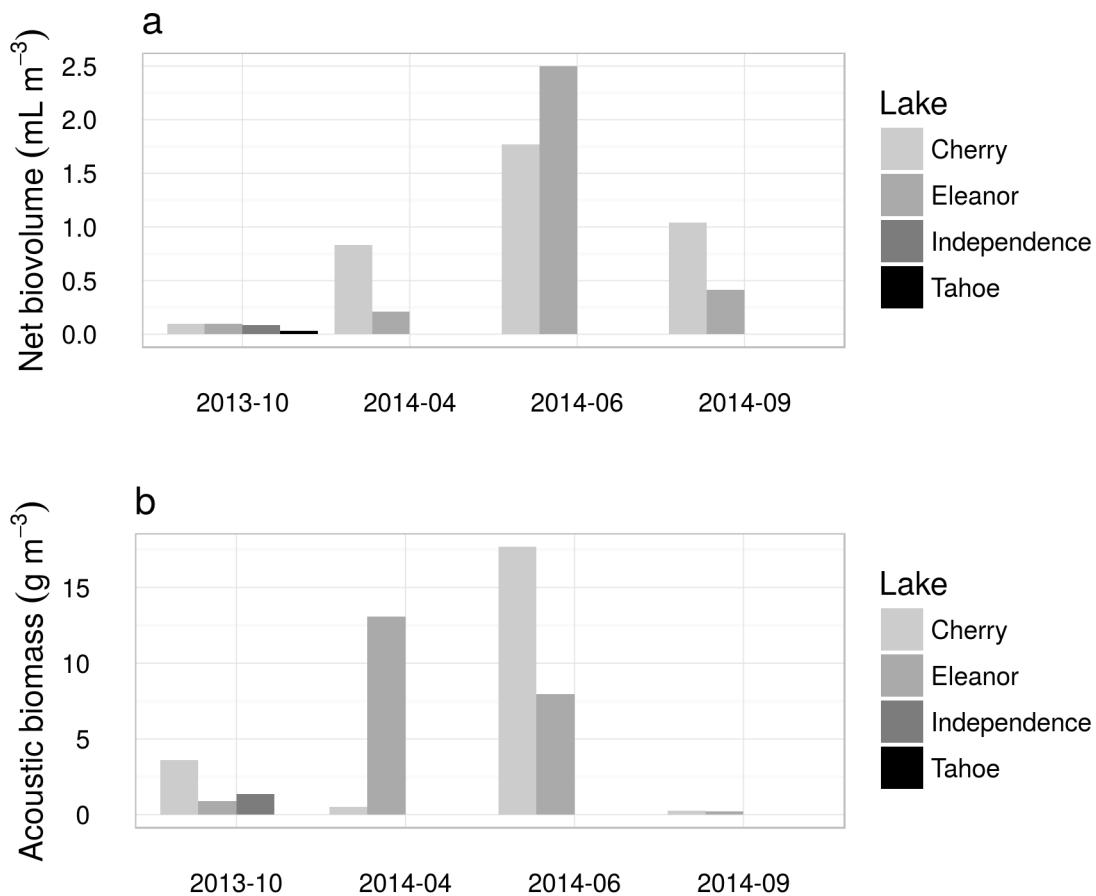
Date	Lake	Intercept	<i>p</i>	Inlet	Shore	<i>p</i>	<i>R</i> ²
				distance	distance		
2013-10	Cherry	-1.37	0.002	0.231	< 0.001	0.0981	0.783 0.32
	Eleanor	0.269	0.044	-0.0112	0.679	-0.485	0.097 0.02
	Independence	-0.613	< 0.001	-0.0191	0.017	1.16	< 0.001 0.12
2014-04	Cherry	0.424	0.477	-0.0843	0.315	-0.419	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

774



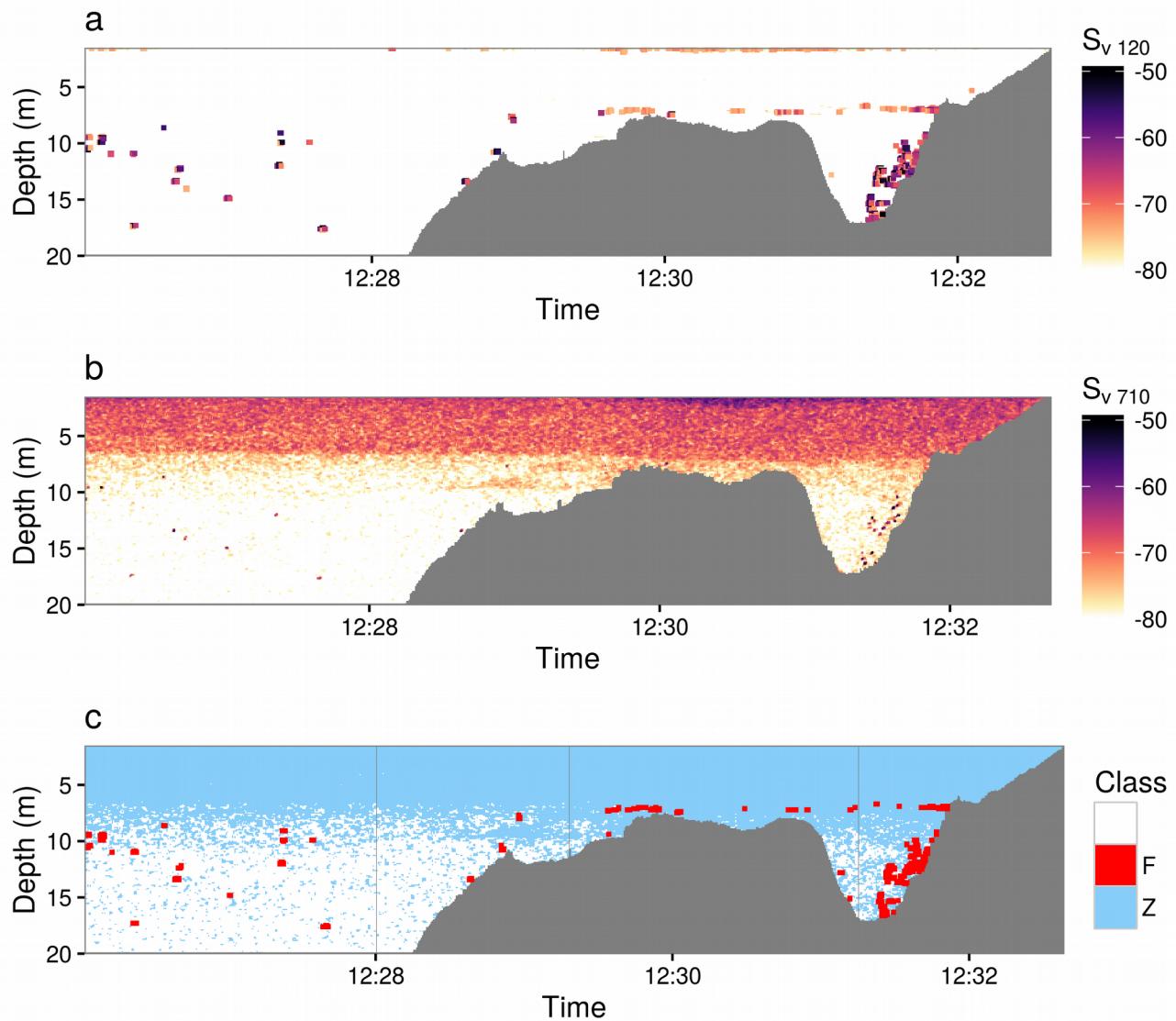
775

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



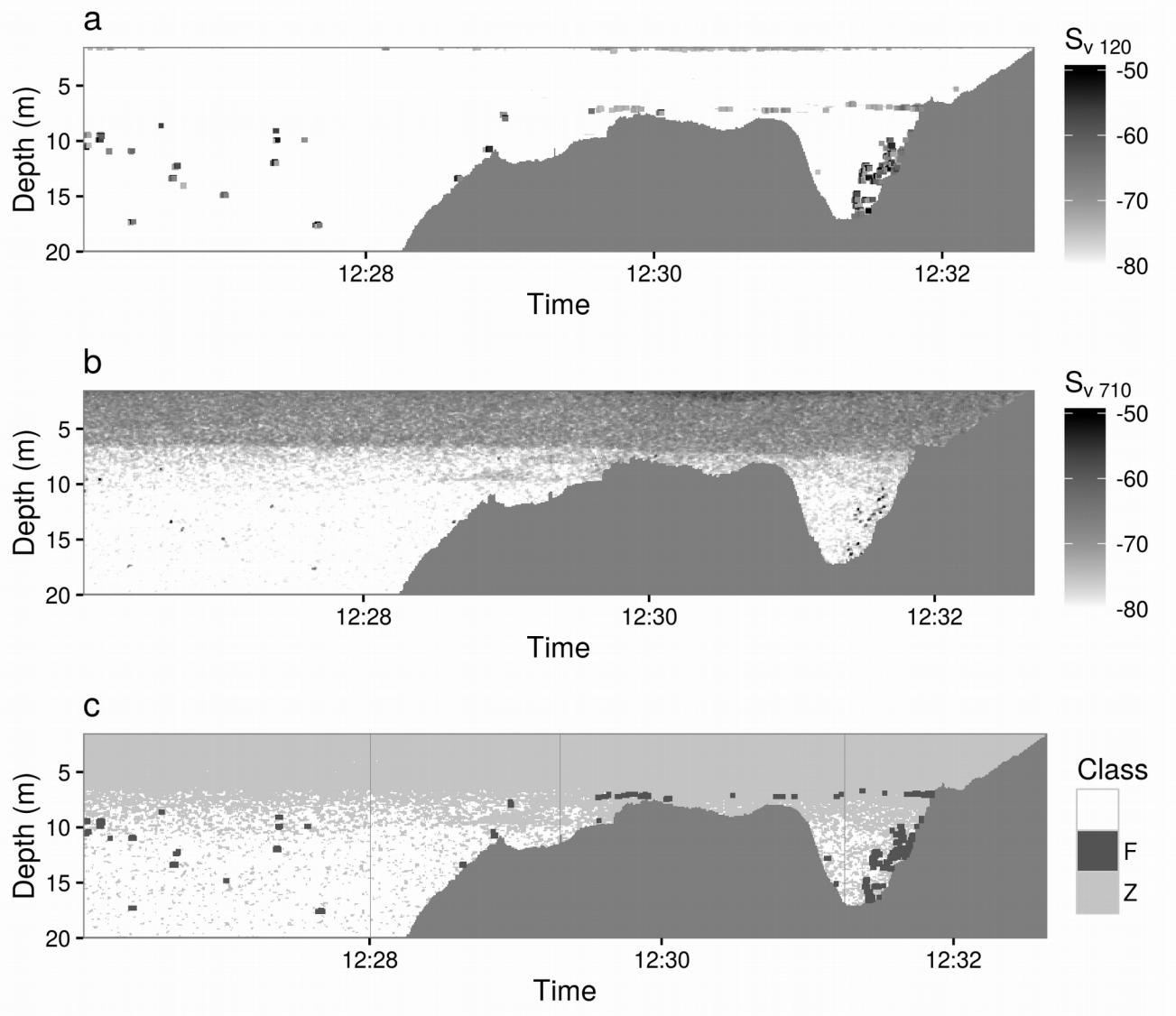
780

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



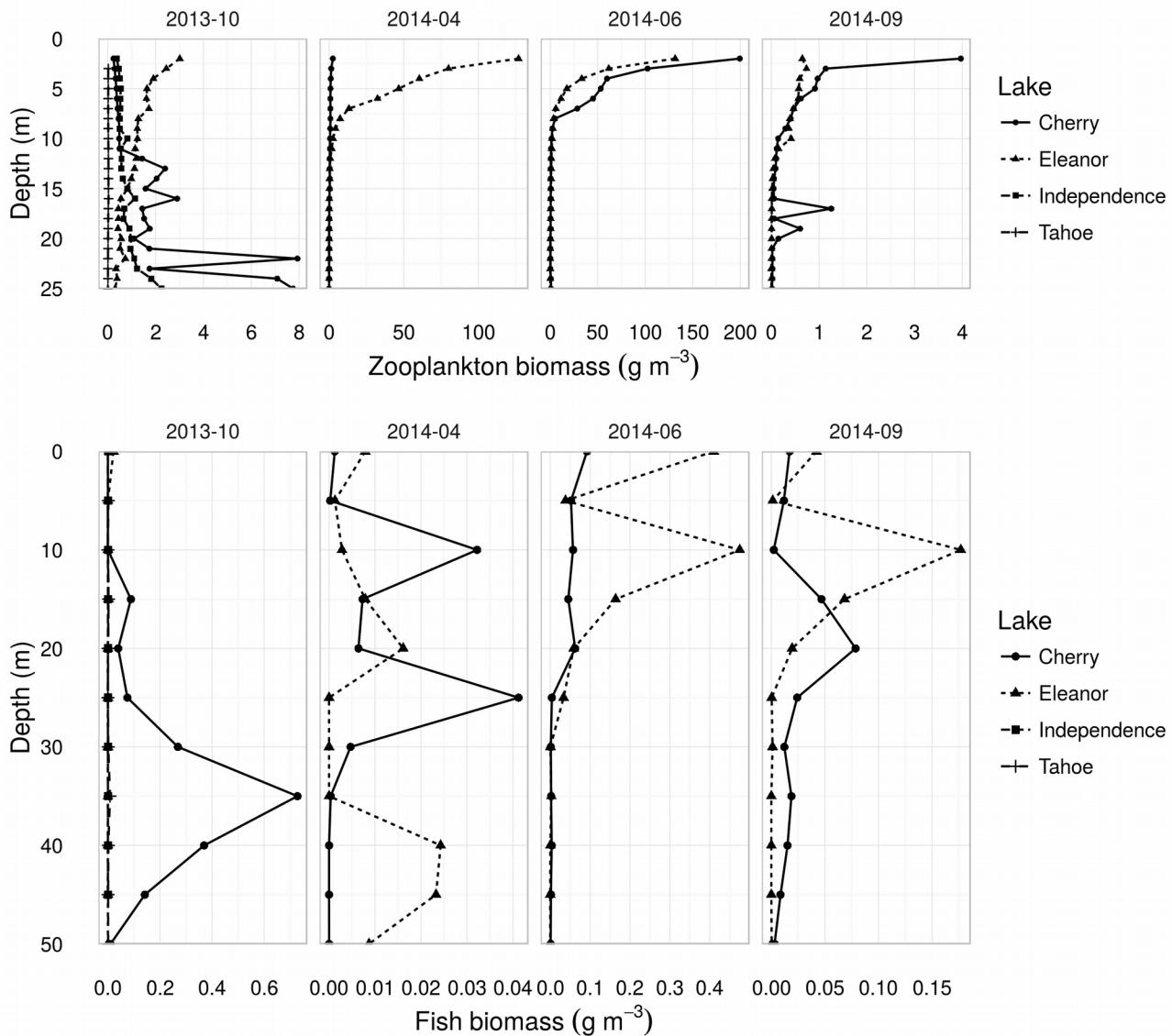
788

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



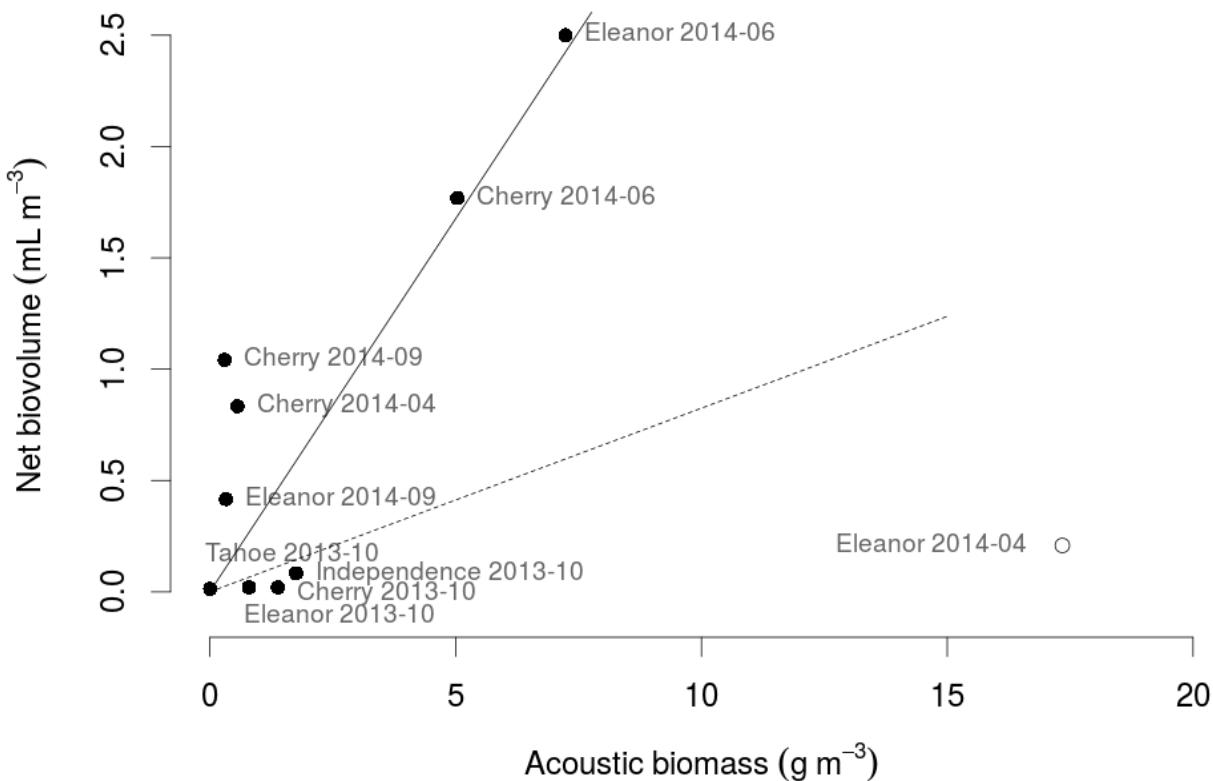
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798 **Figure 3 (Grayscale rendering for print publication)**



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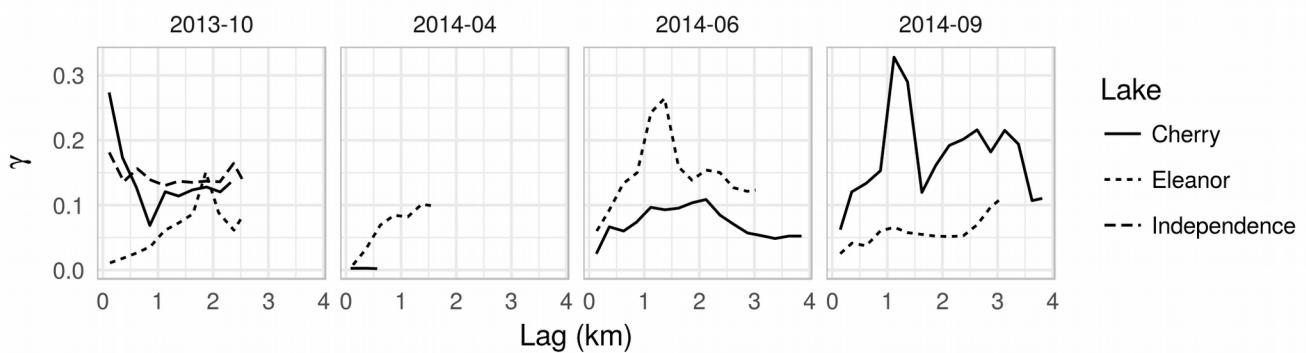
800 **Figure 4.** Depth profiles of zooplankton (top row) and fish (bottom row) wet weight biomass density
 801 measured acoustically in the lakes sampled during each of four seasonal surveys. (Lake Tahoe and
 802 Independence Lake were only sampled in October 2013). Lines show approximate biomass density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



807

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

812



813

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