

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

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4 Running title: Zooplankton & fish in Sierra Nevada lakes

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17 Keywords: acoustics, biomass estimation, fish, patchiness, zooplankton.

18 **Summary**

19

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

39 **Introduction**

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

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

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

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

95 We surveyed the zooplankton and fish in four lakes in the Sierra Nevada mountains of
96 California, USA, between autumn 2013 and autumn 2014: Cherry Lake, Lake Eleanor, Independence
97 Lake, and Lake Tahoe. Cherry and Eleanor are similar in size and shape, and are separated by less than
98 2 km. Lake Tahoe and Independence Lake are located more than 100 km to the north, and are larger
99 (Tahoe) and smaller (Independence) than Cherry and Eleanor. Our primary tool was a two-frequency
100 acoustic system which allowed us to distinguish echoes from fish and zooplankton (Mitson *et al.*, 1996;

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

117

118 **Methods**

119 *Study lakes*

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

Acoustic data collection

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

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

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

181 Independence Lake and Lake Tahoe were sampled on 20 and 21 October 2013 respectively.
182 Cherry Lake and Lake Eleanor were each sampled four times. Cherry was sampled on 29 October
183 2013, and on 2 April, 24 June, and 10 September 2014. Eleanor was sampled one day later, on 30
184 October 2013, 3 April, 25 June, and 11 September 2014. In the three smaller lakes, we attempted to
185 perform a lengthwise transect from one end of the lake to the other. In Independence Lake, we were
186 also able to add a series of zig-zag transects across the main axis of the lake (Figure 1). The April 2014
187 transects in Cherry and Eleanor were shorter due to snowfall, which required slow travel on the
188 mountain roads and reduced the time available for sampling.

189

190 *Direct sampling and target strength models*

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

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

198 Zooplankton were collected on each sampling day near the center of the lake with a vertical tow
199 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
200 equipment problem with the ring net during the October 2013 trip to Cherry and Eleanor, we instead
201 used an open Van Dorn bottle (10 cm diameter) with an elastic nylon mesh ($\sim 100 \mu\text{m}$) over one end.
202 This was hauled vertically through the water column with its uncovered end up, acting like a small-
203 diameter net. Filtered volume was calculated as the depth of the cast multiplied by the cross-sectional
204 area of the net mouth. Samples were preserved in 10% buffered formalin for later analysis. In the lab,
205 the total biovolume of each sample was measured after allowing it to settle in a graduated cylinder.
206 Because of the small diameter of the Van Dorn sampler, the biovolumes of the samples from Cherry
207 and Eleanor in October 2013 were smaller than the finest graduation on our cylinder, preventing a
208 precise measurement. We estimated them at 0.1 mL; our analyses did not appear sensitive to these
209 estimates when they were in the range of 0-1 mL. A subsample of 200-300 animals was split from each
210 original sample and counted under a compound microscope. All of these animals were identified to the
211 lowest possible taxonomic level. In addition, the lengths of the first 30 animals counted from each
212 sample were measured to the nearest 0.1 mm.

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

225 dry weight, W_d , using a published regression for either calanoid nauplii, the calanoid *Diaptomus*
226 *oregonensis*, or *Daphnia galeatea* (Culver *et al.*, 1985). Dry weights were converted to wet weights,
227 W_w , using a relationship from Wiebe *et al.* (1975).

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

231
$$\langle \sigma_{BS, tot} \rangle = \sum_{i=1}^m p_i \langle \sigma_{BS, i} \rangle$$

232
$$\langle W_{w, tot} \rangle = \sum_{i=1}^m p_i \langle W_{w, i} \rangle$$

233 where p_i is the proportional numerical abundance of scattering class i in the net sample and the angled
234 brackets denote an average or expected value. The total numerical density of all zooplankton (number
235 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 $b_{tot} = n_{tot}$

236 $\langle W_{w, tot} \rangle$.

237

238 *Acoustic data processing and analysis*

239 Acoustic data were processed using Echoview Software version 7.0 (Myriax Pty Ltd, 2016).
240 Background noise was estimated and subtracted following De Robertis and Higginbottom (2007), using
241 a 20×5 pixel averaging window (horizontal \times vertical) with noise and SNR thresholds of -110 dB and
242 10 dB. Data were manually scrutinized to correct bottom detection lines, exclude echoes from net and
243 other instrument casts, and eliminate intermittent interference, such as multipath and sidelobe echoes
244 from the steep rocky sides of the lake when close to shore. Data within 2 m of the surface and bottom
245 were excluded to avoid integrating the transducers' ringdown, surface bubbles, or the near-bottom
246 "dead zone." Acoustic data were integrated in cells 1 m deep and 10 m wide along-track and exported
247 for further analysis.

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

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

265 Fish densities were calculated from the integrated 120 kHz backscatter, using the mean TS of
266 the individual fish targets to convert backscatter to fish densities. To obtain approximate estimates of
267 fish biomass, we first converted each fish target's TS to a length (in cm). Because no specific TS-
268 length relationships are available at 120 kHz for the salmonid species in these lakes, we used a generic
269 relationship $TS = 20 \log_{10}(L) - 67.4$ for physoclist fishes from Foote (1987). These lengths were
270 then converted to approximate wet weights using published scaling relationships. Length-weight
271 relationships for fish are usually assumed to follow a power law of the form $\log_{10} W = a + b \log_{10} L$,
272 where a and b are fitted empirically for a particular species or population. Because we could not
273 identify fish targets to species, we averaged the parameters for rainbow trout ($a = -4.898$, $b = 2.99$,
274 Simpkins and Hubert 1996), brook trout ($a = -5.186$, $b = 3.103$, Hyatt and Hubert 2001), and brown
275 trout ($a = -4.867$, $b = 2.96$, Milewski and Brown 1994) to get a single length-weight equation with $a = -$
276 4.98 and $b = 3.02$. These lengths and weights were averaged into mean values for each lake and
277 survey.

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

284

285 *Comparison of net and acoustic biomass*

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

302

303 *Distribution of zooplankton and fish*

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

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

319

320 **Results**

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

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

341 Target strengths predicted for the different classes of zooplankton scatterers using the DWBA
342 varied widely (Table 2). The strongest scatterers were copepods in Lake Tahoe, with an average TS of
343 -104 dB. The weakest were nauplius larvae in Cherry Lake in October 2013, with a mean TS of -148
344 dB. Cladoceran target strengths fell between -113 and -127 dB. Adult copepod target strengths fell in
345 the same broad range, from -104 to -128 dB. Nauplii, due to their much smaller size, were predicted to
346 scatter much less sound, with their mean TS falling between -120 and -148 dB (Table 2). After
347 averaging across all scattering classes, overall mean TS ranged from -127 dB in Lake Eleanor in

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

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

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

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

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

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

393 When depth-integrated and scaled by their respective lake areas, these densities yielded a wide
394 range of estimates for the total biomasses of these trophic levels in the different lakes. In October
395 2013, Cherry Lake contained the most total zooplankton, with an estimated 13,000 kg. In April 2014,
396 the zooplankton wet-weight biomass density in Lake Eleanor had increased to 7.8 g m^{-3} , raising its total
397 biomass estimate to over 31,000 kg. Total zooplankton biomass in Cherry Lake in April was 2,000 kg,
398 15% of its level in the October survey. By June, however, it had increased to 68,000 kg, while the
399 zooplankton biomass in Eleanor dropped to 19,000 kg. During the September 2014 survey,
400 zooplankton populations in both lakes had dropped back to lower levels (Table 4).

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

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

410 significantly different from zero, with a fitted value of 0.85 mL g^{-1} , and a 95% confidence interval from
411 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
412 geometric mean regression, 0.96 mL g^{-1} , was not significantly different from that obtained with the
413 standard regression.

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

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

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

441 values, in \log_{10} -transformed units, imply multiplicative differences (\times/\div) in zooplankton density from
442 0.25 to 1.6 at long ranges, where “long ranges,” as defined by the variograms, are between 1 and 2 km.

443

444 **Discussion**

445

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

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

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

478 Fish biomass did not vary nearly as widely as zooplankton biomass, which is expected given
479 their much longer life spans and generation times. At the height of the zooplankton blooms,
480 zooplankton biomass was several hundred times that of fish, indicating that the former were effectively
481 released from predatory control at those times. In both autumns, the zooplankton:fish ratios were much
482 lower, suggesting a closer match between rates of zooplankton reproduction and fish predation. While
483 fish were scarce in Lake Eleanor in October 2013, our estimate of total biomass (7 kg, Table 4) was
484 probably unrealistic, reflecting error due to the patchy distribution of fish and our limited survey time
485 as much as the true biomass. While zooplankton were found mostly in the surface mixed layer, the fish
486 (at least during our daytime sampling) were found in and below the thermocline, reflecting either light-
487 driven DVM or a preferred thermal niche.

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

502 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 (Table 2), 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 (Figure 5), so this seems unlikely to have affected the comparison. However, weak subsurface zooplankton maxima in Cherry Lake in October 2013 and September 2014 (Figure 5) 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

534 that the patterns observed are biologically meaningful. To avoid similar ambiguities, future studies
535 would benefit from more extensive direct sampling, whether with nets or optical systems. Ultimately,
536 the sound-scattering properties of freshwater zooplankton should be quantified more rigorously, as they
537 have been in many marine species (e.g. Chu and Wiebe, 2005; Smith et al., 2010; Wiebe et al., 2010).

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

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

560 Even after subtracting the lake-scale trend in zooplankton density, spatial autocorrelation was
561 evident in the residuals, as illustrated by the empirical variograms (Figure 7). These should be
562 interpreted with caution, since they were based in most cases on single reciprocal transects down the
563 main axis of each lake which may not have captured any spatial anisotropy present. In particular, the
564 restricted time available to survey Cherry Lake on 2 April 2013 meant that the transect was only about

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

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

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

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

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

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

624 **Acknowledgements**

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

637 **References**

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

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

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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 | | | |

861 **Table 2.** Acoustic properties of crustacean zooplankton. For each class of scatterers (Cladocerans,
862 Copepods, and Nauplii larvae), the mean acoustic target strength (TS, dB re m²) and individual wet
863 weight (W, µg) are displayed, along with the percentage by biomass of the net catch made up of that
864 class of scatterers.

865

| 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 |

866

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

873

| 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 |

874

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.

881

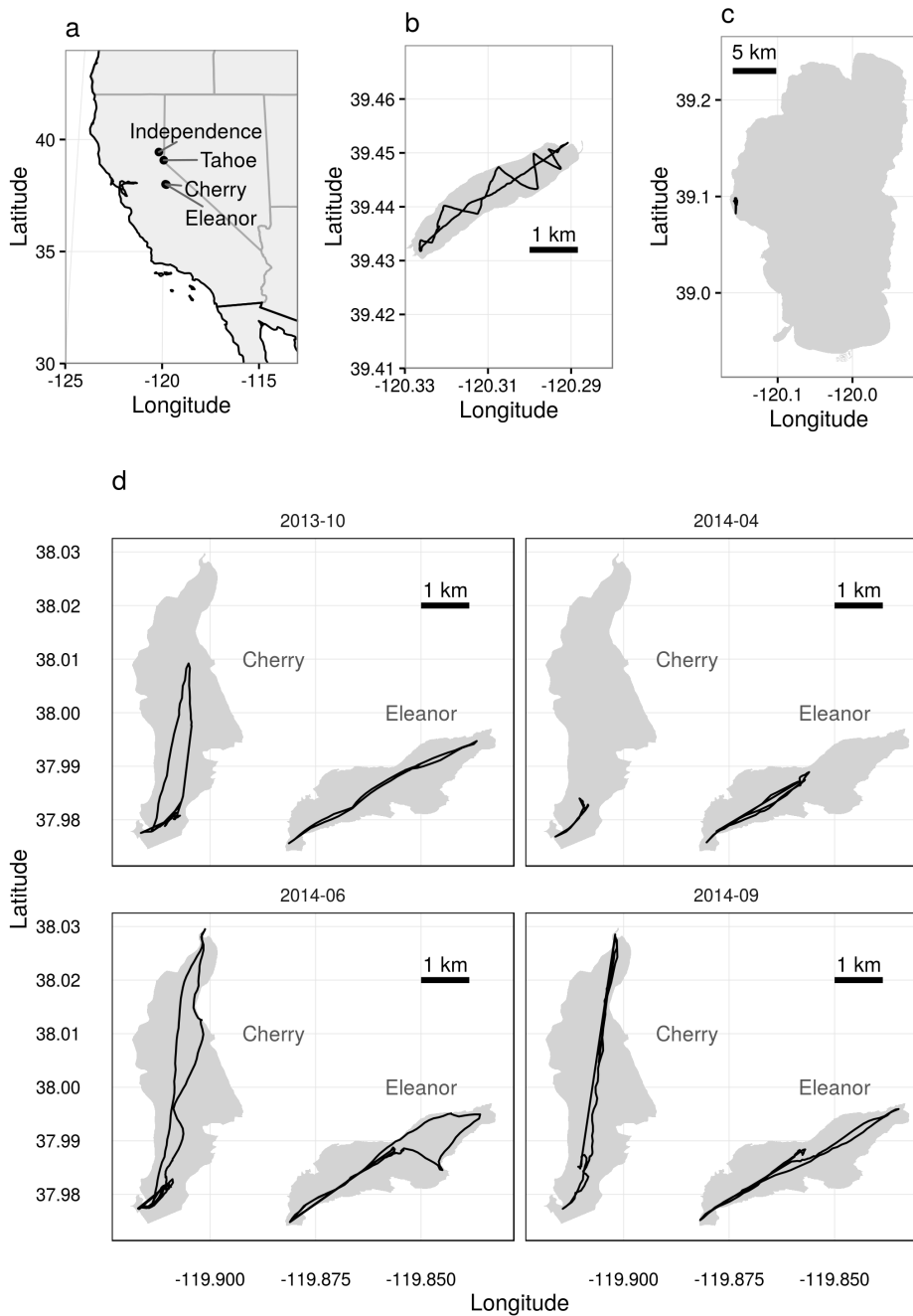
| Date | Lake | Area (km ²) | Zooplankton | | Fish | | Ratio |
|---------|--------------|-------------------------|------------------------------|--------------|------------------------------|--------------|-------|
| | | | Density (g m ⁻²) | Biomass (kg) | Density (g m ⁻²) | Biomass (kg) | |
| 2013-10 | 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 |

882

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

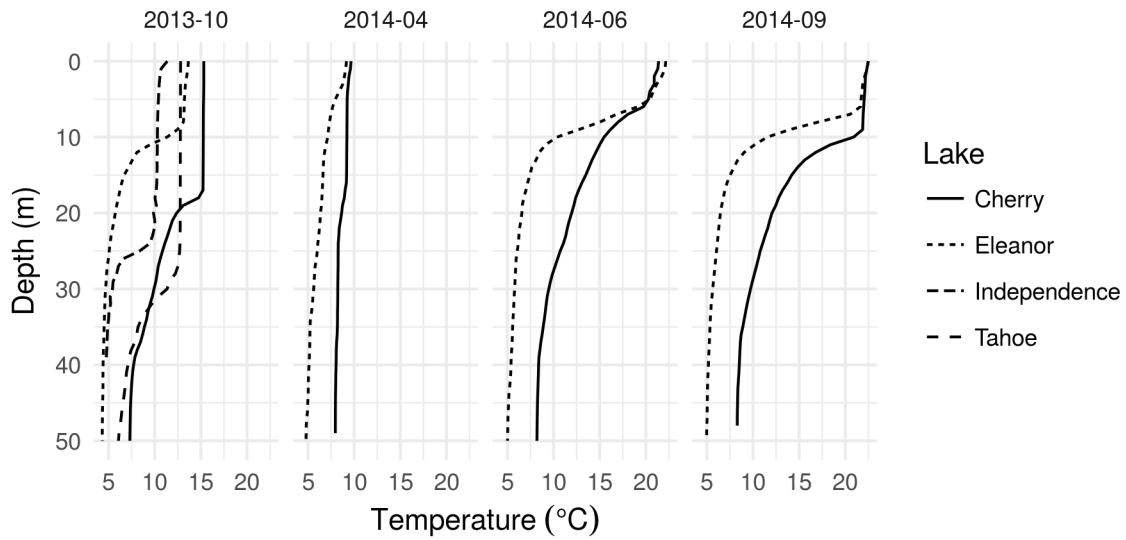
890

| 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 |



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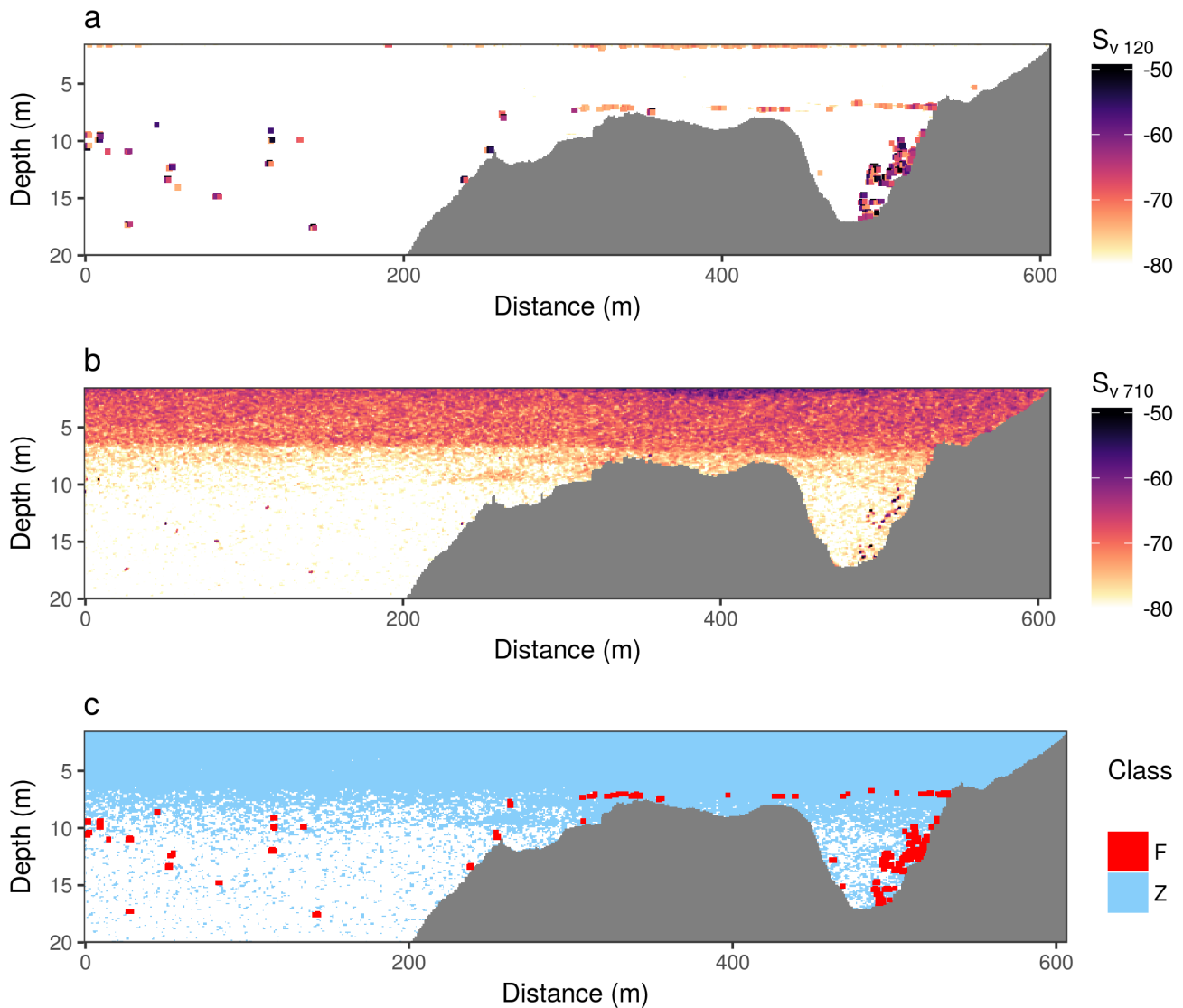
893 **Figure 1.** Maps of study lakes, showing (a) location of the four surveyed lakes in California in the
 894 western United States, survey tracks in October 2013 in (b) Independence Lake and (c) Lake Tahoe,
 895 and (d) repeated surveys in Cherry Lake and Lake Eleanor in October 2013, April 2014,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



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898

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



904

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

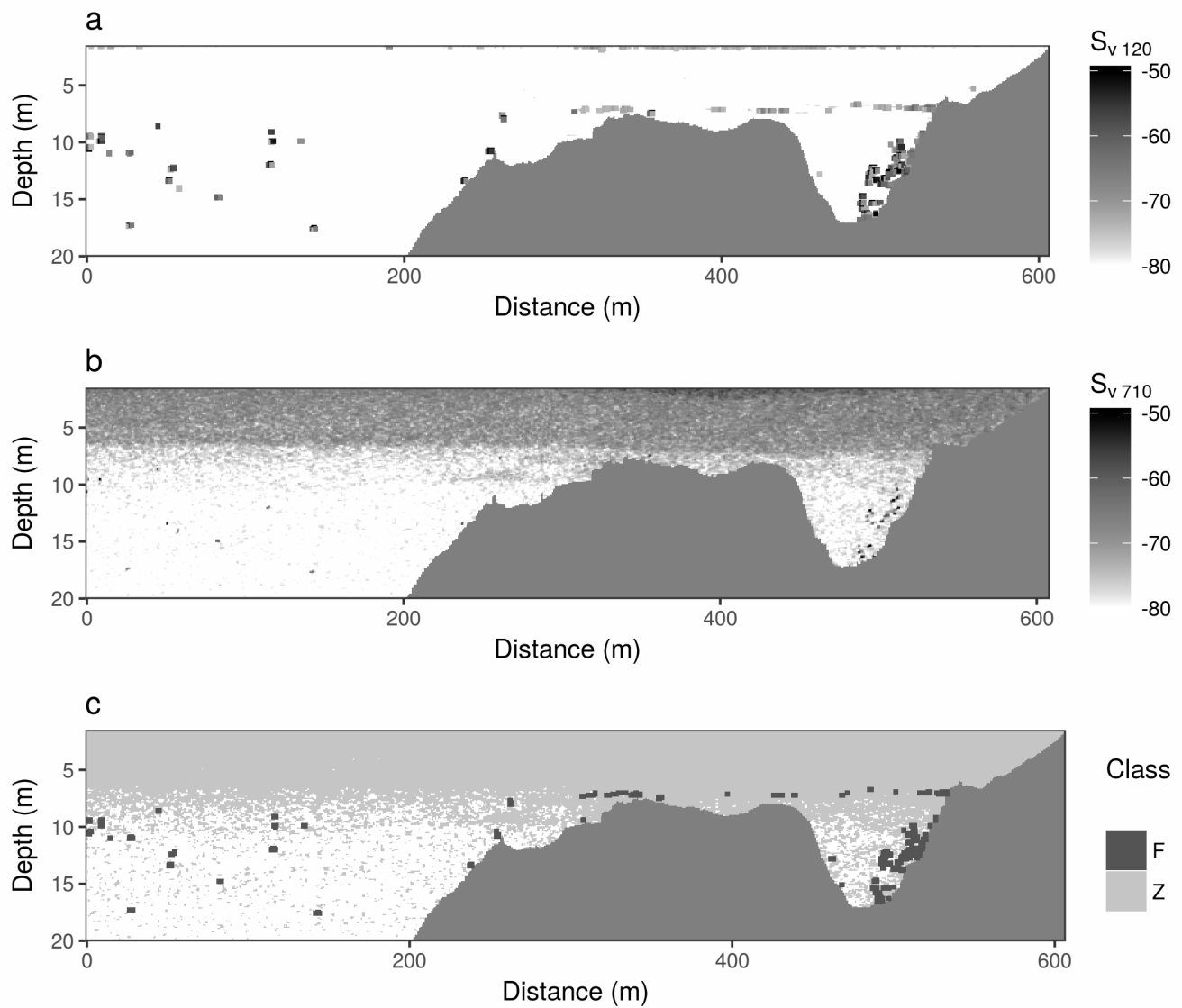
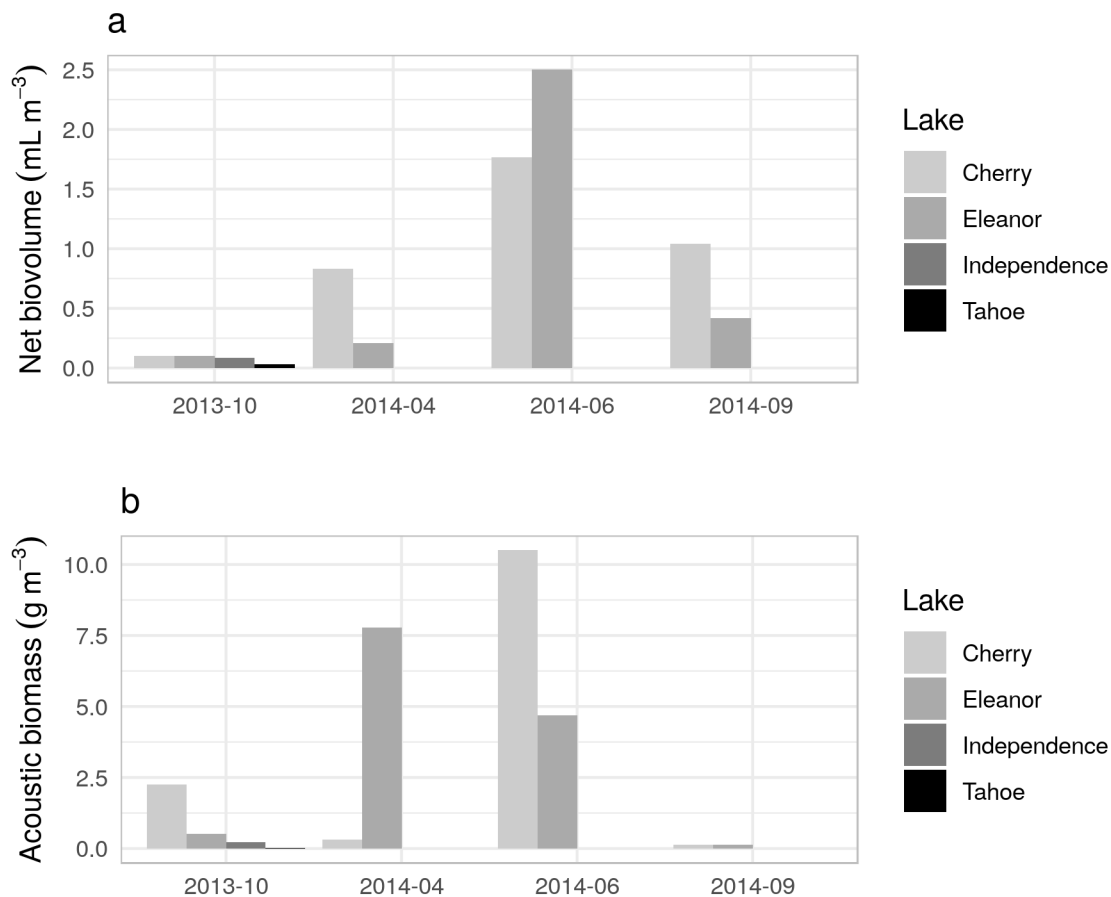


Figure 3 (Grayscale rendering for print publication)

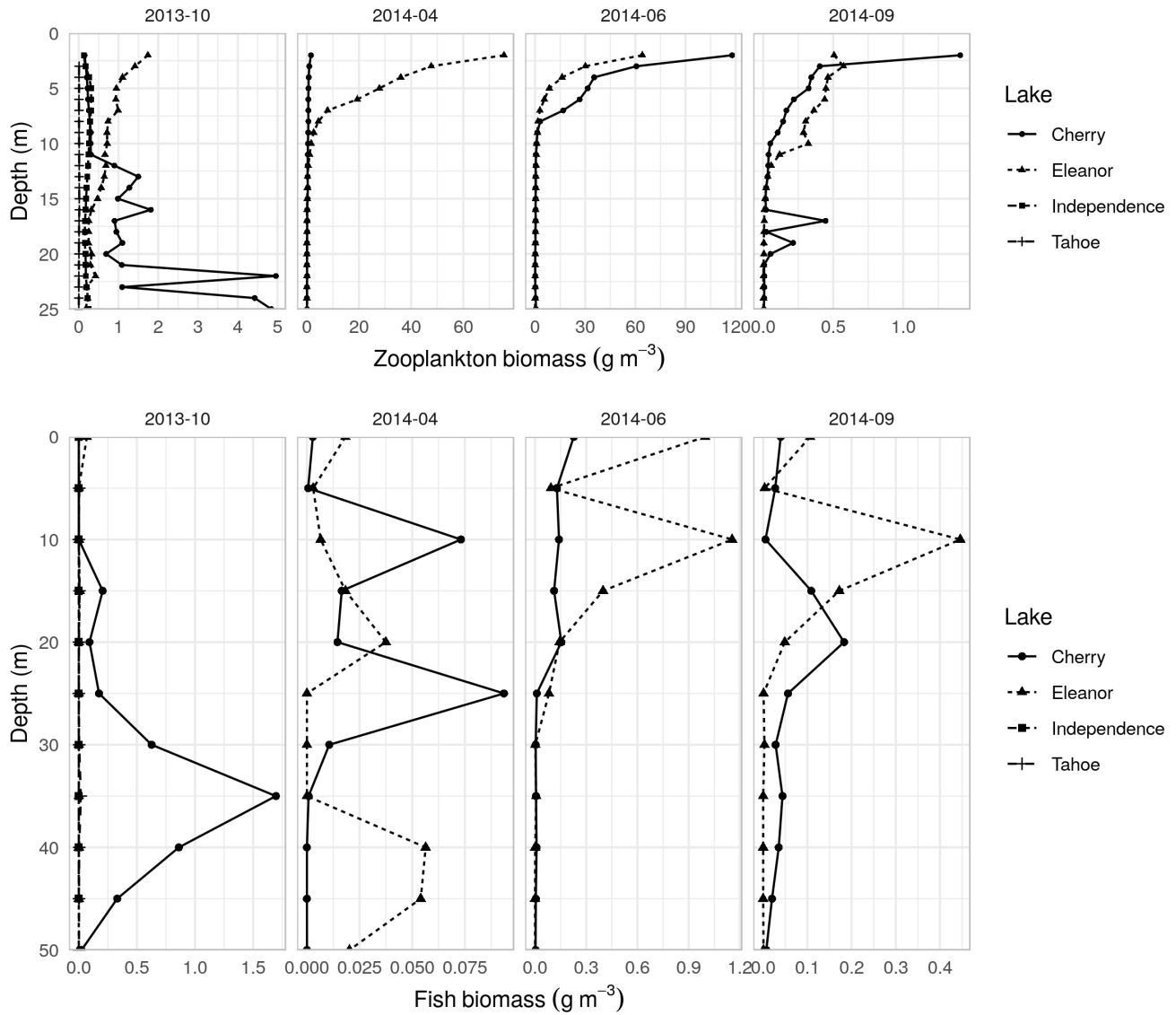


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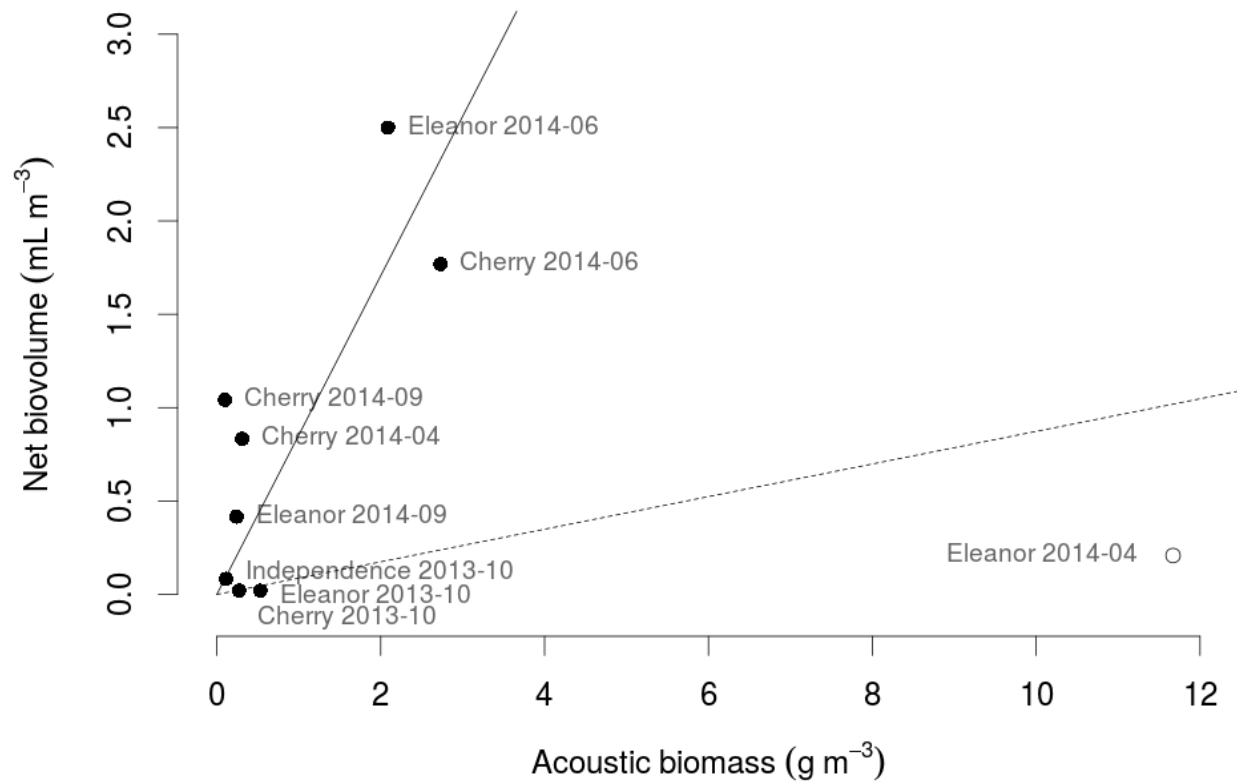
916 Figure 4. Zooplankton abundance measured by nets and acoustics in each of four seasonal surveys.

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

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



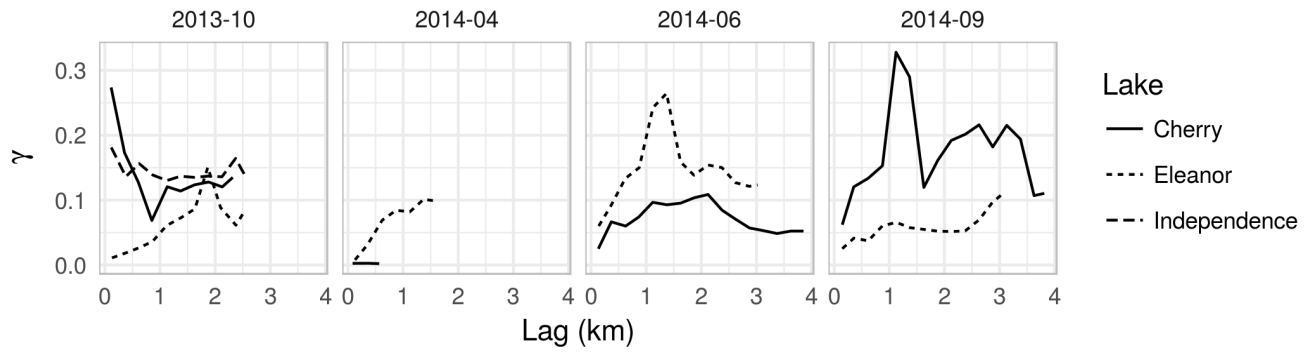
924 **Figure 5.** Depth profiles of zooplankton (top row) and fish (bottom row) wet weight biomass density
 925 measured acoustically in the lakes sampled during each of four seasonal surveys. (Lake Tahoe and
 926 Independence Lake were only sampled in October 2013). Lines show estimated biomass density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



928

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

933



934
 935 **Figure 7.** Empirical variograms of log-transformed zooplankton areal biomass density (i.e., mass of
 936 zooplankton per m² of lake surface) for each lake and survey. Significant spatial autocorrelation (i.e.,
 937 patchiness) was present at scales from 0-2 km in most surveys.