

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

3

4 Running title: Zooplankton & fish in Sierra Nevada lakes

5

6 Samuel S. Urmy¹ and Joseph D. Warren*

7 School of Marine and Atmospheric Sciences

8 Stony Brook University

9 239 Montauk Hwy

10 Southampton, NY 11968, USA

11

12 * Corresponding author: joe.warren@stonybrook.edu

13 ¹ Present address: Monterey Bay Aquarium Research Institute, 7700 Sandholdt Rd, Moss Landing, CA

14 95039, USA

15

16

17 Keywords: acoustics, alpine lakes, frequency response, geostatistics, surveys.

18 **Summary**

19

- 20 1. Zooplankton are important components of lentic ecosystems, affecting phytoplankton, water
21 clarity, and nutrient cycling, as well as transferring primary production to upper trophic levels.
22 Many of these processes are temporally and spatially heterogeneous, but are difficult to observe
23 at fine scales with traditional sampling methods. High-resolution sampling has been especially
24 rare in remote and high-altitude lakes.
- 25 2. We measured the vertical distribution of zooplankton and fish in four lakes in the Sierra Nevada
26 Mountains of California, USA (Independence Lake, Lake Tahoe, Cherry Lake, and Lake
27 Eleanor) using a dual-frequency echosounder, and estimated lake-wide biomass in all lakes
28 except Tahoe. For zooplankton, we also quantified trends and patchiness in their horizontal
29 distribution. In two of the lakes, Cherry and Eleanor, surveys were repeated four times at
30 seasonal intervals between autumn 2013 and autumn 2014.
- 31 3. Zooplankton were most abundant in these lakes in the spring and summer of 2014, with peak
32 wet-weight biomasses estimated at 31 t in Lake Eleanor in April, and 68 t in Cherry Lake in
33 June. The biomass and vertical distribution of fish also varied, increasing and moving
34 shallower in the water column in June in both Cherry Lake and Lake Eleanor.
- 35 4. Zooplankton density was not horizontally homogeneous, displaying gradients at the lake basin
36 scale (5-6 km), and nested patchiness at a range of smaller scales (0-2 km). This small-scale
37 spatial variability may be generated biologically, not physically. While it is well-known that the
38 distribution of zooplankton is often patchy, this aspect of their ecology has not been quantified
39 in most lakes, especially in remote montane locations.
- 40 5. These results illustrate how acoustic sampling can rapidly and simultaneously measure the
41 biomass and spatial distribution of multiple trophic levels in small lakes. This capability
42 provides unique opportunities to study the processes which generate and maintain gradients and
43 patchiness in these components of the ecosystem.

44 **Introduction**

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

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

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

82 In contrast, active acoustics (i.e., scientific echosounders) can measure the density of animals
83 through the water column quickly and at high (sub-meter) resolution. Acoustics are regularly used in
84 lakes to survey fish (e.g. Brandt *et al.* 1991, Rudstam *et al.* 2009, Simonin *et al.* 2012), but have rarely
85 been used for freshwater zooplankton, despite their long use in the marine environment (e.g., Holliday
86 & Pieper, 1995; Parks *et al.*, 2012). This is chiefly because most lake zooplankton scatter sound very
87 weakly at the acoustic frequencies used for fish surveys, with the notable example of some larger
88 genera such as *Mysis* (Rudstam *et al.*, 2008) and *Macrohectopus* (Melnik *et al.*, 1993), and gas-bearing
89 larvae of midges in the families Chaoboridae (Northcote, 1964; Teraguchi and Northcote, 1966) and
90 Chironomidae (Kubecka *et al.*, 2000). Only a few studies have used high-frequency (i.e. > 200 kHz)
91 acoustics to measure the vertical or horizontal distribution of small (< 2 mm) zooplankton (Roman *et*
92 *al.*, 2001; Hembre and Megard, 2003; Parks *et al.*, 2012). Likewise, few studies in lakes have
93 examined the joint distribution of zooplankton with their fish predators at the same fine spatial scale
94 (Pinel-Alloul *et al.*, 1999; Masson *et al.*, 2001). Acoustic methods are uniquely suited to address these
95 questions, though they do have limitations. Most importantly, echoes give limited information on the
96 identity of scattering organisms, so direct sampling is still necessary for identification and as ground-
97 truth for acoustic density estimates. Acoustical techniques are a powerful tool for measuring the
98 distribution of zooplankton, especially when higher frequencies enable the detection of small size
99 classes or abundances of organisms (Warren *et al.*, 2016).

100 We surveyed the zooplankton and fish in four lakes in the Sierra Nevada mountains of
101 California, USA, between autumn 2013 and autumn 2014: Cherry Lake, Lake Eleanor, Independence
102 Lake, and Lake Tahoe. Cherry and Eleanor are similar in size and shape, and are separated by less than
103 2 km. Lake Tahoe and Independence Lake are located more than 100 km to the north, and are larger
104 (Tahoe) and smaller (Independence) than Cherry and Eleanor. Our primary tool was a two-frequency
105 acoustic system which allowed us to distinguish echoes from fish and zooplankton (Mitson *et al.*, 1996;

106 Horne, 2000; Simmonds and MacLennan, 2005) and measure their vertical and horizontal distribution
107 at meter-scale resolution. Acoustic observations were augmented with net samples to identify the
108 zooplankton scatterers, measure their sizes, and parameterize models of their acoustic target strengths
109 (TS). Fish TS were measured in situ. Zooplankton TS and fish TS values were used to convert acoustic
110 backscatter to biomass, yielding estimates of total biomass of two trophic levels. The high-resolution
111 nature of the acoustic data also let us compare the vertical profiles and horizontal trends of zooplankton
112 and fish density among lakes. Changes in the distributions of zooplankton and fish from one season to
113 another were also examined. Finally, we quantified the zooplankton's spatial variability across scales
114 using empirical variograms. Spatially structured variance indicates a patchy distribution, which in turn
115 would imply that the dominant ecological processes are spatially inhomogeneous. Because Cherry
116 Lake and Lake Eleanor are so similar, we expected that the spatial distributions of fish and zooplankton
117 would not vary between these lakes, and that these communities would experience similar seasonal
118 changes. And because Independence, Cherry, and Eleanor are all relatively small (< 6.3 km maximum
119 extent), at similar elevations, and in similar landscapes, we hypothesized that the population dynamics
120 of zooplankton within each lake would be synchronous, and their horizontal distributions
121 homogeneous.

122

123 **Methods**

124 *Study lakes*

125 Surveys were conducted in four lakes in the Sierra Nevada: Cherry Lake, Lake Eleanor,
126 Independence Lake, and Lake Tahoe (Figure 1). Our main focus was on Cherry Lake and Lake
127 Eleanor, located at the border of Yosemite National Park near 38° 0' N, 119° 52.6' W (Figure 1). Both
128 are reservoirs of the San Francisco Public Utilities Commission (SFPUC). Cherry Lake is artificial,
129 created by the damming of Cherry Creek in 1955 (Hennesey, 2012). Lake Eleanor was formed
130 naturally, but enlarged and deepened by the construction of a dam in 1918 (Eckart, 1940). Both lakes
131 are approximately 1,420 m above sea level, placing them in the upper montane forest zone (Kaufman
132 *et al.*, 2007), though their catchments extend up through the subalpine zone and include large areas of
133 bare rock above the treeline. Cherry lake has an area of 6.3 km² and a maximum depth of
134 approximately 80 m, while Lake Eleanor is slightly smaller at 3.9 km² and 68 m. Both lakes have been
135 stocked with fish, including rainbow trout (*Onchoryncus mykiss*), brown trout (*Salmo trutta*), and, in
136 Cherry Lake, eastern brook trout (*Salvelinus fontinalis*) (Bingaman, 1961; United States Forest Service,

2016). Cherry and Eleanor were surveyed in October 2013, April 2014, June 2014, and September 2014 (Figure 1). During this time, an ongoing 5 year drought (2012-2017) in the western United States led the SFPUC to draw down these two reservoirs to maintain water supplies, so that water levels were nearly 8 m lower in September 2014 than in October 2013. In addition to our repeated surveys of Cherry and Eleanor, we surveyed Independence Lake, located at 39° 26.4' N, 120° 18.6' W, and Lake Tahoe, at 39° 10' N, 120° 0' W once each in October 2013. Independence is a natural lake, 2,127 m above sea level, 2.6 km² in area, and 45 m in depth. It has never been stocked with fish, and is one of only two lakes in the world with a self-sustaining population of Lahontan cutthroat trout, *Oncorhynchus clarkii henshawi* (Nielsen and Sage, 2002). Lake Tahoe, at 1,897 m elevation, is much larger and deeper than the other three lakes, with a surface area of 490 km² and maximum depth of 501 m. It is also oligotrophic, in contrast to the three smaller lakes, which are mesotrophic. The watersheds of the three smaller lakes are undeveloped, although significant fractions of the Cherry and Eleanor Creek watersheds were burned during the 2013 Rim Wildfire, which started approximately 20 km southwest of Cherry Lake on 17 August and was not fully contained until several days after the first surveys in October 2013 (National Wildfire Coordinating Group, 2013). Lake Tahoe is bordered by several towns, with a total permanent population of approximately 50,000. All four watersheds are on granitic substrate.

154

155 *Acoustic data collection*

156 Surveys were run from outboard-powered boats trailered to each lake. Because of the recent
157 Rim Fire, camping was not permitted near Cherry Lake or Lake Eleanor, and the survey boats had to be
158 towed in and out over 60 km of mountain roads, restricting our sampling to daylight hours. Acoustic
159 volume backscatter was recorded at two frequencies, 120 and 710 kHz. Volume backscatter can be
160 expressed either in logarithmic form as “mean volume backscattering strength” S_V , or a linear form as
161 “volume backscattering coefficient,” s_V (with units of m⁻¹), related by the equation $S_V = 10\log_{10}(s_V)$
162 (MacLennan *et al.*, 2002). For sound-scattering objects of a given type and size, the volume
163 backscattering coefficient is proportional to their numerical density in the water. The 120 kHz
164 echosounder was a Simrad ES60 with a split-beam transducer (7° beam width), which can accurately
165 measure the target strength of individual targets in situ. The 710 kHz echosounder was a Simrad EK60
166 with a single-beam (2.8° beam width) transducer. This high-frequency system could detect small (<1
167 mm) zooplankton (Holliday and Pieper, 1995; Warren *et al.*, 2016), but its effective range was limited

168 to approximately 30 m due to sound attenuation in water. The transducers were deployed adjacent to
169 one another on a pole mount off the side of the survey boat at depths of 30-50 cm depending on wave
170 conditions. A Global Positioning System antenna attached to the pole directly above the transducers
171 provided georeferenced locations. Vessel survey speeds were approximately 2.5 m s^{-1} . The transducers
172 transmitted simultaneously, generally once per second at of 500 W (120 kHz) and 100 W (710 kHz),
173 with a 0.064 ms pulse length, though these setting were modified in some circumstances. In Lake
174 Tahoe, the pulse length and 120 kHz power were increased to 0.256 ms and 1000 W to increase the
175 penetration depth. The ping rate was also decreased to 0.5 s^{-1} at several points in the smaller lakes to
176 mitigate interference due to multipath echoes and reverberation from the rocky lake bottom.

177 The 120 kHz system was calibrated in Lake Tahoe on 21 October 2013 with a 38.1 mm
178 tungsten carbide standard target sphere (Foote *et al.*, 1987). Because of the 710 kHz transducer's
179 narrow beam width, we were unable to center the sphere in the beam while in the field, and so
180 performed an additional, ex-situ calibration for this instrument in a tank on land. A 166 L barrel, 80 cm
181 deep and 50 cm across (Rubbermaid, Atlanta GA), was filled with fresh water and the transducer
182 mounted at the barrel's center just below the water's surface. The calibration sphere could then be
183 suspended in the center of the beam beyond the transducer's 40 cm near field. Differences from the
184 sphere's theoretical TS of -0.2 dB (120 kHz) and -3 dB (710 kHz) were applied to the acoustic data in
185 post-processing.

186 Independence Lake and Lake Tahoe were sampled on 20 and 21 October 2013 respectively.
187 Cherry Lake and Lake Eleanor were each sampled four times. Cherry was sampled on 29 October
188 2013, and on 2 April, 24 June, and 10 September 2014. Eleanor was sampled one day later, on 30
189 October 2013, 3 April, 25 June, and 11 September 2014. In the three smaller lakes, we attempted to
190 perform a lengthwise transect from one end of the lake to the other. In Independence Lake, we were
191 also able to add a series of zig-zag transects across the main axis of the lake (Figure 1). The April 2014
192 transects in Cherry and Eleanor were shorter due to snowfall, which required slow travel on the
193 mountain roads and reduced the time available for sampling.

194

195 *Direct sampling and target strength models*

196 Temperature profiles were measured from 0-50 m using a conductivity-temperature-depth
197 (CTD) sensor in each lake and on each sampling date. Temperature in Independence Lake was
198 measured with a YSI EXO (YSI Inc., Yellow Springs OH, USA), while temperature in all other lakes

199 were measured using Sea-Bird CTD (Sea-Bird Electronics, Bellevue, WA, USA). A Sea-Bird model 19
200 was used in September 2014, and a model 25 was used on all other trips. We used only data from the
201 down-cast. After inspection for irregular data the temperature values for each lake and date were
202 averaged into 1 m vertical bins.

203 Zooplankton were collected on each sampling day near the center of the lake with a vertical tow
204 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
205 equipment problem with the ring net during the October 2013 trip to Cherry and Eleanor, we instead
206 used an open Van Dorn bottle (10 cm diameter) with an elastic nylon mesh ($\sim 100 \mu\text{m}$) over one end.
207 This was hauled vertically through the water column with its uncovered end up, acting like a small-
208 diameter net. Filtered volume was calculated as the depth of the cast multiplied by the cross-sectional
209 area of the net mouth. Samples were preserved in 10% buffered formalin for later analysis. In the lab,
210 the total biovolume of each sample was measured after allowing it to settle in a graduated cylinder.
211 Because of the small diameter of the Van Dorn sampler, the biovolumes of the samples from Cherry
212 and Eleanor in October 2013 were smaller than the finest graduation on our cylinder, preventing a
213 precise measurement. We estimated them at 0.1 mL; our analyses did not appear sensitive to these
214 estimates when they were in the range of 0-1 mL. A subsample of 200-300 animals was split from each
215 original sample and counted under a compound microscope. All of these animals were identified to the
216 lowest possible taxonomic level. In addition, the lengths of the first 30 animals counted from each
217 sample were measured to the nearest 0.1 mm.

218 To convert acoustic backscatter to animal densities it is necessary to know the backscattering
219 cross-section, σ_{BS} (in m^2), of the scattering organisms. The backscattering cross-section is also
220 expressed in logarithmic form in dB re 1 m^2 , as the target strength, $\text{TS} = 10 \log_{10}(\sigma_{\text{BS}})$ (MacLennan *et*
221 *al.*, 2002). We calculated these values using the distorted-wave born approximation (DWBA, Stanton
222 *et al.* 1998, McGehee *et al.* 1998), implemented as a package, SDWBA.jl (Urmy, 2016) in the Julia
223 language (Bezanson *et al.*, 2012). This package uses models for the body shapes of cladocerans and
224 calanoid copepods from Warren *et al.* (2016), and we assumed density and sound-speed contrasts of
225 1.04 (Stanton and Chu, 2000). For each lake, sampling date, and taxonomic group (i.e., cladocerans
226 and copepods), we calculated the mean body length and its standard deviation (s.d). We then drew
227 1000 random lengths from a normal distribution with these parameters (i.e., a parametric bootstrapping
228 procedure, Efron and Tibshirani 1993). The generic body shape was scaled to each length and its
229 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 galeatea* (Culver *et al.*, 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 $b_{tot} = n_{tot}$

$$\langle W_{w, tot} \rangle.$$

Acoustic data processing and analysis

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

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

Acoustic integration cells were classified as fish if their backscatter was higher at 120 kHz than at 710 kHz, since resonant scattering from fishes' swim bladders makes them stronger targets at the lower frequency (Mitson *et al.*, 1996; Watkins and Brierley, 2002; Simmonds and MacLennan, 2005). Based on the small sizes of the zooplankton, and the fact that they were all fluid-like scatterers, as opposed to gas-bearing ones such as *Chaoborus* (which were not present) the difference in their TS between 120 and 710 kHz was expected to be a robust criterion for classification. Because only 710 kHz data were available in Independence Lake, we used a different approach to eliminate fish backscatter, applying a top threshold to eliminate areas with $S_v > -75$ dB re m^{-1} . This value was determined iteratively by inspecting the echogram and histogram of S_v values and adjusting the threshold until all fish-like targets were excluded.

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). Because no specific TS-length relationships are available at 120 kHz for the salmonid species in these lakes, we used a generic 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 create 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. This was not done in Lake Tahoe, since we felt such an extrapolation was suspect given the patchiness of the animals and the small extent of the survey relative to the lake. We also calculated the ratio of zooplankton biomass to fish biomass in each lake and survey.

Comparison of net and acoustic biomass

291 To test the agreement between acoustic estimates of zooplankton biomass and the direct net
292 sampling, we regressed average acoustic biomass density within 25 m or 10 minutes of each net cast
293 (whichever was less) on the biovolume from the net. These limits ensured the acoustic data used in the
294 regression were close both in space and time to the net haul. Net biovolumes were normalized by the
295 total volume of water filtered to give a biovolume density, in mL m^{-3} . The intercept in the linear
296 regression was fixed at the origin, because a preliminary model showed it was not significantly
297 different from zero (at the $p=0.05$ level), and because it is physically reasonable. Fitting the model
298 without an intercept also added a degree of freedom, increasing power and precision for the slope
299 estimate, which was advantageous given the small sample size ($n=9$). When examining preliminary
300 results, one data point (from Lake Eleanor in April 2014) appeared to be an outlier exerting undue
301 influence on the slope, so we also fit the model without this point for comparison. The significance of
302 the slopes was assessed at the $p=0.05$ level. Several assumptions of the significance test are
303 questionable in this case. The errors may not be homoskedastic, so the resulting p -values must be
304 interpreted with caution. In addition, the independent variable, acoustic biomass, is itself measured
305 with (unknown) error. To address the latter concern, we also conducted a geometric mean regression
306 (Ricker, 1973). These analyses were run using R (R Development Core Team, 2016).

307

308 *Distribution of zooplankton and fish*

309 We investigated horizontal spatial trends and patchiness of zooplankton by averaging their
310 biomass densities vertically through the water column. The densities in this horizontal dataset were
311 \log_{10} -transformed, then regressed on their distances from the shoreline and from each lake's main
312 stream inlet. One multiple regression model (i.e., $\log(\text{biomass}) \sim \text{Intercept} + \text{Shore distance} + \text{Inlet}$
313 distance) was fitted for each lake and survey, to test whether there were any spatial trends in the density
314 of zooplankton. Spatial autocorrelation was assessed by calculating empirical variograms for the
315 residuals of each regression. Two key features of a variogram are its *sill* and *range*. The sill is the
316 variogram's maximum value, indicating the expected absolute differences between biomass densities at
317 widely separated locations. The range is the spatial lag at which the variogram reaches its sill, and
318 characterizes the decorrelation distance. Because we calculated the variograms for \log_{10} -transformed
319 units, they imply multiplicative differences (\times/\div) in zooplankton density in the linear domain.
320 Variograms were calculated at spatial lags from zero to half the distance spanned by the transect in each
321 lake, in bins 0.25 km wide. Lake Tahoe was omitted from these spatial analyses, because it is much

322 larger and fed by many small streams at inlets around its perimeter, and because the sampling schedule
323 did not permit extended transects.

324

325 **Results**

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

333 Over the four sampling dates, more zooplankton species were recorded in Cherry Lake and
334 Lake Eleanor than in the single surveys in Independence and Tahoe (Table 1). In October 2013, the
335 communities in both lakes were 50-60% cladocerans in the genera *Daphnia* and *Diplostraca*, with the
336 remainder mostly composed of cyclopoid copepods in the genus *Eurycyclops*,. The following April,
337 the community in Cherry Lake had similar proportions of cladocerans and copepods (though the former
338 shifted from mostly *Diplostraca* to *Holopedium*), but in Lake Eleanor it had shifted to 59% Copepods,
339 mostly *Epischura nevadensis*. During the final two surveys, in June and September 2014, the
340 communities in both lakes were between 70 and 85% copepods, a large proportion of which were
341 copepodites of unknown calanoid species. The cladocerans, which composed 15-32% of the
342 communities in June and September 2014, were again a mix of *Daphnia*, *Pseudorida*, and unidentified
343 species (Table 1). Biovolumes of zooplankton estimated from the nets ranged from 0.1 mL m⁻³ in Lake
344 Tahoe to 2.5 mL m⁻³ in Lake Eleanor in June 2014 (Figure 2). Biovolumes in both Cherry Lake and
345 Lake Eleanor were highest in June 2014 and lower in the other months.

346 Target strengths predicted for the different classes of zooplankton scatterers using the DWBA
347 varied widely (Table 2). The strongest scatterers were copepods in Lake Tahoe, with an average TS of
348 -104 dB. The weakest were nauplius larvae in Cherry Lake in October 2013, with a mean TS of -148
349 dB. Cladoceran target strengths fell between -113 and -127 dB. Adult copepod target strengths fell in
350 the same broad range, from -104 to -128 dB. Nauplii, due to their much smaller size, were predicted to
351 scatter much less sound, with their mean TS falling between -120 and -148 dB (Table 2). After
352 averaging across all scattering classes, overall mean TS ranged from -127 dB in Lake Eleanor in

353 September 2014 to -105 dB in Lake Tahoe in October 2013 (Table 2). There were no systematic trends
354 in TS between the lakes, or through time.

355 Mean fish target strengths, measured in situ, ranged between -41 and -37 dB re m²,
356 corresponding to mean lengths from 16 to 26 cm, and mean weights from 150 to 590 g (Table 3). In
357 October 2013, the mean TS (and the mean lengths and weights derived from them) were roughly equal
358 in Cherry Lake and Lake Tahoe and higher in Lake Eleanor. In the following three surveys, however,
359 mean TS was 1-3 dB higher in Cherry, with corresponding length and weight differences of 2-9 cm and
360 180-330 g.

361 Water column stratification varied between lakes and over the four sampling dates. In October
362 2013, all four lakes had surface mixed layers between 10 and 15 °C, with Cherry Lake the warmest and
363 Independence lake the coolest (Figure 2). The mixed layer was shallowest in Lake Eleanor
364 (approximately 8 m) and deepest in Lake Tahoe (27 m). In April 2014, both Cherry and Eleanor were
365 vertically mixed with temperatures between 5 and 10 °C. By June, thermoclines had reestablished in
366 both lakes, starting around 6 m depth, though the thermocline in Lake Eleanor was sharper and the
367 water was 2-3 °C cooler at depth than in Cherry Lake. At the end of the summer in September 2014,
368 the temperature profile in Eleanor was similar to that in June, while in Cherry Lake the surface mixed
369 layer was 3 m deeper and the thermocline was better defined.

370 The 710 kHz echosounder was able to detect small zooplankton in the lakes, and the frequency-
371 differencing procedure could clearly separate them from fish echoes (Figure 3). Mean zooplankton
372 wet-weight biomass densities measured acoustically were relatively low (< 10 g m⁻², Table 4) in all
373 lakes, and varied widely among seasons (Figure 4). In October 2013, the mean zooplankton numerical
374 density in all four lakes was low, with less than 5 g of zooplankton wet-weight biomass m⁻³ (Figure 4).
375 Cherry Lake had a subsurface zooplankton maximum (4.5 g m⁻³) between 20 and 25 m, and Lake
376 Eleanor had a weak scattering layer extending from the surface to 15 m, corresponding to an estimated
377 zooplankton biomass density of just under 2 g m⁻³ (Figure 5). In April 2014, Cherry Lake contained
378 zooplankton at similarly low densities, but Lake Eleanor had a denser zooplankton layer near the
379 surface, increasing from near-zero density at 10 m depth to a maximum of 80 g m⁻³ at 2 m depth, the
380 bottom of the echosounder's blind zone (Figure 5). Two months later in June, this layer was still
381 present, though not quite as deep as in April. During this time, a similar layer had also appeared in
382 Cherry Lake, with a maximum density of 125 g m⁻³ at 2 m depth (Figure 5). By September, the surface
383 zooplankton layer in Lake Eleanor had mostly disappeared. The layer in Cherry Lake was much less

384 dense (maximum 1.5 g m^{-3} , Figure 5).

385 Peak fish densities in the lakes ranged between 0.12 and 3.5 fish per 1000 m^{-3} , corresponding to
386 biomass densities of 0.06 to 1.7 g m^{-3} (Figure 5). These fish were mostly found below the zooplankton
387 layers (Figure 5). In the first surveys in October 2013, fish in Cherry Lake were concentrated in a layer
388 centered at 35 m depth, with much higher densities than the other three lakes (Figure 5). The overall
389 mean fish density in October in Cherry Lake was 0.4 per 1000 m^{-3} , compared to 0.02 in Lake Eleanor.
390 The next April, the depth distribution of fish in both lakes was bimodal, grouped in two layers at depths
391 of 10 and 25 m in Cherry Lake, and deeper at 20 and 40 m in Lake Eleanor (Figure 5). In June, fish in
392 both lakes were concentrated in the upper 10-15 m and were more abundant overall than in April, with
393 mean densities of 0.3 (Cherry) and 0.6 (Eleanor) fish per 1000 m^{-3} , corresponding to biomass densities
394 of 0.05 and 0.2 g m^{-3} . In September, the fish in each lake were in one broad layer, between 5 to 20 m
395 depth in Lake Eleanor and from 10 to 30 m in Cherry Lake. Overall densities were lower than in June,
396 at 0.2 fish per 1000 m^{-3} in Cherry Lake and 0.1 fish per 1000 m^{-3} in Lake Eleanor, giving biomass
397 densities of 0.043 and 0.054 g m^{-3} .

398 When depth-integrated and scaled by their respective lake areas, these densities yielded a wide
399 range of estimates for the total biomasses of these trophic levels in the different lakes. In October
400 2013, Cherry Lake contained the most total zooplankton, with an estimated 13,000 kg. In April 2014,
401 the zooplankton wet-weight biomass density in Lake Eleanor had increased to 7.8 g m^{-3} , raising its total
402 biomass estimate to over 31,000 kg. Total zooplankton biomass in Cherry Lake in April was 2,000 kg,
403 15% of its level in the October survey. By June, however, it had increased to 68,000 kg, while the
404 zooplankton biomass in Eleanor dropped to 19,000 kg. During the September 2014 survey,
405 zooplankton populations in both lakes had dropped back to lower levels (Table 4).

406 Estimates for total fish biomass were much lower than those for zooplankton. The highest
407 estimate was 1,700 kg in Cherry Lake, in October 2013. Fish biomass in Cherry Lake and Lake
408 Eleanor was lowest the following April, increasing somewhat in the following two surveys in June and
409 September. Fish biomass did not vary as widely as zooplankton biomass. In all surveys, zooplankton
410 outweighed fish by a factor of 2 to 510.

411 Net and acoustic estimates of zooplankton density were positively related (Figure 6). The
412 regression of net-caught zooplankton biovolume on acoustically-estimated biomass was not statistically
413 significant when all data points were included ($p=0.1$, $R^2=0.19$), though the fitted slope was positive.
414 When the outlying measurement from Lake Eleanor in April 2014 was excluded, the fitted slope was

415 significantly different from zero, with a fitted value of 0.85 mL g^{-1} , and a 95% confidence interval from
416 0.46 to 1.2 mL g^{-1} . This model fit the data fairly well, with an adjusted R^2 of 0.76 . The slope from the
417 geometric mean regression, 0.96 mL g^{-1} , was not significantly different from that obtained with the
418 standard regression.

419 Zooplankton biomass density displayed significant trends with respect to distance from the inlet
420 and shore in most surveys, though the directions of these trends were variable (Table 5). The most
421 pronounced trend was in Cherry Lake in June 2014, where zooplankton biomass density was an order
422 of magnitude higher near the lake's inlet than near the dam at the other end. In seven out of the nine
423 surveys, the signs of the coefficients for distance from shore and distance from the inlet were the same.
424 The surveys in Independence Lake and Lake Eleanor in September 2014 were the exceptions, with
425 biomass density increasing closer to the inlet and decreasing closer to shore. In three of the four
426 surveys in Cherry Lake, zooplankton density increased towards the shore and inlet. In Lake Eleanor,
427 the reverse was true: three out of four surveys showed zooplankton density higher away from shore and
428 the inlet (Table 5). These spatial regressions explained a low-to-moderate amount of the variability in
429 the data, with R^2 values ranging from approximately zero in Lake Eleanor in October 2013, to 0.73 in
430 Cherry Lake in June 2014 (Table 5).

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

439 In June, the sill of the variogram in Lake Eleanor had increased to 0.15 at a range of 2 km
440 (Figure 7), implying an expected difference in biomass on the order of 50% when transformed back to
441 linear units. In Cherry Lake, the variogram was relatively flat (Figure 7), showing little evidence for
442 spatial structure other than the lakewide trends described above. Spatial variability in Lake Eleanor
443 decreased somewhat between June and September 2014. However, the variogram for Cherry Lake in
444 the final survey showed higher overall variability, peaking at 0.37 at a lag of 1 km and a sill near 0.2
445 beyond 1.5 km . Overall, the variogram sill values ranged from approximately 0.1 to 0.2 . These

446 values, in \log_{10} -transformed units, imply multiplicative differences (\times/\div) in zooplankton density from
447 0.25 to 1.6 at long ranges, where “long ranges,” as defined by the variograms, are between 1 and 2 km.

449 Discussion

450
451 This study used multifrequency acoustics to biomass and distribution of zooplankton and fish in four
452 peri-alpine lakes in the Sierra Nevada Mountains. To our knowledge, these are the first biomass
453 estimates (for any trophic level) ever made in Independence Lake, Cherry Lake, and Lake Eleanor. As
454 expected, the zooplankton communities in Cherry and Eleanor were broadly similar in their
455 composition, seasonality, and distribution, although there were measurable differences, indicating that
456 these two neighboring lakes do not share identical dynamics. The measurements in Independence Lake
457 and Lake Tahoe represent only a single snapshot of the zooplankton and fish in each lake, and should
458 not be over-interpreted, though our estimate of zooplankton density in Lake Tahoe (2,200 individuals
459 m^{-3}) was consistent with prior measurements (e.g. 0-23,00 individuals m^{-3} , Goldman et al., 1979).
460 Contrary to our expectations, the horizontal distribution of zooplankton in Independence, Cherry, and
461 Eleanor was not uniform, with significant spatial variability at scales of 10s to 100s of meters. The
462 causes of this fine-scale patchiness are unknown, and present an interesting opportunity for future
463 research.

464 A spring bloom of zooplankton occurred in both Cherry Lake and Lake Eleanor, with peak
465 biomass densities of 100-200 g m^{-3} . In spring and summer, the zooplankton were concentrated in the
466 upper 5-10 m of the water column, closely associated with the stratified surface layer. In 2014, the
467 bloom appeared to begin earlier in Lake Eleanor than in Cherry Lake, since a near-surface zooplankton
468 layer was present in Eleanor, but not Cherry, during the early April survey. In fact, the surface
469 zooplankton layer in Lake Eleanor was present before the lake’s surface waters warmed and stratified.
470 By June, both lakes had similar zooplankton densities, and by September, zooplankton populations in
471 both lakes had declined by an order of magnitude. At this point there were still more zooplankton in
472 Cherry Lake, however, suggesting that the bloom there, which started later, also took longer to collapse
473 in the autumn. This pattern, of a spring and summer increase in zooplankton as they respond to
474 blooming phytoplankton, is consistent with standard models of seasonal cycles in lake ecosystems
475 (Sommer *et al.*, 1986, 2012). While the seasonal changes in Cherry Lake and Lake Eleanor were
476 similar there were also distinct differences, both in the vertical distribution of fish and zooplankton, and

477 the timing of seasonal blooms. These differences were greater than expected given the apparent
478 similarities between the sizes, depths, and catchments of the two lakes, and emphasize that ecological
479 dynamics can follow different trajectories even in similar environments. Though both lakes had near-
480 identical surface temperatures, Lake Eleanor was cooler at depth and more strongly stratified. This
481 difference may have affected primary and secondary production, perhaps accounting for some of the
482 differences seen in zooplankton biomass and distribution.

483 Fish biomass did not vary nearly as widely as zooplankton biomass, which is expected given
484 their much longer life spans and generation times. At the height of the zooplankton blooms,
485 zooplankton biomass was several hundred times that of fish, indicating that the former were effectively
486 released from predatory control at those times. In both autumns, the zooplankton:fish ratios were much
487 lower, suggesting a closer match between rates of zooplankton reproduction and fish predation. While
488 fish were scarce in Lake Eleanor in October 2013, our estimate of total biomass (7 kg) was probably
489 unrealistic, reflecting error due to the patchy distribution of fish and our limited survey time as much as
490 the true biomass. While zooplankton were found mostly in the surface mixed layer, the fish (at least
491 during our daytime sampling) were found in and below the thermocline, reflecting either light-driven
492 DVM or a preferred thermal niche.

493 Our seasonal sampling interval may have caused us to miss shorter-scale variability in
494 zooplankton populations, due either to sub-seasonal population dynamics, or responses to
495 environmental forcings such as runoff from rainstorms or mixing of the water column by wind. This
496 study also only covers one year, leaving changes due to longer-term trends and extreme events, such as
497 the 2012-2017 drought and the Rim Wildfire, unknown. Both the drought and Rim Fire are likely to
498 have affected the lakes. Fires can increase runoff from burned watersheds, deposit ash from the air, or
499 alter the characteristics of incident solar radiation via drifting smoke plumes (Urmy *et al.*, 2016;
500 Williamson *et al.*, 2016), though their effects on a lake's zooplankton are not necessarily large (Patoine
501 *et al.*, 2002). While the drought probably contributed to the fire's severity, it may have actually
502 mitigated some of the fire's effects on Cherry and Eleanor: precipitation during the winter of 2013-
503 2014 was well below normal (California Department of Water Resources, 2014), meaning that runoff
504 and erosion in the burned areas were much less than they might have been in a more normal year.
505 Unfortunately, the limited sampling schedule made it impossible to separate these effects from the
506 expected seasonal cycle for a temperate lake.

507 Fish target strengths, and the corresponding estimated lengths, were in the expected range for

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

There was good agreement between the acoustic and net-based estimates of zooplankton biomass. However, the data from Lake Eleanor in April 2014 formed a notable outlier, with the net-based biovolume much lower relative to the acoustic biomass than expected, based on the other samples. That day, a relatively strong scattering layer was visible near the surface along the entire survey track. This layer, along with weaker-than-average TS predicted for zooplankton, accounted for the high acoustic biomass estimate. The small biovolume estimate is accurate, at least based on the net sample (0.5 mL of zooplankton from a total filtered volume of 15 m³). The discrepancy between these two measures is probably due to some combination of random variability in the net sample and uncertainty in our TS estimates. Regardless, regressions with and without this outlier produced positive slopes. Without it, the slope was significantly different from zero with a value of 0.85 mL g⁻¹. Wiebe *et al.* (1975) found that displacement biovolume DV and wet weight WW of marine zooplankton were related by the equation $\log_{10}(DV) = 0.078 + 1.026 \log_{10}(WW)$ which, in linear terms, implies a slope of approximately 1.2 mL g⁻¹, within the 95% confidence limits of our estimate (0.24 to 1.24 mL g⁻¹). Although the net sampled more of the water column than the 710 kHz echosounder (50 m vs ~30 m), zooplankton density was never more than 10 g m⁻³ below about 10 m in all surveys, so this seems unlikely to have affected the comparison. However, weak subsurface zooplankton maxima in Cherry Lake in October 2013 and September 2014 do raise the possibility of deeper zooplankton layers, which might have been sampled by the net but not the echosounder. The spatial extent of our net sampling was quite limited compared with that of the acoustics, so these results should thus be interpreted with some caution. However, our procedures do produce realistic biomass values, with agreement between nets and acoustics, increasing our confidence that the patterns observed are biologically meaningful.

539 To avoid similar ambiguities, future studies would benefit from more extensive direct sampling,
540 whether with nets or optical systems. Ultimately, the sound-scattering properties of freshwater
541 zooplankton should be quantified more rigorously, as they have been in many marine species (e.g. Chu
542 and Wiebe, 2005; Smith et al., 2010; Wiebe et al., 2010).

543 We did not calculate confidence intervals on our acoustic biomass estimates because the
544 conversion process from acoustic backscatter to biovolume includes multiple sources of uncertainty,
545 from the material properties of the scatterers to geostatistical error. To assess their (nonlinear)
546 cumulative effect would entail additional assumptions and conditional simulations, which we felt went
547 beyond the scope of this paper. Previous studies of uncertainty in acoustic surveys have found that
548 measurement errors (i.e., due to calibration, target strength uncertainty, length-weight conversion, etc.)
549 are typically minor compared with errors due to limited sampling of heterogeneously distributed
550 animals. In these studies total error, expressed as a coefficient of variation with respect to the estimated
551 biomass, ranged from ~10-170% (Demer, 2004; Rose, Gauthier, & Lawson, 2000). If confidence
552 intervals are required (e.g., if biomass estimates are to be used in management decisions), procedures
553 exist to calculate them (Demer, 2004; Simmonds and MacLennan, 2005).

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

565 Even after subtracting the lake-scale trend in zooplankton density, spatial autocorrelation was
566 evident in the residuals, as illustrated by the empirical variograms. These should be interpreted with
567 caution, since they were based in most cases on single reciprocal transects down the main axis of each
568 lake which may not have captured any spatial anisotropy present. In particular, the restricted time
569 available to survey Cherry Lake on 2 April 2013 meant that the transect was only about 1 km long,

570 limiting our ability to draw conclusions about the spatial distribution of zooplankton. Regardless, most
571 of the variograms in Cherry Lake and Lake Eleanor did show evidence of spatial patchiness in the
572 distribution of zooplankton, with approximate spatial scales, based on the variogram ranges, between
573 500 and 2000 m. These ranges are well below the sizes of the lake basins, suggesting that ecological
574 processes in these lakes are not spatially uniform.

575 This result was unexpected given the relatively small sizes of Independence, Cherry, and
576 Eleanor. It is unknown what processes generate and maintain patchiness in these lakes. In the ocean,
577 patchiness in zooplankton appears to be driven mostly by bottom-up processes, with scales of
578 biological variability mirroring scales of physical variability (Denman *et al.*, 1977; Mackas *et al.*, 1985;
579 Urmy *et al.*, 2012). At smaller scales, animal behavior and ecological interactions become more
580 important in generating spatial variability (Pinel-Alloul, 1995; Folt and Burns, 1999), though these
581 scales and processes are harder to observe and have been studied less in the field. It seems unlikely
582 that these lakes (with the possible exception of Tahoe) are large enough to support horizontal physical
583 structures larger than internal waves or wind-driven Langmuir circulations on the scale of 10s of m, so
584 the km-scale patchiness in the zooplankton is probably due to other processes, such as aggregation
585 (e.g., Byron *et al.* 1983) or local predation by schooling fish. In this interpretation, the lake's finite
586 boundaries act like a high-pass filter, preventing large-scale physical processes (e.g. fronts, gyres,
587 nutrient upwelling) from creating spatial variability that masks patchiness due to smaller-scale,
588 biological processes (swarming, predator-prey interactions, etc.). If this interpretation is correct, future
589 studies could use appropriately-sized lakes as model systems to study biogenic patchiness free of
590 interference from larger-scale processes.

591 The acoustic methods used here offer a number of advantages over traditional direct sampling
592 methods, though they also come with their own uncertainties and caveats. Identification of scatterers is
593 often a challenge with acoustics. However, using a two (or more) frequency system, as in this study,
594 reliably separates areas of backscatter from zooplankton and fish. Furthermore, direct net sampling of
595 the zooplankton community, especially in relatively small lakes such as Independence, Cherry, and
596 Eleanor, lets us confidently identify the main classes of zooplankton scatterers. The main source of
597 uncertainty when interpreting acoustic backscatter as an estimate of biomass density is in the target
598 strengths assumed for the scattering organisms. The DWBA is an accurate and widely used method to
599 calculate zooplankton target strengths, but it depends, sensitively, on the values of the scatterers'
600 material properties—namely the density- and sound-speed-contrasts g and h . To our knowledge, these

601 values have never been measured for any freshwater zooplankton. In their absence, we used generic
602 values from the literature, based on marine zooplankton (Stanton and Chu, 2000). These are reasonable
603 defaults, but they may not be accurate for the species considered here, introducing a degree of unknown
604 error into the TS and hence biomass estimates. Measurements of the material properties of freshwater
605 zooplankton would be a worthwhile objective for future research.

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

616 Perhaps most importantly, multi-frequency echosounders allow the biomass of multiple trophic
617 levels to be measured efficiently, and at the same spatial resolution, providing valuable data for food
618 web models such as Ecopath with Ecosim/Ecospace (Langseth *et al.*, 2012; Musinguzi *et al.*, 2017),
619 and ultimately ecosystem-based management decisions (Slocombe, 1985; Allan and Johnson, 1997;
620 Link, 2002). In a relatively small lake such as Cherry, Eleanor, or Independence, the ability to survey
621 large volumes of water quickly means that a virtual census of the lake's fauna is feasible. The time
622 available for our acoustic surveys was somewhat constrained by the need to collect other optical,
623 chemical, and biological data not reported in this study, as well as the time required to trailer the boat to
624 each lake. However, we were still able to run full-length transects of the lakes in most of the surveys,
625 and with just a few more hours it would be possible to survey the lakes quite thoroughly, producing
626 detailed three-dimensional maps of the distribution of fish and zooplankton as well as accurate
627 estimates of their numbers and biomass. As this study demonstrates, such a goal is achievable and
628 offers an exciting prospect for studies of predator-prey interactions and lake food webs.

629 **Acknowledgements**

630 Many of the logistical aspects of this project were planned and executed on short notice, and
631 could not have succeeded without help from a number of people. The staff of the UC Davis Tahoe
632 Environmental Research Center (TERC), in particular Raph Townsend, Katie Senft, and Brant Allen,
633 got us in and out of the lakes safely in conditions that were usually difficult and at times dangerous.
634 Taylor Leach and Jennifer Brentrup assisted with field work in Independence Lake and Lake Tahoe,
635 helped process some of the zooplankton samples, and supplied the CTD cast from Independence Lake.
636 CTD data in Tahoe, Cherry, and Eleanor were provided by Shohei Watanabe of UC Davis TERC. Maria
637 Anderson, Kayla Hartigan, Michaela Miller, and Helena Nierer identified, counted, and measured the
638 zooplankton. Erin Overholt maintained her good humor while dealing with reimbursements for a
639 dozen cross-country flights, booked on short notice. This project was funded by the National Science
640 Foundation's Division of Environmental Biology RAPID grant 13-60066, awarded to Craig E.
641 Williamson and S. Geoffrey Schladow. The authors declare no conflicts of interest.

642 **References**

643 Data and code to reproduce the analysis, tables, and figures in this paper are available at

644 <https://github.com/ElOceanografo/rimfire>.

645

646 Allan, J. D., & Johnson, L. B. (1997). Catchment-scale analysis of aquatic ecosystems. *Freshwater*
647 *Biology*, 37, 107–111. <https://doi.org/10.1046/j.1365-2427.1997.00155.x>

648 Beauchamp, D. a, Baldwin, C. M., Vogel, J. L., & Gubala, C. P. (1999). Estimating diel, depth-specific
649 foraging opportunities with a visual encounter rate model for pelagic piscivores. *Canadian*
650 *Journal of Fisheries and Aquatic Sciences*, 56(S1), 128–139. <https://doi.org/10.1139/f99-217>

651 Bezanson, J., Karpinski, S., Shah, V. B., & Edelman, A. (2012). Julia: A fast, dynamic language for
652 technical computing. *ArXiv Preprint, arXiv:1209*. <https://doi.org/10.1109/APS.2015.7305314>

653 Bingaman, J. W. (1961). *Guardians of the Yosemite: A Story of the First Rangers* (1st ed.). Desert
654 Printers. Retrieved from http://www.yosemite.ca.us/library/guardians_of_the_yosemite/

655 Bradford, D. F., Cooper, S. D., Jenkins, Jr., T. M., Kratz, K., Sarnelle, O., Brown, A. D., ... Brown, A.
656 D. (1998). Influences of natural acidity and introduced fish on faunal assemblages in California
657 alpine lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(11), 2478–2491.
658 <https://doi.org/10.1139/f98-128>

659 Brandt, S. B., Mason, D. M., Patrick, E. V, Argyle, R. L., Wells, L., Unger, P. A., & Stewart, D. J.
660 (1991). Acoustic measures of the abundance and size of pelagic planktivores in Lake Michigan.
661 *Canadian Journal of Fisheries and Aquatic Science*, 48(5), 894–908. [https://doi.org/10.1139/f91-](https://doi.org/10.1139/f91-106)
662 106

663 Byron, E. R., Whitman, P. T., & Goldman, C. R. (1983). Observation of copepod swarms in Lake
664 Tahoe. *Limnology and Oceanography*, 28(2), 378–382. <https://doi.org/10.4319/lo.1983.28.2.0378>

665 California Department of Water Resources. (2014). 2014 Water Year Monthly Precipitation. Retrieved
666 January 10, 2017, from <http://cdec.water.ca.gov/cgi-progs/reports/PRECIPOUT.BSN.2014>

667 Culver, D. A., Boucherle, M. M., Bean, D. J., & Fletcher, J. W. (1985). Biomass of Freshwater
668 Crustacean Zooplankton from Length–Weight Regressions. *Canadian Journal of Fisheries and*
669 *Aquatic Sciences*, 42(8), 1380–1390. <https://doi.org/10.1139/f85-173>

670 De Robertis, A., & Higginbottom, I. (2007). A post-processing technique to estimate the signal-to-noise
671 ratio and remove echosounder background noise. *ICES Journal of Marine Science*, 64(6), 1282–
672 1291. <https://doi.org/10.1093/icesjms/fsm112>

673 Demer, D. A. (2004). An estimate of error for the CCAMLR 2000 survey estimate of krill biomass.
674 *Deep-Sea Research Part II: Topical Studies in Oceanography*, 51(12–13 SPEC.ISS.), 1237–1251.
675 <https://doi.org/10.1016/j.dsr2.2004.06.012>

- 676 Denman, K., Okubo, A., & Platt, T. (1977). The chlorophyll function spectrum in the sea. *Limnology*
677 *and Oceanography*, 22(6), 1033–1038. <https://doi.org/10.4319/lo.1977.22.6.1033>
- 678 Eckart, N. A. (1940). The Water Supply System of San Francisco. *Journal (American Water Works*
679 *Association)*, 32(5), 751–794.
- 680 Efron, B., & Tibshirani, R. J. (1993). *An Introuction to the Bootstrap*. New York: Chapman & Hall.
- 681 Finlay, K., Beisner, B. E., & Barnett, a J. D. (2007). The use of the Laser Optical Plankton Counter to
682 measure zooplankton size, abundance, and biomass in small freshwater lakes. *Limnology and*
683 *Oceanography-Methods*, 5, 41–49. <https://doi.org/10.4319/lom.2007.5.41>
- 684 Folt, C. L., & Burns, C. (1999). Biological drivers of zooplankton patchiness. *Trends in Ecology and*
685 *Evolution*, 14(8), 300–305. [https://doi.org/10.1016/S0169-5347\(99\)01616-X](https://doi.org/10.1016/S0169-5347(99)01616-X)
- 686 Foote, K. G. (1987). Fish target strengths for use in echo integrator surveys. *The Journal of the*
687 *Acoustical Society of America*, 82(3), 981. <https://doi.org/10.1121/1.395298>
- 688 Foote, K. G., Knudsen, H. P., Vestnes, G., MacLennan, D. N., & Simmonds, E. J. (1987). *Calibration*
689 *of acoustic instruments for fish density estimation: a practical guide. ICES Cooperative Research*
690 *Report* (Vol. 144). Copenhagen. Retrieved from [http://www.ices.dk/sites/pub/Publication Reports/](http://www.ices.dk/sites/pub/Publication Reports/Cooperative Research Report (CRR)/crr144/crr144.pdf)
691 *Cooperative Research Report (CRR)/crr144/crr144.pdf*
- 692 Goldman, C. R., Morgan, M. D., Threlkeld, S. T., & Angeli, N. (1979). A population dynamics analysis
693 of the cladoceran disappearance from Lake Tahoe, California-Nevada. *Limnology and*
694 *Oceanography*, 24(2), 289–297. <https://doi.org/10.4319/lo.1979.24.2.0289>
- 695 Grünbaum, D. (2012). The logic of ecological patchiness. *Interface Focus*, 2(2), 150–155.
696 <https://doi.org/10.1098/rsfs.2011.0084>
- 697 Guisande, C., Bartumeus, F., Ventura, M., & Catalan, J. (2003). Role of food partitioning in structuring
698 the zooplankton community in mountain lakes. *Oecologia*, 136(4), 627–634.
699 <https://doi.org/10.1007/s00442-003-1306-4>
- 700 Hembre, L. K., & Megard, R. O. (2003). Seasonal and diel patchiness of a *Daphnia* population: An
701 acoustic analysis. *Limnology and Oceanography*, 48(6), 2221–2233.
702 <https://doi.org/10.4319/lo.2003.48.6.2221>
- 703 Hennesey, B. (2012). *Hetch Hetchy*. Charleston, SC: Arcadia Publishing.
- 704 Higley, Carrick, H. J., Brett, M. T., Luecke, C., & Goldman, C. R. (2001). The effects of ultraviolet
705 radiation and nutrient additions on periphyton biomass and composition in a sub-alpine lake
706 (Castle Lake, USA). *International Review of Hydrobiology*, 86(2), 147–163.
707 [https://doi.org/10.1002/1522-2632\(200104\)86:2<147::AID-IROH147>3.0.CO;2-Y](https://doi.org/10.1002/1522-2632(200104)86:2<147::AID-IROH147>3.0.CO;2-Y)
- 708 Holliday, D. V., & Pieper, R. E. (1995). Bioacoustical oceanography at high frequencies. *ICES Journal*

- 709 *of Marine Science*, 52(3–4), 279–296. [https://doi.org/10.1016/1054-3139\(95\)80044-1](https://doi.org/10.1016/1054-3139(95)80044-1)
- 710 Hyatt, M. W., & Hubert, W. a. (2001). Proposed Standard-Weight Equations for Brook Trout. *North*
 711 *American Journal of Fisheries Management*, 21(May), 253–254. [https://doi.org/10.1577/1548-](https://doi.org/10.1577/1548-8675(2001)021<0253:PSWEFB>2.0.CO;2)
 712 8675(2001)021<0253:PSWEFB>2.0.CO;2
- 713 Kaufman, J. A. F., Rundel, P., Stephenson, N., & Weixelman, D. A. (2007). Montane and subalpine
 714 vegetation of the Sierra Nevada and Cascade Ranges. In M. G. Barbour, T. Keeler-Wolf, & A. A.
 715 Schoenherr (Eds.), *Terrestrial Vegetation of California* (3rd ed., pp. 456–501). Oakland, CA:
 716 University of California Press. Retrieved from <http://www.jstor.org/stable/10.1525/j.ctt1pnqfd.21>
- 717 Knapp, R. A., Matthews, K. R., & Sarnelle, O. (2001). Resistance and resilience of alpine lake fauna to
 718 fish introductions. *Ecological Monographs*, 71(3), 401–421. [https://doi.org/10.1890/0012-](https://doi.org/10.1890/0012-9615(2001)071[0401:raroal]2.0.co;2)
 719 9615(2001)071[0401:raroal]2.0.co;2
- 720 Link, J. J. S. (2002). What does ecosystem-based fisheries management mean? *Fisheries (Bethesda)*,
 721 27(4), 18–21. Retrieved from [http://www.scopus.com/inward/record.url?eid=2-s2.0-](http://www.scopus.com/inward/record.url?eid=2-s2.0-1942490119&partnerID=40&md5=dc5321eb52a4acd1ddaaa7072670c40%5Cnhttp://www.nmfs.noaa.gov/pr/sars/improvement/pdfs/meaning.pdf)
 722 1942490119&partnerID=40&md5=dc5321eb52a4acd1ddaaa7072670c40%5Cnhttp://
 723 www.nmfs.noaa.gov/pr/sars/improvement/pdfs/meaning.pdf
- 724 Lorke, A., Weber, A., Hofmann, H., & Peeters, F. (2008). Opposing diel migration of fish and
 725 zooplankton in the littoral zone of a large lake. *Hydrobiologia*, 600(1), 139–146.
 726 <https://doi.org/10.1007/s10750-007-9183-1>
- 727 Mackas, D. L., Denman, K. L., & Abbott, M. R. (1985). Plankton patchiness: biology in the physical
 728 vernacular. *Bulletin of Marine Science*, 37(2), 653–674.
- 729 Mackas, D. L., Tsurumi, M., Galbraith, M. D., & Yelland, D. R. (2005). Zooplankton distribution and
 730 dynamics in a North Pacific Eddy of coastal origin: II. Mechanisms of eddy colonization by and
 731 retention of offshore species. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 52(7–
 732 8), 1011–1035. <https://doi.org/10.1016/j.dsr2.2005.02.008>
- 733 MacLennan, D. N., Fernandes, P. G., MacLennan, J. D., Fernandes, D. N., MacLennan, D. M., &
 734 Fernandes, P. G. (2002). A consistent approach to definitions and symbols in fisheries acoustics.
 735 *ICES Journal of Marine Science*, 59(2), 365–369. <https://doi.org/10.1006/jmsc.2001.1158>
- 736 Masson, S., Angeli, N., Guillard, J., & Pinel-Alloul, B. (2001). Diel vertical and horizontal distribution
 737 of crustacean zooplankton and young of the year fish in a sub-alpine lake: an approach based on
 738 high frequency sampling. *Journal of Plankton Research*, 23(10), 1041–1060.
 739 <https://doi.org/10.1093/plankt/23.10.1041>
- 740 McGehee, D. E., O’Driscoll, R. L., & Traykovski, L. V. M. (1998). Effects of orientation on acoustic
 741 scattering from Antarctic krill at 120 kHz. *Deep-Sea Research Part II: Topical Studies in*
 742 *Oceanography*, 45(7), 1273–1294. [https://doi.org/10.1016/S0967-0645\(98\)00036-8](https://doi.org/10.1016/S0967-0645(98)00036-8)

- McNaught, A. S., Schindler, D. W., Parker, B. R., Paul, A. J., Anderson, R. S., Donald, D. B., & Agbeti, M. (1999). Restoration of the food web of an alpine lake following fish stocking. *Limnology and Oceanography*, 44(1), 127–136. <https://doi.org/10.4319/lo.1999.44.1.0127>
- Melnik, N. G., Timoshkin, O. A., Sidleva, V. G., Pushkin, S. V., & Mamylov, V. S. (1993). Hydroacoustic measurement of the density of the Baikal macrozooplankton *Macrohectopus branickii*. *Limnology and Oceanography*, 38, 425–434. <https://doi.org/10.4319/lo.1993.38.2.0425>
- Milewski, C. L., & Brown, M. L. (1994). Proposed Standard Weight (Ws) Equation and Length-Categorization Standards for Stream-Dwelling Brown Trout (*Salmo trutta*). *Journal of Freshwater Ecology*, 9(2), 111–116. <https://doi.org/10.1080/02705060.1994.9664437>
- Myriax Pty Ltd. (2016). Echoview Software. Hobart, Tasmania. Retrieved from <http://www.echoview.com>
- National Wildfire Coordinating Group. (2013). *Rim Fire Final Update*. Retrieved from <http://inciweb.nwcg.gov/incident/article/3660/21586/>
- Nielsen, J. L., & Sage, G. K. (2002). Population Genetic Structure in Lahontan Cutthroat Trout. *Transactions of the American Fisheries Society*, 131, 376–388. [https://doi.org/10.1577/1548-8659\(2002\)131<0376:PGSILC>2.0.CO;2](https://doi.org/10.1577/1548-8659(2002)131<0376:PGSILC>2.0.CO;2)
- Northcote, T. G. (1964). Use of a high-frequency echo sounder to record distribution and migration of *Chaoborus* larvae. *Limnology and Oceanography*, 9(1), 87–91. <https://doi.org/10.4319/lo.1964.9.1.0087>
- Parks, S. E., Warren, J. D., Stamieszkin, K., Mayo, C. A., & Wiley, D. (2012). Dangerous dining: surface foraging of North Atlantic right whales increases risk of vessel collisions. *Biology Letters*, 8(1), 57–60. <https://doi.org/10.1098/rsbl.2011.0578>
- Patoine, A., Pinel-Alloul, B., & Prepas, E. E. (2002). Effects of catchment perturbations by logging and wildfires on zooplankton species richness and composition in Boreal Shield lakes. *Freshwater Biology*, 47(10), 1996–2014. <https://doi.org/10.1046/j.1365-2427.2002.00947.x>
- Pinel-Alloul, B. (1995). Spatial heterogeneity as a multiscale characteristic of zooplankton community. *Hydrobiologia*, 300(1), 17–42.
- Pinel-Alloul, B., & Ghadouani, A. (2007). Spatial heterogeneity of planktonic microorganisms in aquatic systems. In *The spatial distribution of microbes in the environment* (pp. 203–310). Netherlands: Springer.
- Pinel-Alloul, B., Guay, C., Angeli, N., Legendre, P., Dutilleul, P., Balvay, G., ... Guillard, J. (1999). Large-scale spatial heterogeneity of macrozooplankton in Lake of Geneva. *Canadian Journal of Fisheries and Aquatic Sciences*, 56(8), 1437–1451. <https://doi.org/10.1139/cjfas-56-8-1437>
- Pugnetti, A., & Bettinetti, R. (1999). Biomass and species structure of the phytoplankton of an high

777 mountain lake (Lake Paione Superiore, Central Alps, Italy). *Journal of Limnology*, 58(2), 127–
778 130. <https://doi.org/10.4081/jlimnol.1999.127>

779 R Development Core Team. (2016). R: A language and environment for statistical computing. Vienna,
780 Austria: R Foundation for Technical Computing. Retrieved from <http://r-project.org>

781 Ricker, W. E. (1973). Linear regressions in fishery research. *Journal of the Fisheries Research Board*
782 *of Canada*, 30(3), 409–434.

783 Roman, M. R., Holliday, D. V., & Sanford, L. P. (2001). Temporal and spatial patterns of zooplankton
784 in the Chesapeake Bay turbidity maximum. *Marine Ecology Progress Series*, 213, 215–227.
785 <https://doi.org/10.3354/meps213215>

786 Rose, G., Gauthier, S., & Lawson, G. (2000). Acoustic surveys in the full monte: Simulating
787 uncertainty. *Aquatic Living Resources*, 13(5), 367–372. [https://doi.org/10.1016/S0990-](https://doi.org/10.1016/S0990-7440(00)01074-3)
788 [7440\(00\)01074-3](https://doi.org/10.1016/S0990-7440(00)01074-3)

789 Rose, K. C., Williamson, C. E., Saros, J. E., Sommaruga, R., & Fischer, J. M. (2009). Differences in
790 UV transparency and thermal structure between alpine and subalpine lakes: implications for
791 organisms. *Photochemical & Photobiological Sciences*, 8, 1244–1256.
792 <https://doi.org/10.1039/b905616e>

793 Rudstam, L. G., Knudsen, F. R., Balk, H., Gal, G., Boscarino, B. T., & Axenrot, T. (2008). Acoustic
794 characterization of *Mysis relicta* at multiple frequencies. *Canadian Journal of Fisheries and*
795 *Aquatic Sciences*, 65(12), 2769–2779. <https://doi.org/10.1139/F08-179>

796 Rudstam, L. G., Parker-Stetter, S. L., Sullivan, P. J., & Warner, D. M. (2009). Towards a standard
797 operating procedure for fishery acoustic surveys in the Laurentian Great Lakes, North America.
798 *ICES Journal of Marine Science*.

799 Schabetsberger, R., Luger, M. S., Drozdowski, G., & Jagsch, A. (2009). Only the small survive:
800 Monitoring long-term changes in the zooplankton community of an Alpine lake after fish
801 introduction. *Biological Invasions*, 11(6), 1335–1345. <https://doi.org/10.1007/s10530-008-9341-z>

802 Simmonds, J., & MacLennan, D. (2005). *Fisheries acoustics: Theory and practice: Second edition*.
803 *Fisheries Acoustics: Theory and Practice: Second Edition* (2nd ed.). Oxford: Blackwell Science.
804 <https://doi.org/10.1002/9780470995303>

805 Simonin, P. W., Parrish, D. L., Rudstam, L. G., Sullivan, P. J., & Pientka, B. (2012). Native rainbow
806 smelt and nonnative alewife distribution related to temperature and light gradients in Lake
807 Champlain. *Journal of Great Lakes Research*, 38(SUPPL. 1), 115–122.
808 <https://doi.org/10.1016/j.jglr.2011.06.002>

809 Simpkins, D. G., & Hubert, W. A. (1996). Proposed revision of the standard-weight equation for
810 rainbow trout., 11(3), 3–9.

811 Slocombe, D. S. (1985). Implementing Ecosystem-based Management. *BioScience*, 43(9), 612–622.

812 Sommer, U., Adrian, R., De Senerpont Domis, L., Elser, J. J., Gaedke, U., Ibelings, B., ... Winder, M.
813 (2012). Beyond the Plankton Ecology Group (PEG) Model: Mechanisms Driving Plankton
814 Succession. *Annual Review of Ecology, Evolution, and Systematics*, 43(1), 429–448.
815 <https://doi.org/10.1146/annurev-ecolsys-110411-160251>

816 Sommer, U., Gliwicz, Z. M., Lampert, W., & Duncan, A. (1986). The PEG-model of seasonal
817 succession of planktonic events in fresh waters. *Archiv Fur Hydrobiologie*, 106(4), 433–471.
818 <https://doi.org/10.1111/j.1469-185X.1969.tb01218.x>

819 Stanton, T. K., & Chu, D. (2000). Review and recommendations for the modelling of acoustic
820 scattering by fluid-like elongated zooplankton: euphausiids and copepods. *ICES Journal of*
821 *Marine Science*, 57, 793–807. <https://doi.org/10.1006/jmsc.1999.0517>

822 Stanton, T. K., Chu, D., & Wiebe, P. H. (1998). Sound scattering by several zooplankton groups. II.
823 Scattering models. *The Journal of the Acoustical Society of America*, 103(1), 236–253.
824 <https://doi.org/10.1121/1.421110>

825 Temming, A., Floeter, J., & Ehrich, S. (2007). Predation hot spots: Large scale impact of local
826 aggregations. *Ecosystems*, 10(6), 865–876. <https://doi.org/10.1007/s10021-007-9066-3>

827 Teraguchi, M., & Northcote, T. G. (1966). Vertical distribution and migration of *Chaoborus flavicans*
828 larvae in Corbett Lake, British Columbia. *Limnology and Oceanography*, 11(2), 164–176.

829 Tessier, A. J. (1983). Coherence and horizontal movements of patches of *Holopedium gibberum*
830 (Cladocera). *Oecologia*, 60(1), 71–75.

831 Thorne, P. D., & Hanes, D. M. (2002). A review of acoustic measurement of small-scale sediment
832 processes. *Continental Shelf Research*, 22(4), 603–632. [https://doi.org/10.1016/S0278-](https://doi.org/10.1016/S0278-4343(01)00101-7)
833 [4343\(01\)00101-7](https://doi.org/10.1016/S0278-4343(01)00101-7)

834 United States Forest Service. (2016). Stanislaus National Forest - Cherry Lake. Retrieved November
835 17, 2016, from <http://www.fs.usda.gov/recarea/stanislaus/recarea/?recid=14973>

836 Urmy, S. S. (2016). SDWBA.jl: A Julia package for modeling acoustic backscatter from zooplankton.
837 <https://doi.org/http://doi.org/10.5281/zenodo.56814>

838 Urmy, S. S., Horne, J. K., & Barbee, D. H. (2012). Measuring the vertical distributional variability of
839 pelagic fauna in Monterey Bay. *ICES Journal of Marine Science*, 69(2), 184–196.
840 <https://doi.org/10.1093/icesjms/fsr205>

841 Urmy, S. S., Williamson, C. E., Leach, T. H., Schladow, S. G., Overholt, E. P., & Warren, J. D. (2016).
842 Vertical redistribution of zooplankton in an oligotrophic lake associated with reduction in
843 ultraviolet radiation by wildfire smoke. *Geophysical Research Letters*, 43(8), 3746–3753.
844 <https://doi.org/10.1002/2016GL068533>

- 845 Warren, J. D., Leach, T. H., & Williamson, C. E. (2016). Measuring the distribution, abundance, and
846 biovolume of zooplankton in an oligotrophic freshwater lake with a 710 kHz scientific
847 echosounder. *Limnology and Oceanography: Methods*, 14(4), 231–244.
848 <https://doi.org/10.1002/lom3.10084>
- 849 Warren, J. D., & Wiebe, P. H. (2008). Accounting for biological and physical sources of acoustic
850 backscatter improves estimates of zooplankton biomass. *Canadian Journal of Fisheries and*
851 *Aquatic Sciences*, 65(7), 1321–1333. <https://doi.org/10.1139/F08-047>
- 852 Wiebe, P. H., Boyd, S., & Cox, J. L. (1975). Relationships between zooplankton displacement volume,
853 wet weight, dry weight, and carbon. *Fishery Bulletin*, 73(4), 777–786.
- 854 Wiebe, P. H., Lawson, G. L., Lavery, A. C., Copley, N. J., Horgan, E., & Bradley, A. (2013). Improved
855 agreement of net and acoustical methods for surveying euphausiids by mitigating avoidance using
856 a net-based LED strobe light system. *ICES Journal of Marine Science*, 70(3), 650–664.
857 <https://doi.org/10.1093/icesjms/fst005>
- 858 Williamson, C. E., Overholt, E. P., Brentrup, J. A., Pilla, R. M., Leach, T. H., Schladow, S. G., ...
859 Neale, P. J. (2016). Sentinel responses to droughts, wildfires, and floods: Effects of UV radiation
860 on lakes and their ecosystem services. *Frontiers in Ecology and the Environment*, 14(2), 102–109.
861 <https://doi.org/10.1002/fee.1228>

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

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>Diaphanosoma</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>Eurycyclops</i>	22.8	14.9	0	4.1
		<i>Eurytemora</i>	2.2	0	0	4.1
		<i>Leptodiptomus</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>Diaphanosoma</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>Eurycyclops</i>	27.7	0	1.1	2.8
		<i>Eurytemora</i>	1.7	0	0	0
		<i>Leptodiptomus</i>	1.7	0	2.6	1.6
		<i>Orthocyclops</i>	0	0	2.6	0
		Unk. Copepodite	4.8	20.9	67.4	73.8
Independence	Cladocerans	<i>Bosmina</i>	6.3			
		<i>Daphnia</i>	45.8			
	Copepods	<i>Diacyclops</i>	47.9			
Tahoe	Cladocerans	<i>Bosmina</i>	1.2			
		<i>Daphnia</i>	0.3			
	Copepods	<i>Epischura</i>	21.9			
		<i>Leptodiptomus</i>	55.9			

Table 2. Acoustic properties of crustacean zooplankton. For each class of scatterers (Cladocerans, Copepods, and Nauplii larvae), the mean acoustic target strength (TS, dB re m²) and individual wet weight (W, µg) are displayed, along with the percentage by biomass of the net catch made up of that class of 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	-118.5	48.1	59	-121.1	65.8	31	-148.4	1.3	10	-119.7	48.8
	Eleanor	-112.7	115.3	64	-113.5	89.5	32	—	—	—	-113.2	101.6
	Independence	-114.1	94.9	50	-117.1	81.1	46	—	—	—	-115.3	88.2
	Tahoe	—	—	—	-104	189.7	86	-130.5	3.9	12	-104.7	163.4
2014-04	Cherry	-113.4	100.8	43	-112	84.4	19	-120.3	7.4	38	-114.5	62.2
	Eleanor	-126.9	31	18	-123.8	49.8	38	-127.8	3.4	44	-125.7	26.1
2014-06	Cherry	-119.5	41.2	30	-123.1	50.8	58	-134	2.2	13	-122.1	41.8
	Eleanor	-117.4	63.5	23	-128.3	34.6	11	-125.4	5.4	67	-122.1	21.6
2014-09	Cherry	-123.4	39	32	-128	32	22	-125.4	5.4	46	-125.1	22
	Eleanor	-117.9	72.7	15	-110.8	152.6	11	-118.5	7.5	73	-116.6	33.3

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

878

Date	Lake	TS (dB)	(Estimated)		n
			L (cm)	W (g)	
2013-10	Cherry	-37 ± 7.4	26 ± 18	590 ± 930	7467
	Eleanor	-40 ± 7	18 ± 15	290 ± 600	217
	Tahoe	-37 ± 7.8	25 ± 20	610 ± 1100	136
2014-04	Cherry	-41 ± 8.2	15 ± 14	180 ± 390	522
	Eleanor	-39 ± 7.6	21 ± 17	370 ± 700	909
2014-06	Cherry	-41 ± 6.7	17 ± 11	150 ± 260	4226
	Eleanor	-39 ± 8.6	19 ± 17	330 ± 640	457
2014-09	Cherry	-41 ± 7.2	16 ± 13	200 ± 450	2442

879

Table 4. Acoustic estimates of wet-weight zooplankton and fish biomass in each lake and survey. Biomasses are presented both as areal densities (in g m⁻²) and scaled by lake areas to total biomasses (in kg). The ratio of zooplankton to fish biomass is also presented. Seasonal changes in the different trophic levels are evident, as well as inter-lake differences. Fish biomass was not estimated in Independence Lake due to the lack of reliable target strength estimates, and neither biomass was estimated in Lake Tahoe due to the small extent of the survey relative to the lake's size.

886

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	2.3	13,000	0.26	1,700	7.8
	Eleanor	3.9	0.53	2,000	0.0018	7	300
	Independence	2.6	0.23	570	—	—	—
	Tahoe	490	0.0082	—	—	—	—
2014-04	Cherry	6.3	0.32	2,000	0.014	94	21
	Eleanor	3.9	7.8	31,000	0.015	60	510
2014-06	Cherry	6.3	10.5	68,000	0.043	280	240
	Eleanor	3.9	4.7	19,000	0.16	640	30
2014-09	Cherry	6.3	0.14	910	0.043	280	3.3
	Eleanor	3.9	0.14	560	0.054	210	2.7

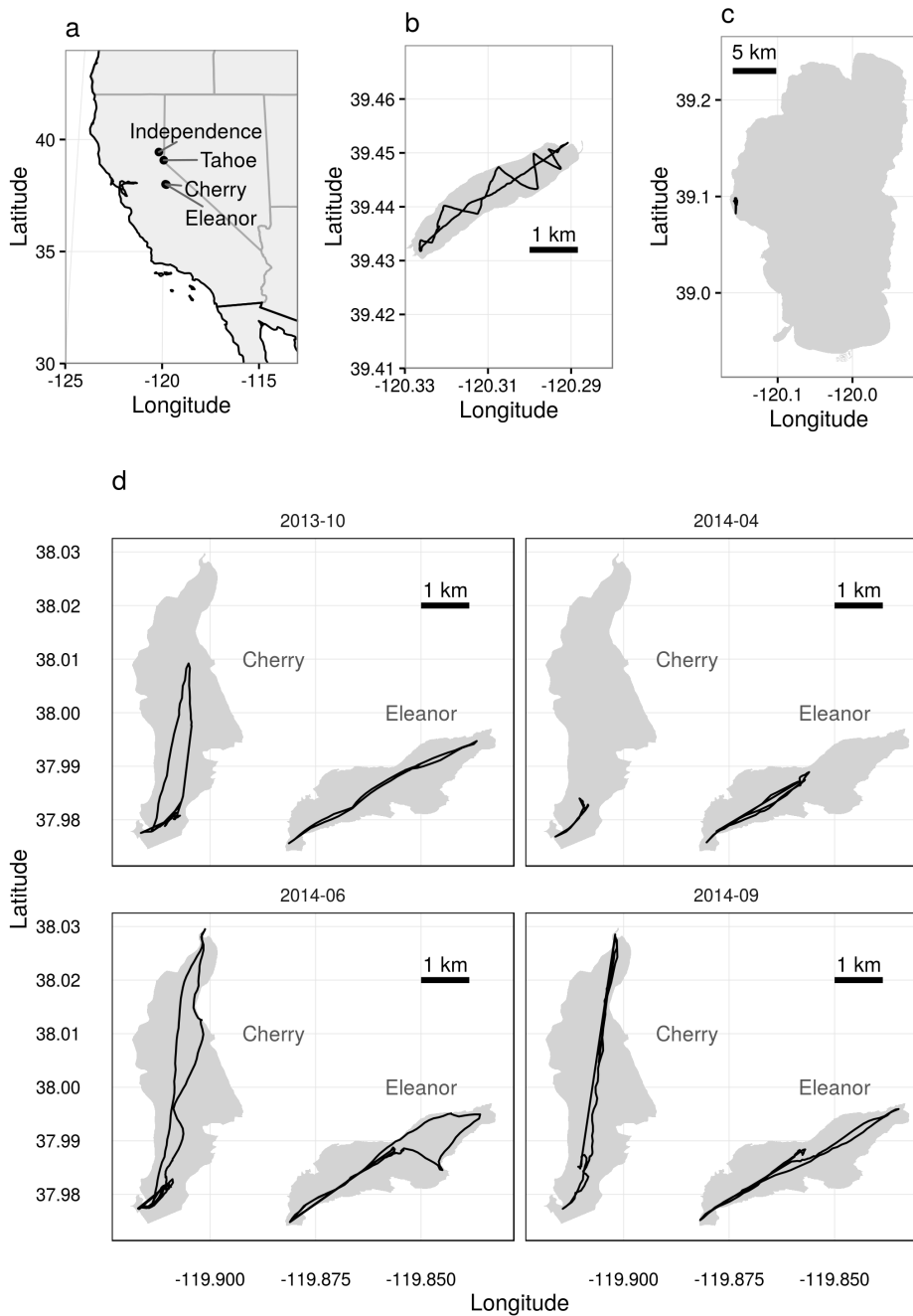
887

888 **Table 5.** Summary of multiple-regression models for spatial trends in biomass density of zooplankton
889 by lake and survey. The average wet-weight biomass density of zooplankton (in g m⁻³), was averaged
890 through the water column, log₁₀-transformed, and modeled as a linear function of distance (in km) from
891 the lake's inlet and from the shore. The columns "Intercept", "Inlet distance", and "Shore distance"
892 give the regression intercept and coefficients associated with each covariate. Their respective *p*-values
893 are in the columns to their right. These trends were not estimated in Lake Tahoe because only a small
894 proportion of the lake's area was surveyed (Figure 1).

895

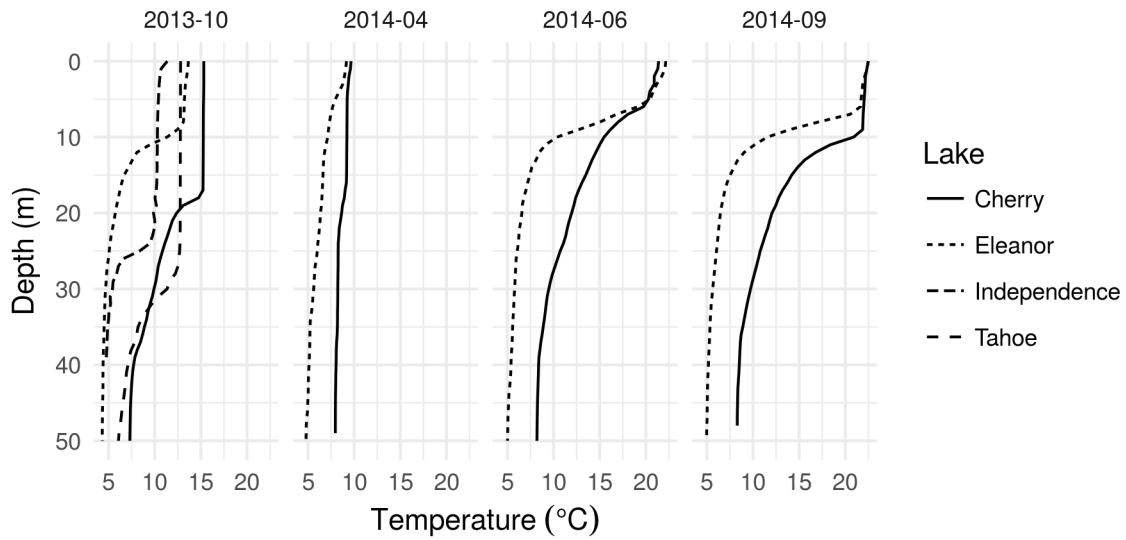
Date	Lake	Intercept	<i>p</i>	Inlet distance	<i>p</i>	Shore distance	<i>p</i>	<i>R</i> ²
2013-10	Cherry	-1.62	< 0.001	0.231	< 0.001	0.0981	0.783	0.32
	Eleanor	0.02	0.878	-0.0112	0.679	-0.485	0.097	0.02
	Independence	-1.07	< 0.001	0.0419	< 0.001	0.808	< 0.001	0.23
2014-04	Cherry	0.202	0.733	-0.0843	0.315	-0.419	0.063	0.17
	Eleanor	0.33	0.019	0.219	< 0.001	0.206	0.276	0.45
2014-06	Cherry	2.06	< 0.001	-0.184	< 0.001	-0.76	< 0.001	0.73
	Eleanor	0.521	< 0.001	0.0111	0.637	0.687	0.002	0.05
2014-09	Cherry	0.197	0.093	-0.109	< 0.001	-1.44	< 0.001	0.44
	Eleanor	-0.0942	0.224	0.0161	0.242	-1.68	< 0.001	0.55

896



897

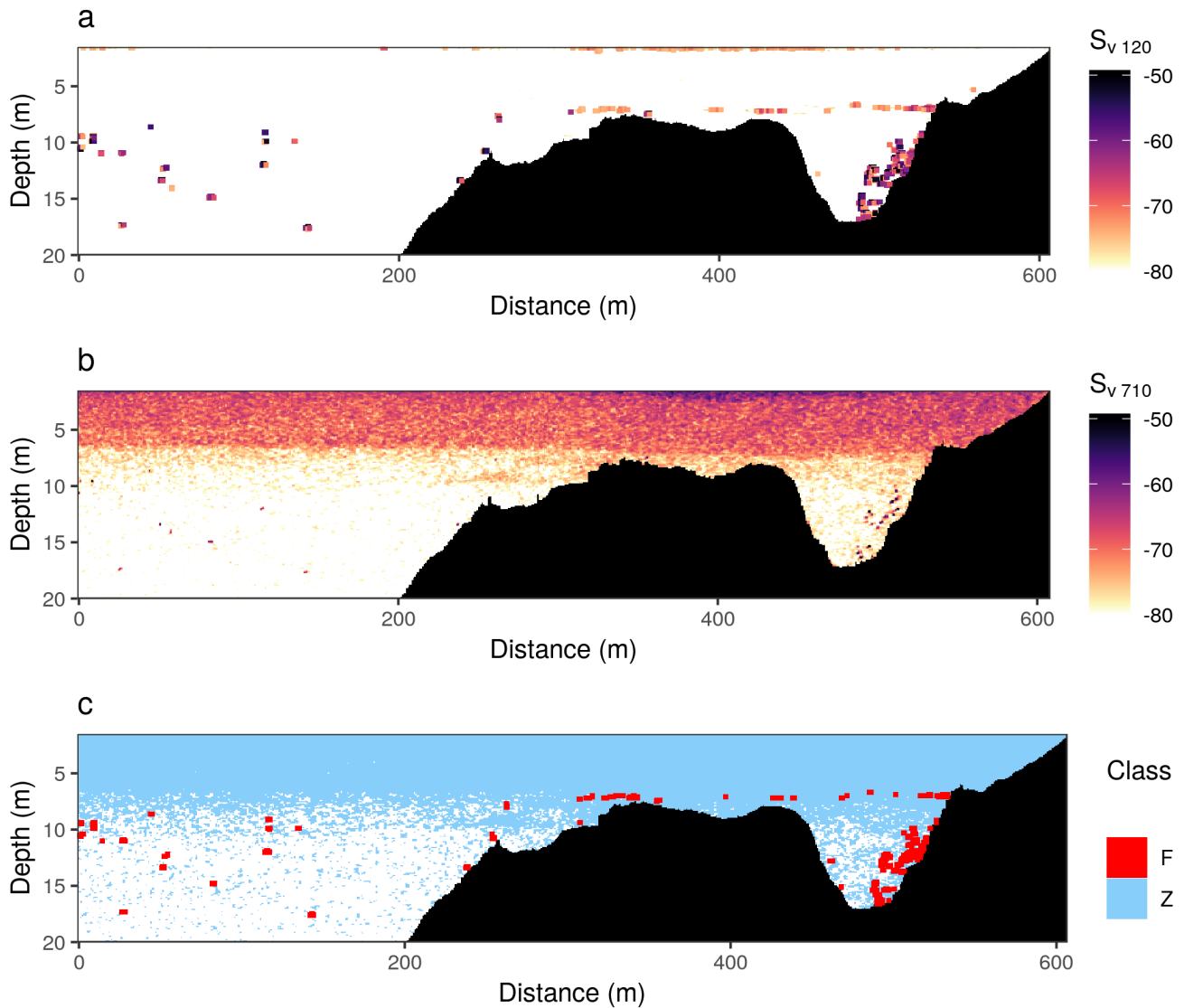
898 Figure 1. Maps of study lakes, showing (a) location of the four surveyed lakes in California in the
 899 western United States, survey tracks in October 2013 in (b) Independence Lake and (c) Lake Tahoe,
 900 and (d) repeated surveys in Cherry Lake and Lake Eleanor in October 2013, April 2014, June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



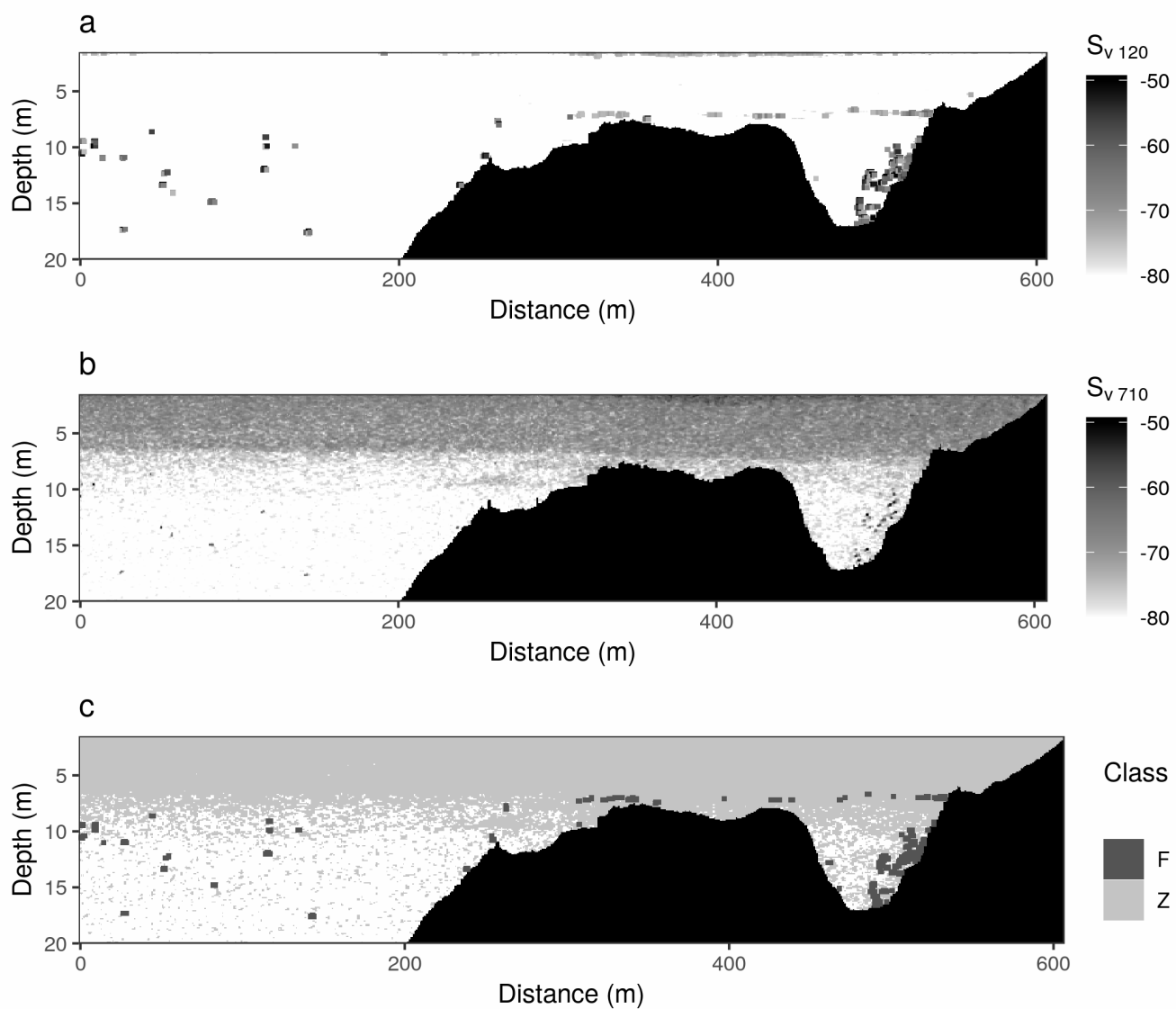
902

903

904 Figure 2: Temperature profiles measured in the lakes during four seasonal surveys. (Lake Tahoe and
 905 Independence Lake were only sampled in October 2013.) All four lakes had mixed layers between 30
 906 m (Tahoe) and 10 m (Eleanor) in October 2013. Cherry and Eleanor were fully mixed in April 2014,
 907 but thermoclines were reestablished around 10 m by June and had strengthened by the end of the
 908 summer.

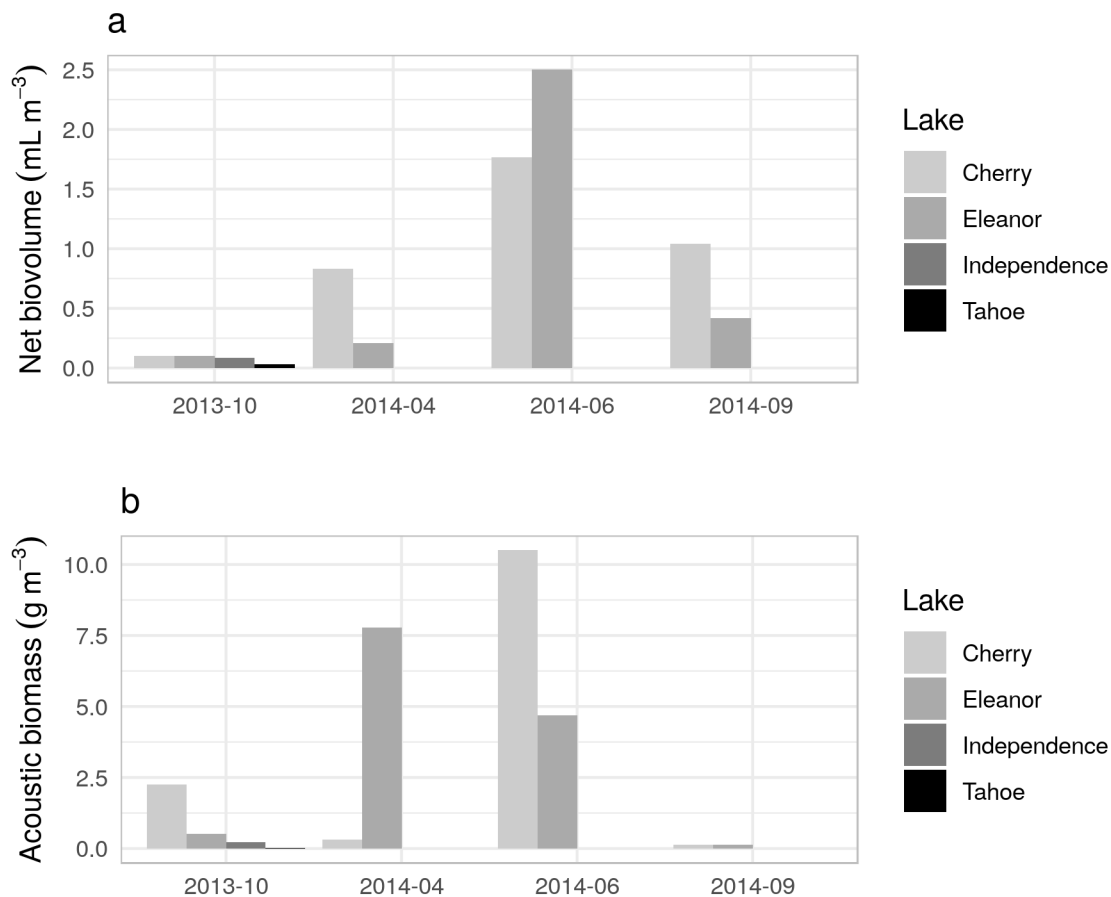


910 Figure 3. Acoustic profile through part of Cherry Lake on 24 June 2014, showing acoustic backscatter
 911 at (a) 120 kHz and (b) 710 kHz. Isolated dots are echoes from individual fish, while the zone of
 912 scattering between ~7 m and the surface represents echoes from zooplankton, which are only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



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

919

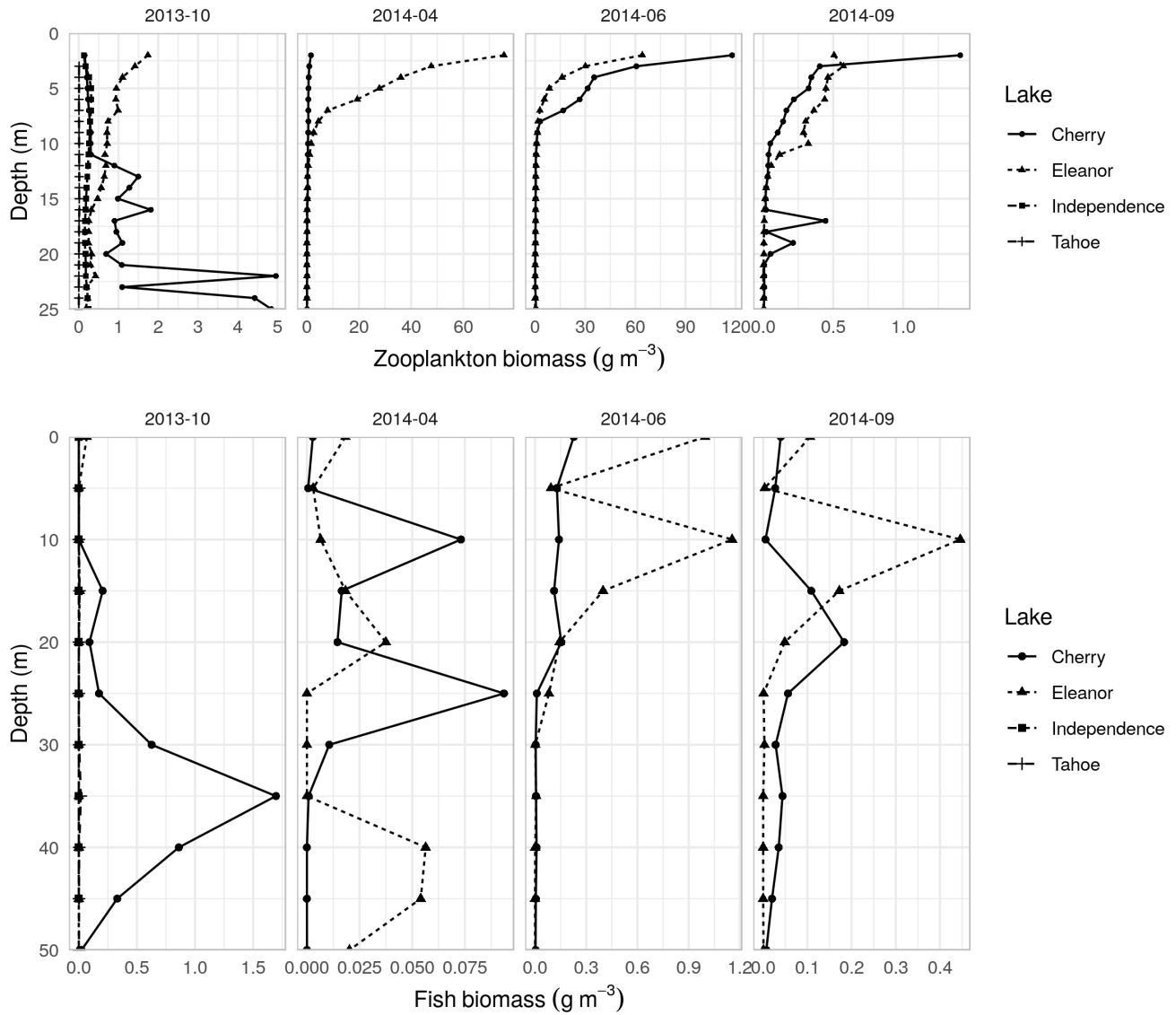


920

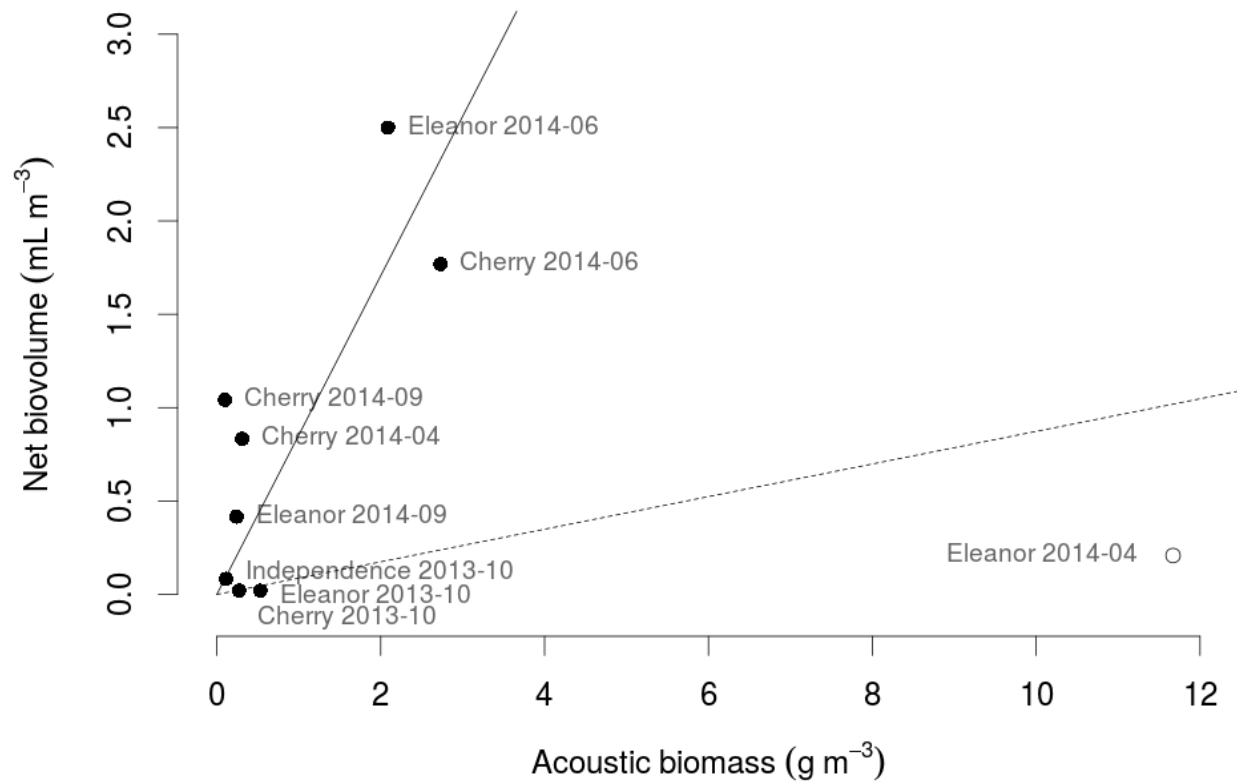
921 Figure 4. Zooplankton abundance measured by nets and acoustics in each of four seasonal surveys.

922 The color of each bar indicates the lake; note that Independence and Tahoe were only sampled in
 923 October 2013, and that the acoustic biomass density in Tahoe was too low to be visible on the graph.

924 (a) Biovolume of zooplankton caught in vertical net tows. These values are normalized by the volume
 925 of water filtered, giving units of mL of biovolume per cubic meter of lake water. (b) Wet-weight
 926 biomass of zooplankton per cubic meter, estimated from acoustic surveys, using measured zooplankton
 927 lengths and species identities to parameterize target strengths and length-weight relationships.



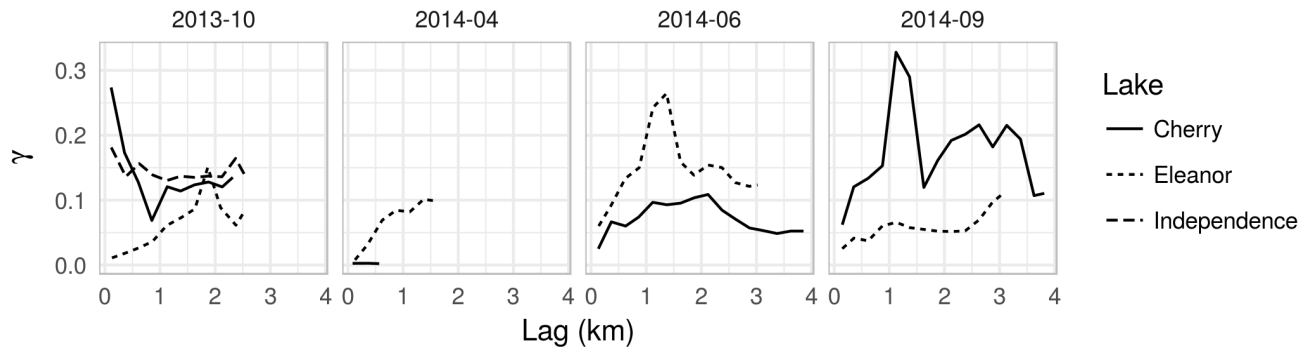
929 Figure 5. Depth profiles of zooplankton (top row) and fish (bottom row) wet weight biomass density
 930 measured acoustically in the lakes sampled during each of four seasonal surveys. (Lake Tahoe and
 931 Independence Lake were only sampled in October 2013). Lines show estimated biomass density of all
 932 zooplankton or fish as a function of depth. Note differing x-axis scales in each plot.



933

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

938



939
 940 Figure 7. Empirical variograms of log-transformed zooplankton areal biomass density (i.e., mass of
 941 zooplankton per m² of lake surface) for each lake and survey. Significant spatial autocorrelation (i.e.,
 942 patchiness) was present at scales from 0-2 km in most surveys.