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Key Points:

- Wildfire smoke selectively reduced incident ultraviolet solar radiation in Lake Tahoe, CA
- When smoke was present, zooplankton were positioned higher in the water column
- Wildfires appear capable of remotely altering the distribution of zooplankton in clear lakes

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Vertical redistribution of zooplankton in an oligotrophic lake associated with reduction in ultraviolet radiation by wildfire smoke

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Abstract We used a natural experiment to test whether wildfire smoke induced changes in the vertical distribution of zooplankton in Lake Tahoe by decreasing incident ultraviolet radiation (UV). Fires have a variety of effects on aquatic ecosystems, but these impacts are poorly understood and have rarely been observed directly. UV is an important driver of zooplankton vertical migration, and wildfires may alter it over large spatial scales. We measured UV irradiance and the distribution of zooplankton on two successive days. On one day, smoke haze from a nearby wildfire reduced incident UV radiation by up to 9%, but not irradiance in the visible spectrum. Zooplankton responded by positioning themselves, on average, 4.1 m shallower in the lake. While a limited data set such as this requires cautious interpretation, our results suggest that smoke from wildfires can change the UV environment and distribution of zooplankton. This process may be important in drought-prone regions with increasingly frequent wildfires, and globally due to widespread biomass burning.

1. Introduction

Fires, both naturally occurring and anthropogenic, are global phenomena [*Flannigan et al.*, 2009] that may have widespread impacts on the UV environment of lakes [*France et al.*, 2000] and oceans [*Herman et al.*, 1997]. Fires can alter the transparency of water bodies locally by depositing ash and particulates, either directly or via later erosion and runoff from burned watersheds. Fires may also have remote effects, by aerially depositing ash into lakes or by attenuating solar radiation underneath smoke plumes. These processes can affect lakes in entirely different watersheds than the fire itself. The importance of these effects on lake ecosystems is largely unknown, but as wildfires are expected to become more frequent and severe due to climate warming and shifts in precipitation in many parts of the world [*Flannigan et al.*, 2009], the issue is worthy of investigation. The western United States, including the Sierra Nevada Mountains of California, is one area where the frequencies of droughts and wildfires are expected to increase in future decades [*Westerling et al.*, 2006; *Miller et al.*, 2009].

The diel vertical migration (DVM) of aquatic organisms is likely the largest animal migration event on Earth [*Hays*, 2003]. Throughout the world's oceans and lakes, numerous fish and zooplankton exhibit this behavior, swimming up to hundreds of vertical meters twice a day [*Hardy*, 1936; *Cushing*, 1951; *van Haren and Compton*, 2013], causing large shifts in the distribution of animal biomass and altering the biogeochemistry of the water column [*Steinberg et al.*, 2000]. Because sunlight attenuates rapidly in water, photosynthesis and visual predation are both most efficient near the surface. DVM is classically explained as a compromise: animals stay deep during the day to avoid visual predators and only move to shallower depths, where food is more abundant, after dark. In fact, many different environmental factors can affect DVM, including UV radiation [*Leech and Williamson*, 2001]. Various natural events and processes can also alter "standard" DVM, including eclipses [*Kampa*, 1975], phases of the Moon [*Ochoa et al.*, 2013], ice cover [*Wallace et al.*, 2010], and water turbidity [*Frank and Widder*, 2002; *Rose et al.*, 2012].

A recent synthesis, the transparancy-regulator hypothesis (TRH) [*Williamson et al.*, 2011], classifies these drivers of DVM as "structural" or "dynamic" depending on whether or not they vary strongly on daily time scales. The TRH predicts that avoidance of damaging UV radiation will be an important dynamic driver of DVM, especially in very clear water. This prediction has been supported in laboratory and field studies [*Leech and Williamson*, 2001; *Leech et al.*, 2005; *Fischer et al.*, 2015]. UV can have other effects as well, such as inactivating waterborne parasites

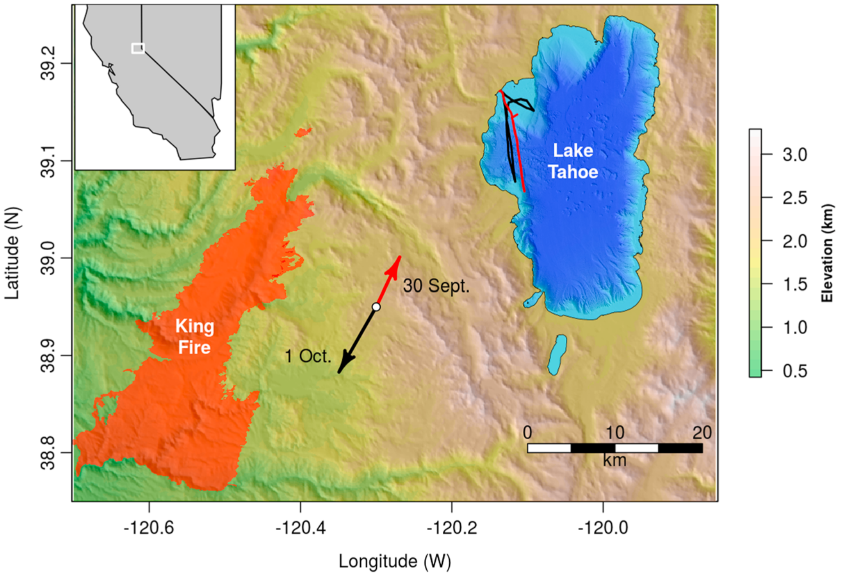

Figure 1. Geography of King Fire and Lake Tahoe. King Fire burn area is shown in red, with Lake Tahoe to the northeast (inset shows location at the border of California and Nevada, USA). Green-to-white shading shows elevation above sea level, while blue shading indicates bathymetric depth in Lake Tahoe, from the surface (0 m) to a maximum of 501 m. Black and red lines on the lake show the boat transects on 30 September (red) and 1 October (black). The arrows at the center indicate mean wind direction during the 12 h prior to sampling on 30 September (red) and 1 October (black). Arrow length is proportional to the mean wind speed, 2.4 m s^{-1} on 30 September, and 3.6 m s^{-1} on 1 October.

like *Cryptosporidium* [*King et al*., 2008]. Wildfires are one widespread natural process that may affect aquatic ecosystems by changing their UV environments. The extent and larger implications of these effects are not well known, but they may be significant at continental or global scales, as persistent smoke plumes from natural and anthropogenic burning can span continents and oceans [*Williamson et al*., 2016].

The King Fire in the Sierra Nevada Mountains of California, USA, presented an opportunity to test the remote effects of wildfires on zooplankton vertical distribution. The King Fire was started by arson on 13 September 2014 and burned a total of 39,545 ha over the next 24 days [*National Wildfire Coordinating Group*, 2014a]. Depending on wind direction, the fire's smoke plume blew over Lake Tahoe, a large, deep, oligotrophic lake located 1897 m above sea level on the California-Nevada border (Figure 1). Lake Tahoe is exceptionally clear, with 320 nm UV, 380 nm UV, and 400–700 nm photosynthetically active radiation (PAR) generally penetrating deeper than 20, 40, and 50 m [*Rose et al*., 2009; *Williamson et al*., 2016], and an average Secchi depth in 2014 of 23.7 m [*Tahoe Environmental Research Center*, 2015]. UV radiation is therefore likely to have a larger influence on the vertical migration and distribution of zooplankton than it would in more turbid lakes [*Williamson et al*., 2011]. The alternating presence and absence of smoke over Lake Tahoe, selectively attenuating incident UV radiation relative to visible light in the atmosphere, set up a natural test of the effects of smoke plumes on zooplankton vertical distribution. We expected incident UV radiation to be lower when smoke was present and that zooplankton would be distributed shallower in the water column as a result.

2. Materials and Methods

2.1. Vessel and Survey

We collected acoustic and optical data on Lake Tahoe from 14:25 to 18:01 on 30 September (day 1) and from 15:16 to 18:25 1 October 2014 (day 2). Only data from the overlapping times (i.e., 15:16 to 18:01) were analyzed to ensure comparability. Weather conditions were similar on both days except for the wind, which blew from the southwest on day 1 and the east on day 2 (Figure 1). Weather data were taken from buoy TB1 in the center of Lake Tahoe. These winds caused smoke haze from the King Fire to blow over Lake Tahoe on the first day, and away from it on the second. The weather on both days was fair, with no clouds over the lake. Surveys were conducted from the R/V *Bob Richards*. On each day, we ran two reciprocal transects (length ~11 km), along the western shore of the lake roughly parallel to the isobaths (Figure 1).

2.2. Optical and Limnological Data

Optical data were logged once per second during the survey using a Biospherical Instruments Cosine (BIC) radiometer (San Diego, CA) mounted on the roof of the vessel's pilothouse. Care was taken to orient the instrument vertically and keep it out of shadows from the boat's mast, antennas, and radar. Irradiance was recorded in three UV wavelengths (305, 320, and 380 nm), and in the range of photosynthetically active radiation (PAR, 400–700 nm). Irradiances were recorded in units of μmol photons $m^{-2}\,s^{-1}$ but were converted to $W\,m^{-2}$, using the per-photon energy hc/λ, where h is Planck's constant, c is the speed of light, and λ is the wavelength. In addition, vertical casts with a submersible BIC radiometer were made on 22 September, 30 September, and 7 October from the surface to 45 m, measuring downwelling irradiance in the same four spectral bands, as well as water temperature. These data were averaged into 1 m depth bins and used to calculate light extinction coefficients k for each wavelength in the lake. On the same three dates, a SeaBird SBE25 conductivity-temperature-depth measured chlorophyll fluorescence from the surface of the lake to 100 m depth. Finally, near-surface temperatures were recorded every 2 min by thermistor chains (depths of 0.5, 1, 1.5, 2, 3, 4, 5, and 5.5 m) at four data buoys in the central lake for the duration of the study.

2.3. Acoustic Data

We measured the density of zooplankton and fish in the epilimnion using a two-frequency acoustic system, consisting of a single-beam 710 kHz Simrad EK60 and a split-beam 120 kHz Simrad ES60. The 710 and 120 kHz transducers had 2.8° and 7.0° beam angles, respectively. The 710 kHz system had an effective range of 30 m and could detect small (<1 mm) zooplankton [*Holliday and Pieper*, 1995; *Warren et al.*, 2016]. The 120 kHz system had a greater range (200 m) but could only detect stronger targets (large zooplankton and fish). The transducers were deployed on a pole mount near the boat's bow. The transducer depth was 35 cm on the first day, but was increased to 55 cm the second day to avoid bubble sweepdown from slightly larger waves. Transmitted power was 1000 W for the 120 kHz sounder and 100 W for the 710 kHz sounder. Both operated with a pulse length of 0.064 ms and a ping rate of 1 s^{-1}. Both echosounders were calibrated during a previous deployment using the standard-sphere method [*Foote et al.*, 1987].

2.4. Acoustic Data Processing

We removed background noise from the acoustic data using the method of *De Robertis and Higginbottom* [2007] with an averaging window of 20 pings by 10 vertical bins and a maximum signal-to-noise ratio of 10 dB. We smoothed the data with a 3 × 3 pixel median filter to remove isolated noise spikes and then integrated it in 0.5 × 10 m bins (depth × along-track distance). Acoustic data were processed using Echoview version 6.1 [*Myriax Pty Ltd*, 2014]. After integration, a total of 3642 individual depth profiles were available for analysis (1417 on 30 September and 2225 on 1 October) [*R Development Core Team*, 2014]. The backscatter-weighted mean depth, or acoustic center of mass CM [*Urmy et al.*, 2012], was calculated for both frequencies. We only calculated this metric where the lake was more than 30 m deep, to minimize any influence of the lake bottom on the distribution of animals. The significance of changes in the CM between days was assessed using two-tailed Student's t tests, considered significant at the 0.05 level.

2.5. Direct Zooplankton Sampling

We conducted a net tow on day 1 to ground truth the acoustic data and identify the zooplankton present. The net was a 0.75 m diameter opening, 3 m long conical net with 80 μm mesh, and was hauled vertically from 60 m to the surface. Filtered volume was estimated using a General Oceanics flow meter. Due to wind drift the net's actual path was 73 m instead of 60 m, and the volume filtered was 55 m^3. The zooplankton were preserved in 10% buffered formalin. A subsample was split from the original sample and counted under a compound microscope, with all animals identified to species and their total (prosome and urosome) lengths measured.

2.6. Data Analysis

We aligned the irradiance time series from the two afternoons by time of day and calculated the ratio of irradiance with smoke haze to that under clear skies (I_{smoke}/I_{clear}). Under the hypothesis that avoidance of UV is a driver of vertical migration, a simple but reasonable model for zooplankton behavior is that they attempt to remain below a depth of constant irradiance. Using the standard extinction equation, $I(z) = I_0 e^{-kz}$, where z is depth, I_0 is irradiance at the surface, and k is the extinction coefficient, we can predict the change in zooplankton depth resulting from a change in surface irradiance. We assume that zooplankton change their depth to track a certain (unknown) isolume, i.e., changing their z so that $I(z) = I_{\mathrm{opt}}$. Given two different surface irradiances I_1 and I_2, we can write the relation

$$I_{\mathrm{opt}} = I_1 e^{-kz_1} = I_2 e^{-kz_2}, \tag{1}$$

where z_1 and z_2 are preferred depths associated with incident intensities I_1 and I_2. Rearranging and simplifying, we find

$$\Delta z = z_2 - z_1 = \frac{1}{k} \ln\left(\frac{I_2}{I_1}\right). \tag{2}$$

This equation lets us predict a change in zooplankton depth given a change in irradiance at the surface and an extinction coefficient, without having to know the absolute irradiance the zooplankton prefer. Extinction coefficients for each wavelength were calculated from the irradiance profiles by fitting linear regressions to the natural log of irradiance as a function of depth; the slopes of these lines are the extinction coefficients. We only used data shallower than 10 m, since this was where most zooplankton were found, and the slopes steepened slightly, diverging from linearity, at deeper depths.

3. Results and Discussion

During the 12 h before the survey on 30 September, winds on Lake Tahoe averaged 2.4 m s^{-1} from the southwest, while during the same period on 1 October they averaged 3.6 m s^{-1} from the northeast (Figure 1). Despite rain and snowfall on 26–27 September and the 92% containment of the fire by the first survey day [*National Wildfire Coordinating Group*, 2014b], smoke was still rising from the burn area on 30 September. The southwesterly winds blew this smoke over the lake, causing a visible haze (Figure 2a) and a noticeable smell of burning. In contrast, the northeasterly winds on 1 October prevented any smoke from reaching the Lake. The air was clearer (Figure 2b) and the smell of smoke was absent. Other than the wind and smoke, the weather on both days was similar with clear skies.

Daytime (before 16:30 local time) UV radiation at 305 nm was 8% lower when smoke haze was present (Figure 2c). The decrease was less pronounced for longer UV wavelengths (−4% and −1% for 320 and 380 nm). Visible PAR increased very slightly (<1%). After 16:30, the smoky-to-clear irradiance ratios shifted: differences were less pronounced at 305 and 320 nm (−6% and 0%) and were positive at 380 nm and in PAR (+4% and +9%). This change is attributed to indirect scattering from particulates in the smoke haze, partially offsetting the effects of attenuation when the Sun was low. All differences from zero were highly significant (two-tailed Student's t test, $p < 0.001$). The presence of smoke haze thus significantly reduced UV radiation during the middle of the day, especially at the shortest wavelength.

The vertical distribution of zooplankton shifted significantly between the two days. Based on the net sample, the adult zooplankton community was composed of the calanoid copepods *Epischura nevadensis* and *Leptodiaptomus tyrrelli* (78% and 22% by number, mean lengths 0.6 and 0.7 mm). On the smoky 30 September, a shallow layer of zooplankton was present at the surface, with its upper edge extending into the echosounder's surface exclusion zone (1 m) and possibly all the way to the surface (Figure 3a). On the clear 1 October, the same layer was present but was located lower in the water column and was clearly separated from the lake's surface (Figure 3b). These changes were reflected in the CM, which was 4.1 m shallower on 30 September. Total depth-integrated backscatter at 710 kHz was 20% less on 30 September, possibly because some of the zooplankton were in the echosounder's blind zone. These results are consistent with zooplankton repositioning themselves in response to dynamic changes in UV radiation.

The extinction coefficient at 320 nm was estimated at 0.15 m^{-1} on 30 September. A week before and after it was 0.14 and 0.15 m^{-1}, indicating water transparency was essentially constant over this period. Using the extinction coefficient of $k = 0.15$ m^{-1} from 30 September, zooplankton were predicted to be located 0.3 m (±0.005 standard error, s.e.) deeper on 1 October, based on the observed increases in UV. The observed difference in depth was much larger, at 4.1 m—suggesting that this calculation does not include all the important drivers of zooplankton distribution. Regardless, repeating the same calculation for PAR using the extinction coefficient of $k = 0.088$ m^{-1} (also calculated from the 30 September radiometer profile) predicts that zooplankton would have moved *closer* to the surface by 0.06 m (±0.02 m s.e.) on 1 October if they had been tracking an isolume of visible light. The difference in sign and magnitude between these two predictions supports the

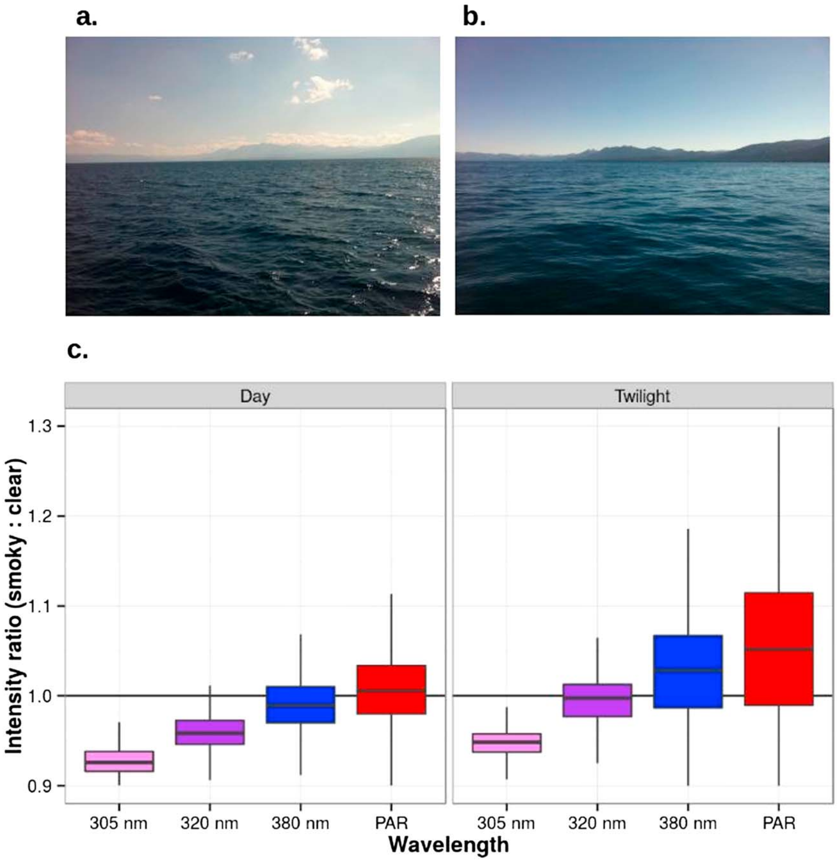

Figure 2. Changes in air quality and UV radiation. Photographs show (a) smoke haze on 30 September and (b) clear air on 1 October. Both were taken near Tahoe City facing south toward Rubicon Peak at approximately 15:00 local time. (c) Short-wavelength UV light was attenuated more by the smoke than longer-wavelength UV or visible (PAR) light. Ratios of light intensity with smoke present to intensity with clear air ($I_{\text{smoke}}/I_{\text{clear}}$) were calculated by time of day in each of four spectral bands, from shortwave ultraviolet (305 nm, light purple) to photosynthetically active radiation (400–700 nm, red). Boxplots show 5th, 25th, 50th, 75th, and 95th percentiles of the observed ratios. Values above (below) unity indicate measurements that were brighter (dimmer) when smoke haze was present. The two panels show ratios before and after 16:30 local time, representing high and low solar angles during daytime and twilight. Clear/smoke irradiance ratios are less pronounced or reversed when the Sun was low, probably due to indirect scattering from particulates in the smoke haze.

hypothesis that UV was an important driver of zooplankton vertical migration and that wildfire-induced changes in incident UV from one day to another are sufficient to alter the distribution of zooplankton.

The highest recorded irradiances (at 14:37) were 0.7, 7.5, and 20.5 W m^{-2} at 305, 320, and 380 nm, and 1994 W m^{-2} for PAR. Values at local noon would have been slightly higher. Again using the 30 September extinction coefficient, the midday dose of 320 nm UV expected for zooplankton 5 m below the surface was at least 3.7 W m^{-2}, or 13 kJ h^{-1}. Natural solar UV causes sublethal effects at only 0.3 kJ m^{-2} for the copepod *Boeckella gracilipes* [*Zagarese*, 1997]. [*Fischer et al.*, 2006] At a depth of 5 m at midday in Lake Tahoe, this exposure would be reached in less than 2 min. However, some zooplankton species have the ability to photoenzymatically repair DNA damage, which may substantially decrease mortality rates for UV damage in natural sunlight, when both damaging UV and photorepair radiation (longwave UV-A) are present [*Fischer et al.*, 2006]. While the UV sensitivities and photorepair capabilities of *Epischura nevadensis* and *Leptodiaptomus tyrrelli* in Lake Tahoe are not known, naturally occurring UV levels in the upper water column may nonetheless be high enough to cause UV damage. The widespread ability of calanoid copepods to respond behaviorally to UV [*Overholt et al.*, 2016] supports the potential for behavioral avoidance to drive changes in zooplankton distribution in this study.

Ultraviolet radiation is not the only driver of zooplankton vertical migration in Lake Tahoe, although it is an important one. The location of food (i.e., phytoplankton) and predators can influence vertical distribution,

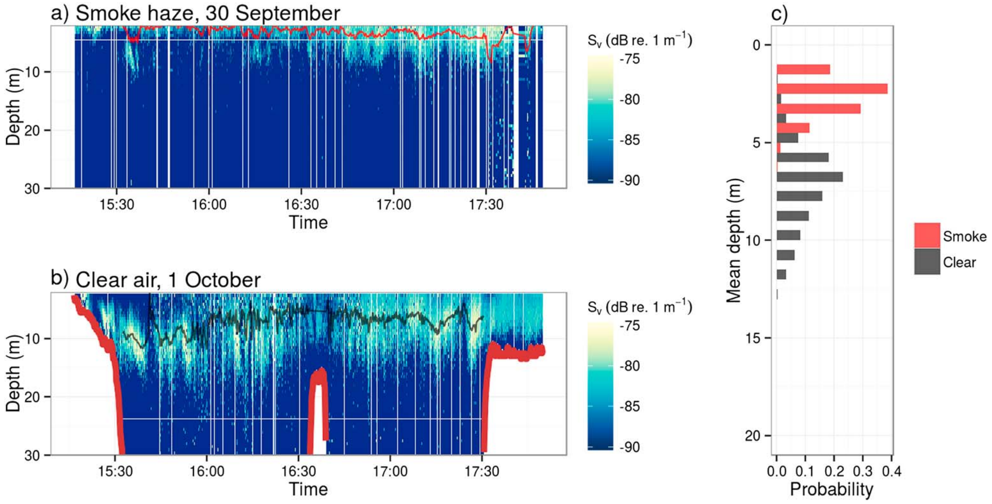

Figure 3. Vertical distribution of zooplankton in Lake Tahoe. Acoustic backscatter, a proxy for zooplankton density, is shown as a function of depth (*y* axis) and time (*x* axis) (a) with and (b) without smoke haze. White vertical stripes are data gaps, due to system reboots. The brown lines indicate the lake bottom. Overplotted on each echogram is a time series showing the acoustic center of mass (CM), i.e., the mean depth of backscatter in each ping. The CM lines have been smoothed with a five-point running mean to improve visibility. The CM highlights the shallower distribution of zooplankton under smoky conditions (30 September, Figure 3a). (c) Histograms of the two CM series (red for smoke haze, black for clear air) show that the average CM was 3.0 m higher in the water column when smoke haze was present (*t* test, $p < 0.001$).

as can temperature and physical mixing. The average chlorophyll concentration in the upper 30 m of the water column was 1.77 μg L^{-1} on 30 September. Samples taken a week before and after, on 22 September and 7 October, differed by less than 0.05 μg L^{-1}. On all three of these dates, a subsurface chlorophyll maximum between 3.0 and 3.7 μg L^{-1} was present at 67–82 m depth, well below the near-surface zooplankton layer. The abundance and distribution of phytoplankton thus remained nearly constant and were unlikely to have driven the observed changes in zooplankton depth.

The 120 kHz echosounder effectively measured the vertical distribution of predators, since the only pelagic animals in Lake Tahoe large enough to return echoes at this frequency are fish and the predatory zooplankton *Mysis relicta* [*Rudstam et al*., 2008]. At 120 kHz, scattered aggregations were observed from 20 to 60 m depth,

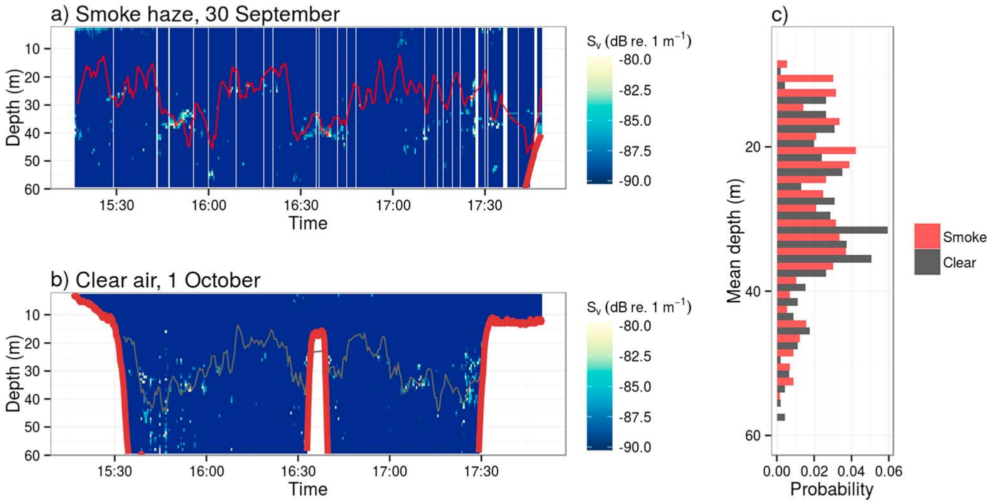

Figure 4. Vertical distribution of zooplankton predators (fish or mysid shrimp) in Lake Tahoe. Same as Figure 3 but showing acoustic backscatter and its center of mass at 120 kHz instead of 710 kHz. Note that the vertical scale is larger than in Figure 3, due to the longer range of the 120 kHz echosounder. Predators were located below the zooplankton layers and did not change their depth significantly between the two days.

well below the zooplankton layer (Figure 4). Their average CM was 1.6 m shallower when smoke was present, but the variance in the 120 kHz CM was large (Figure 4c) and the change in depth was not statistically significant ($p = 0.08$). Changes in predation cannot explain the observed differences in zooplankton distribution, either.

The vertical temperature profile taken the morning of 30 September showed a mixed layer from the surface to 20 m depth, well below the zooplankton. This layer represented previous, rather than active, mixing, since the thermistor chains showed that solar heating was able to set up a weak (0.3 to 0.7°C) stratified layer in the upper 2 m of the Lake on 30 September. This thin surface layer disappeared after sunset and did not reform the next day, probably due to mixing by the higher winds (mean 3.6 m s^{-1} on 1 October, versus 2.4 m s^{-1} on 30 September). Wind-driven mixing could redistribute a near-surface concentration of zooplankton over the mixed layer, increasing its mean depth. This may partly explain why the change in zooplankton depth was greater than predicted based on changes in isolume depth. However, downmixing of a surface zooplankton layer would produce a uniform distribution over the mixed layer, while the observed zooplankton distribution had a distinct subsurface peak (Figure 3b), indicating zooplankton actively aggregated at a preferred depth. Like food and predation, physical mixing does not appear to explain the changes in zooplankton distribution, leaving smoke-mediated changes in UV the most likely driver.

Our conclusions come with the obvious caveat that they are based on only two days of sampling. This study was an opportunistic response to an unexpected wildfire near Lake Tahoe, and logistical and meteorological constraints prevented more extensive data collection. Other experiments, in other bodies of water, are needed to further test the teleconnections we propose between fires, smoke plumes, and aquatic ecosystems. Subsequent experiments would clearly be improved by round-the-clock sampling to capture the diel cycle and repeated sampling on multiple days. Extended spatial coverage is also important, because abiotic events such as windstorms can affect the large-scale distribution of fish and zooplankton in lakes [*Rinke et al.*, 2009].

Though we cannot conclusively eliminate all other drivers of DVM, the change in zooplankton vertical distribution between 30 September and 1 October appears to be explained best by changes in incident UV, caused by wildfire smoke. Between the two days, none of the other factors known to affect zooplankton vertical migration adequately explain the change in their vertical distribution. The distribution of food did not change. Predators were distributed far below the zooplankton and their depth did not change significantly. Visible light (PAR) did not change or changed in the wrong direction. Changes in surface water temperatures between the two days were small (−0.2 to −0.5°C). Finally, while some amount of wind-driven mixing took place on 1 October, it cannot account for the observed differences alone. Eliminating these other explanations, UV radiation appears to have driven the change in zooplankton depth, suggesting that short-term events such as wildfires can affect the distribution of zooplankton.

4. Conclusion

Diel vertical migration of zooplankton is a large-scale phenomenon in the world's oceans and lakes, structuring aquatic ecosystems and affects higher-trophic-level predators [*Hays*, 2003]. Some of these predators support important commercial or recreational fisheries, and ignorance of DVM can lead to poor management decisions and outcomes [*Richards and Goldman*, 1991]. At larger scales, 17–40% of the total carbon export from the epipelagic can be attributed to active transport by vertically migrating animals [*Davison et al.*, 2013]. The effects of smoke plumes on incident UV radiation may in fact be important globally, since large areas of the world's oceans are affected by UV-absorbing aerosols from biomass burning [*Herman et al.*, 1997] and the existence of a long-term increase in aerosol optical depth [*Hsu et al.*, 2012]. Our findings here underline the importance of UV as a dynamic driver of zooplankton vertical migration and illustrate the potential for fire smoke to drive changes in the vertical distribution of zooplankton.

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