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### Key Points:

- Wildfire smoke reduced ultraviolet-B and photosynthetically active radiation
- Lake habitats respond differently to changes in light from smoke, pelagic primary production increased with no change to littoral metabolism
- Smoke alters energy flows with implications for food web structure in lakes

### Supporting Information:

Supporting Information may be found in the online version of this article.

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## Wildfire Smoke Effects on Lake-Habitat Specific Metabolism: Toward a Conceptual Understanding

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**Abstract** The impacts of wildfire smoke on lake habitats remains unclear. We determined the metabolic response to smoke in the epi-pelagic and two littoral habitats in Castle Lake, California. We compared light regime, gross primary production, ecosystem respiration, and net ecosystem production in years with and without smoke. During the smoke period incident ultraviolet-B (UV-B) radiation and photosynthetically active radiation (PAR) decreased by 53% and 28%, respectively, while the water column extinction coefficient of UV-B and PAR increased by 20% and 18% respectively. Epi-pelagic productivity increased during smoke cover because of decreased solar inputs. PAR values remained sufficient to saturate productivity, suggesting observed differences were primarily the result of changes in UV-B. Littoral-benthic productivity did not change, possibly reflecting adaptation to high-intensity UV-B light in these habitats. Our results highlight the importance of understanding how prolonged wildfire smoke alters the amount of energy produced from specific habitats in lakes.

**Plain Language Summary** Large wildfires are increasing worldwide, but the impacts of wildfire smoke on lakes are unknown. We determined how photosynthetic activity and organism's respiration respond to smoke in the offshore and nearshore habitats in a mountain lake. Smoke limited the damage to algae caused by ultraviolet-B radiation, resulting in increased offshore photosynthesis. Photosynthesis in the nearshore habitat did not change during smoke cover, possibly because organisms in shallow habitats have adapted to the higher intensity of damaging ultraviolet-B radiation. Our results highlight the importance of understanding how prolonged smoke conditions can alter lakes' energy flows and food webs.

## 1. Introduction

Wildfires have increased globally in recent decades (Dennison et al., 2014; Doerr & Santín, 2016). Wildfires modify the land, water, and atmospheric dynamics by burning the landscape, exporting particles and nutrients to distant locations by wind, and attenuating incoming solar radiation through smoke cover (McLaughlan et al., 2020). In the western United States, wildfires have increased over time because of changes in climate (Westerling, 2016), historic management (Dennison et al., 2014), and changes in land use (Nagy et al., 2018; Radeloff et al., 2018). In 2020, the most destructive wildfire year on record in the USA, a total of 9,917 fires burned an area of 1,723,096 ha in California alone (Cal Fire, 2020). While the impacts of wildfire on terrestrial systems are closely studied, the impacts of wildfire smoke, on aquatic systems, remains virtually unknown.

Aquatic ecosystems have a high risk of exposure to wildfires (McCullough et al., 2019). Indirect effects are mediated by the transport of smoke and particles from local and regional fires to nearby and distant lakes (Scordo et al., 2021; Williamson et al., 2016). Wildfire smoke combines gaseous pollutants, water vapor, and particulate matter (PM). PM is a mixture of solid particles suspended in the air with diameters between 0.1 and 10  $\mu\text{m}$ . Particles  $\leq 2.5 \mu\text{m}$  in diameter ( $\text{PM}_{2.5}$ ), represent  $\sim 90\%$  of total particle mass emitted from wildfire smoke (Vicente et al., 2013). The type and amount of  $\text{PM}_{2.5}$  contributed by fires depends on the size and duration of the fire, burning conditions and material (Jaffe et al., 2008). Most notably, smoke reduces incident radiation and deposits particles on lakes (Scordo et al., 2021; Williamson et al., 2016; Figure 1a). Particulates in smoke reduce incoming ultraviolet B radiation (UV-B) that would enter the water column, effectively increasing the ratio of photosynthetically active radiation (PAR) to UV-B (Williamson et al., 2016; Figure 1a). Moreover, reductions in incident

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solar radiation can decrease water temperatures and affect physical mixing dynamics (David et al., 2018; Scordo et al., 2021; Figure 1a).

Smoke particles deposited directly on lakes or transported into lakes through runoff from the watershed affect aquatic ecosystems by suppressing light and altering nutrient supply to algae (Goldman et al., 1990; Scordo et al., 2021; Figure 1a). The deposition of particles may contribute nutrients (Earl & Blinn, 2003) and stimulate pelagic primary productivity (Tang et al., 2021). In ecosystems with high water clarity, declines in incident and underwater PAR and UV-B may increase productivity by alleviating photoinhibition through multiple mechanisms (Campbell & Serôdio, 2020; Long et al., 1994), allowing phytoplankton to photosynthesize at their maximum rate for a larger proportion of daylight hours (Falkowski & Raven, 2007; Figures 1c–1e). The combination of reduced UV-B radiation and increased production have several notable effects on lake structure and the behavior of organisms. Under reduced UV light conditions zooplankton alter their behavior to inhabit the upper waters more frequently (Urmy et al., 2016), which increases grazing pressure on phytoplankton. Although these effects of wildfire smoke have been observed across the pelagic habitat of lakes and oceans, to our knowledge the effects of smoke on littoral habitats remain undocumented.

Conceptually, there is reason to believe metabolic processes in the pelagic and littoral habitats respond differently to smoke effects (Figures 1c–1e). Production in the littoral may not have a detectable response to reduced UV-B light exposure produced by the smoke conditions (Figure 1d). Benthic algal communities have characteristics (e.g., taxa that can migrate into the substrate, excrete screening compounds, or develop large filamentous colonies) that allow them to persist under high UV conditions (Karsten & Garcia-Pichel, 1996; Vinebrooke & Leavitt, 1999). Additionally, littoral-benthic habitats consistently exhibit higher rates of productivity compared to pelagic habitats in clear lakes (Sadro, Melack, & Macintyre, 2011; Scordo et al., 2022; Figure 1e), emphasizing the need to understand habitat-specific responses in metabolic rates to the effects of wildfire smoke.

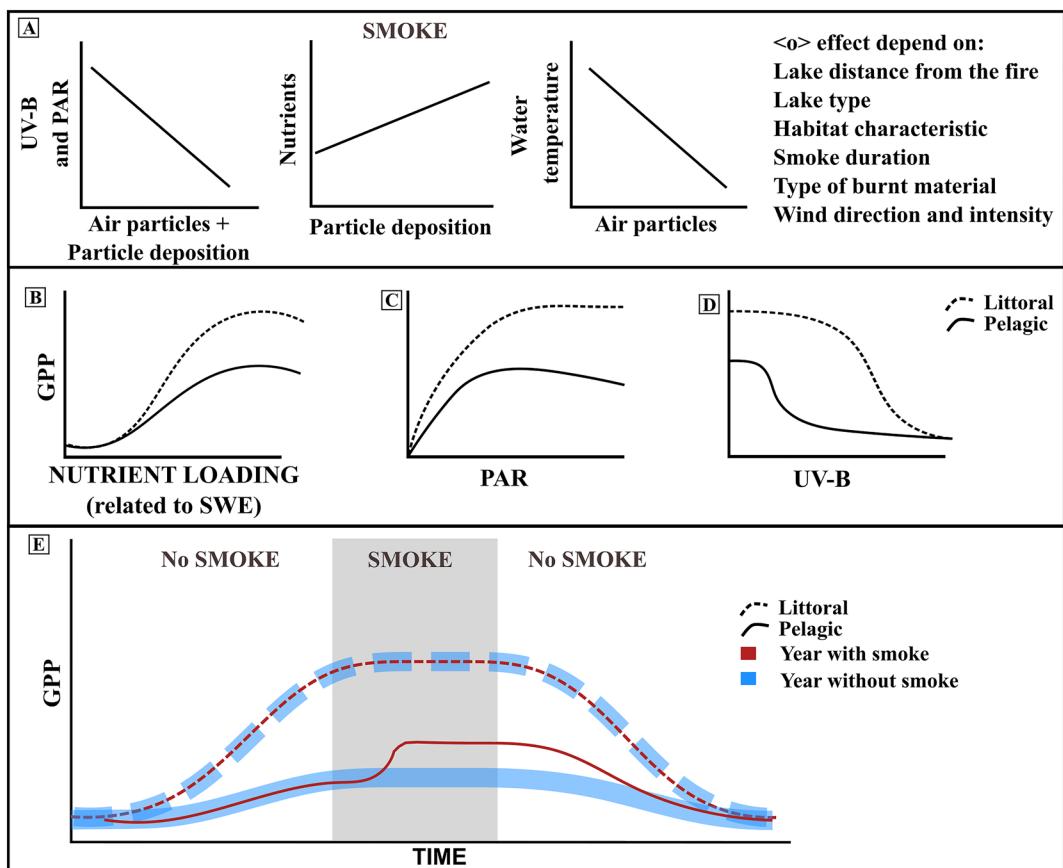
Addressing the effects of smoke and ash from wildfire to lake metabolism requires us to differentiate smoke effects from hydrologic effects (Figure 1b). In western mountain lakes of the United States, ice-out date and snow water equivalent (SWE) affect inter-annual productivity (Goldman et al., 1989; Figures 1b and 1e). SWE determines the duration of the ice-free period (Smits et al., 2021) and inflow during the spring (Sadro et al., 2019), which sets the conditions for summer production and phytoplankton biomass accumulation (Sadro et al., 2018; Figures 1b and 1e). Ice-out timing determines heat content in the water column and the seasonal timing of maximum primary producers' biomass (Park et al., 2004). Littoral-benthic habitats have short retention times of water and nutrients, making them sensitive to changes in ice out and SWE (Scordo et al., 2022; Figures 1b and 1e). In this study, we examined three non-smoke years with differing hydrological climates to account for changes in ice out and SWE when examining the influence of smoke effects alone.

We examined the influence of wildfire smoke on gross primary production (GPP), ecosystem respiration (ER), and net ecosystem production (NEP) for both epi-pelagic and littoral lake habitats in a year with heavy smoke cover (2018) and years without smoke (2015, 2016, 2019). We (a) determine if the metabolic response to wildfire smoke differs between epi-pelagic and littoral habitats and (b) use these observations to provide a conceptual framework to understand how smoke alters littoral and epi-pelagic processes in a mesotrophic, subalpine lake. We expect the metabolic rates in the epi-pelagic habitat to be higher in 2018 than in non-smoke years, owing to wildfire smoke's suppression of UV-B light (Figure 1e). We expect littoral productivity to fall within the range of variability of non-smoke years because benthic algae productivity is less sensitive to UV-B light suppression.

## 2. Material and Methods

### 2.1. Study Site and Data Collection

Castle Lake is a meso-oligotrophic, dimictic, subalpine lake (1,646 m. a.s.l., surface area of  $0.2 \text{ km}^2$ ,  $z_{\max} = 35 \text{ m}$ , and  $z_{\text{mean}} = 11.4 \text{ m}$ ) located in California, USA (Figures 2a and 2b). Snow and ice cover the lake typically from the end of November until April. The ice-free summer season averages  $\sim 135$  days. We analyzed how a smoky year (2018) affected the metabolism rates in late summer (August and September) in two locations of the littoral habitat and one location in the deepest point of the pelagic habitat (Figures 2c–2e). Since the littoral habitat of Castle Lake is variable due to the adjacent landscapes and sediment compositions, we calculate metabolism in two different littoral sites ("Littoral 1" and "Littoral 2"; Figure 2e). Littoral 1 is dominated by fine-organic

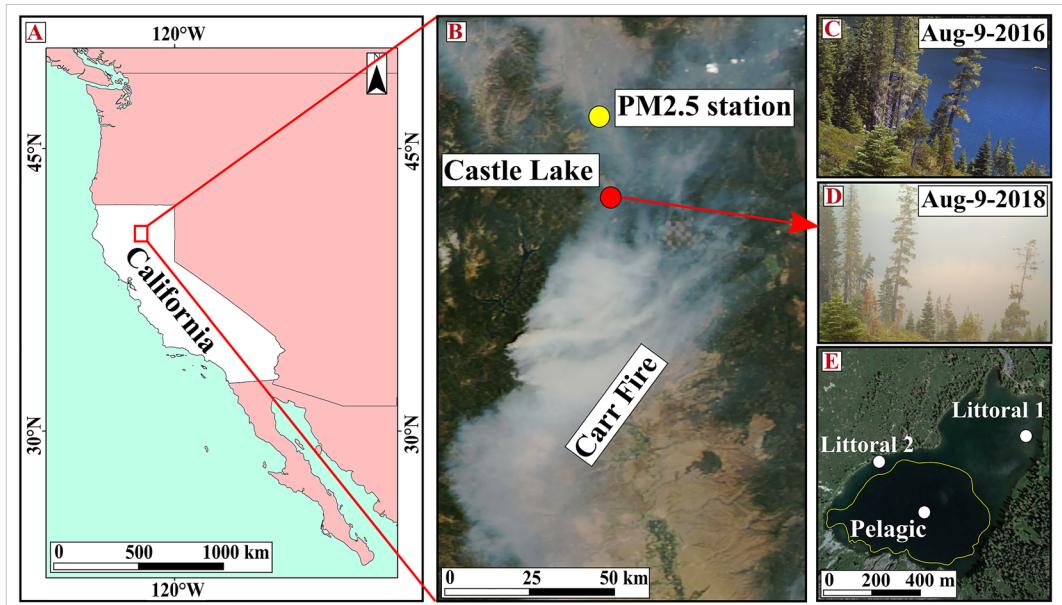


**Figure 1.** Conceptual framework to understand how smoke alters littoral and pelagic processes in a lake. Wildfire smoke reduces light regimes, lake heat content, and contributes nutrients to lakes (a). When the SWE accumulated by the start of ice-break melts, nutrients from the watershed start flowing into the lake. By mid-summer (July to August), the lake productivity cannot keep growing as it is nutrient-limited and light inhibited during a large part of the day (UV-B and PAR) (c and d). Productivity starts declining by the end of the summer when light and temperature decrease. If smoke covers the study lake when productivity is light inhibited, then reduced UV-B light due to smoke presence can produce an increase in epi-pelagic metabolic rates (e). Littoral benthic algal communities have different mechanisms to adapt to high solar UV-B radiation. Therefore, reduced UV-B light may not produce a change in littoral metabolic rates (d and e). The influence of smoke likely depends on the distance between the lake and the wildfire, wind conditions, type of material combusted, duration of smoke, and lake type.

sediments, regular terrestrial leaf inputs, and inputs from groundwater seepage. Littoral 2 is dominated by coarser sediments with no spring influences and less immediate connections to terrestrial leaf inputs.

We compared the smoke year of 2018 with multiple years (2015, 2016, and 2019) that encapsulated the total observed variability in SWE (4–1,047 mm) and ice out date (February 20th to June 1st) from the last 60 years of observation. This approach suggests that any novel patterns that we detected in 2018, relative to previously observed variability, are likely not related to unusual ice-out timing or snowpack that year but rather to the unusual smoke conditions. The year 2018 was an average year in terms of ice out date (April 7th), and dry in terms of SWE (135 mm; <https://nsidc.org/data/g02158>).

We defined the degree of ‘smokiness’ in all years by quantifying atmospheric particulate loads and using two game cameras overlooking the lake that took daily, midday photos. Fine particulate matter ( $PM_{2.5} \leq 2.5 \mu\text{m}$  diameter) in concentrations  $>20 \mu\text{g m}^{-3}$  indicates the presence of smoke in fire prone areas (Liu et al., 2017). The  $PM_{2.5}$  data obtained from a nearby monitoring station in Yreka (<https://www.epa.gov/outdoor-air-quality-data/download-daily-data>), confirms the visible evidence from the cameras that the hazy images resulted from wildfire smoke plumes.



**Figure 2.** (a) Location of the study area in California (USA). (b and d) Photo of the smoke plume of Carr Fire (9 August 2018) covering Castle Lake. (c) Photo of Castle Lake without smoke cover on 9 August 2016. (e) Site location where metabolism was determined.

We evaluated how smoke altered the underwater intensity of light (UV-B and PAR) and water temperature. We measured the midday (1 p.m.) intensity of incident UV-B and PAR at the surface of the lake and the extinction coefficient of both wavelengths using a Biospherical Instruments 2104P radiometer once per week.

We made high-frequency *in situ* measurements of water temperature and dissolved oxygen (DO) at 10-min intervals (PME miniDOT) in pelagic and littoral habitats. The pelagic sensor was deployed 3 m below the surface within the pooled mixed layer, each of two littoral sensors were deployed 0.1 m above lake sediments where total depth was 3 m (Figure 2e).

We estimated metabolic rates using a modeling approach based on Phillips (2020) and Lottig et al. (2021). This model requires high-frequency measurements of DO concentration ( $\text{mg L}^{-1}$ ), water temperature ( $^{\circ}\text{C}$ ), PAR ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), wind speed ( $\text{m s}^{-1}$ ), and barometric pressure (mbar). The model generates daily estimates ( $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ) of GPP, R, and NEP (NEP = GPP - R). A detailed description of the model can be found in the Text S1 of Supporting Information S1 and Lottig et al. (2021). Metabolism estimates were calculated from August 1st to September 17th for the Littoral 1 and the epi-pelagic sites, while for the Littoral 2 site, data was available from August 13th to September 17th.

To estimate habitat specific metabolic rate contributions to whole-lake productivity within the epilimnion, we partitioned the lake into littoral and pelagic zones based on area-volume information obtained from the bathymetric map of Castle Lake. We defined the littoral zone as areas with depth  $\leq 6$  m and epi-pelagic zone as areas with depth  $> 6$  m, each of which comprise 50% of the total 107,000  $\text{m}^2$  lake area (Vander Zanden et al., 2007). The mixed layer depth was used to define the lower boundary for littoral and epi-pelagic habitats, and a hypsographic curve was used to determine the total water volume for each. The daily volumetric rates ( $\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ) obtained from the model at the littoral (average of the Littoral 1 and Littoral 2) and the epi-pelagic sites were multiplied by the total volume ( $\text{m}^3$ ) of each habitat to obtain habitat specific metabolism. We present the proportion of total GPP, R, and NEP contributed by each habitat during the study period by summing the daily values of total littoral and epi-pelagic metabolism for the period August 13th to September 17th.

## 2.2. Statistical Analyses

We tested the proportion of days with  $\text{PM}_{2.5}$  higher than  $20 \mu\text{g m}^{-3}$  using a binomial generalized linear model (GLM) with “logit” as a link function. The year acted as a fixed effect in the model, using the “glm” function in

the R “stats” package (R Core Team, 2020). We used linear mixed-effects models (LMM) to test for significant differences in GPP, NEP, and R among sites (epi-pelagic, Littoral 1, and Littoral 2) with site as a fixed effect. The model was built using the “gls” function in R’s “nlme” package (Pinheiro et al., 2020). Similarly, we used LMM to test our hypotheses regarding differences among PAR, UV-B, GPP, NEP, and R with smoke condition as a fixed effect. We used the Wald statistic to test the significance of the fixed effects in each of the models (Zuur et al., 2009), using the “gls” function in the “nlme” package (Pinheiro et al., 2020). We compared the fixed effects of the model with Tukey’s HSD post hoc test (Lenth, 2021). We considered the specific variance-covariance structure for repeated-measures data in each model, and when residuals did not meet the assumption of homoscedasticity, we modeled the variance.

For each variable analyzed in this study (water temperature, PAR, UV-B, GPP, NEP, and R), we calculated the mean, standard error, and 95% confidence interval for non-smoke years. Next, we determined if the data from the smoke-impacted year of 2018 fell within the 95% confidence interval of the non-smoke years. To calculate the 95% confidence interval, we used a Student’s t-distribution. All the analyses were performed in the statistical software R version 4.0.2 (R Core Team, 2020). Data and metadata are available in Scordo and Chandra (2022).

### 3. Results

#### 3.1. Extent of Smoke

The period between July 15th and 30 September 2018 had a significantly ( $p < 0.01$ ) higher number of days with smoke (60%) than the other three years, which combined had only 6% of days with smoke cover (Figure 3a). Also, the year 2018 had the highest mean ( $51 \pm 5 \mu\text{g m}^{-3}$ ) and maximum ( $143 \mu\text{g m}^{-3}$ ) value of  $\text{PM}_{2.5}$  when smoke was present (Figure 3a). During 2018, our study period began on August 1st, 13 days after the smoke conditions started (Scordo et al., 2021). Within our study period, smoke cover occurred between August 1–19, August 21–25, August 29–30, and September 5–10. Field notes and camera images corroborate the  $\text{PM}_{2.5}$  data; smoke was present on the same days  $\text{PM}_{2.5}$  increased (Figure 2c).

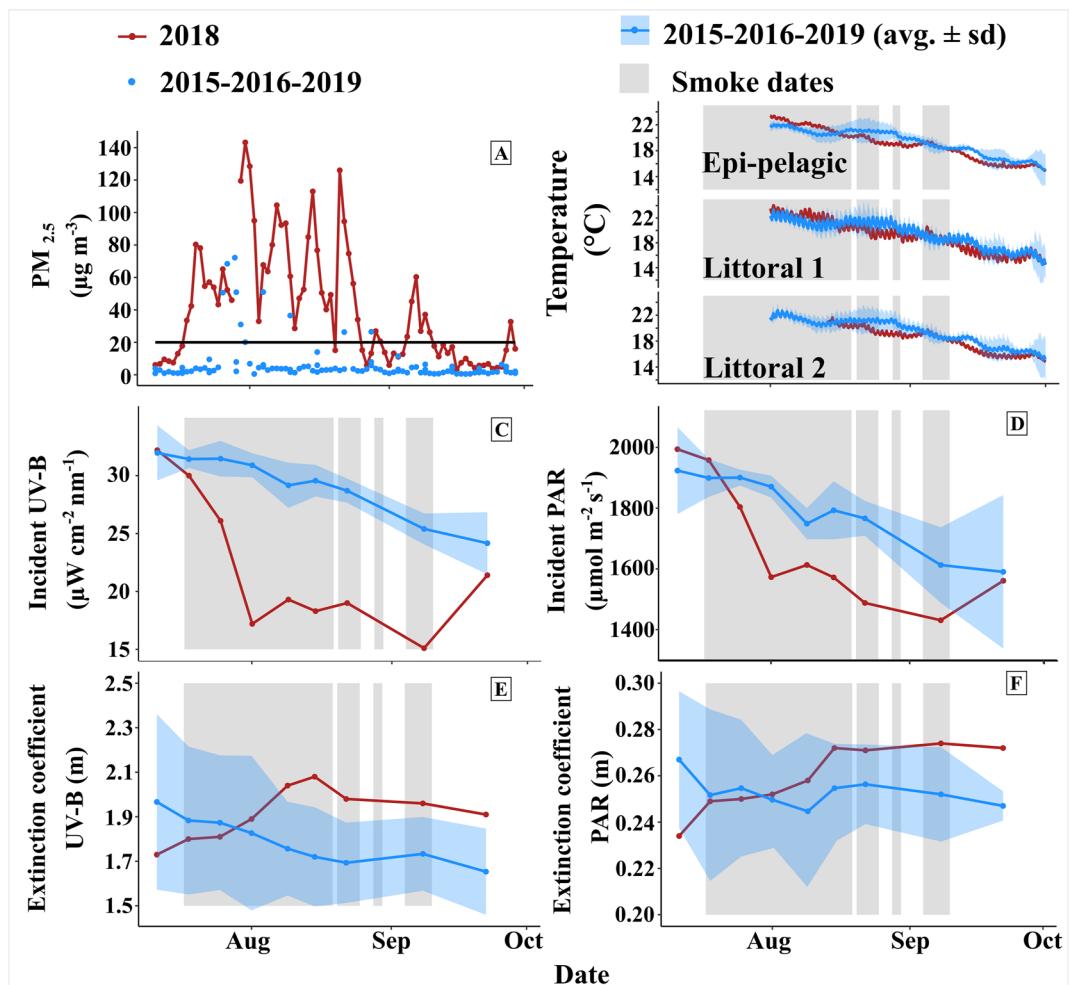
#### 3.2. Effects of Smoke on Light and Temperature Within the Lake

During smoke cover periods of 2018, we found a significant decrease in incident light intensity and increases in the extinction coefficient of UV-B and PAR. Incident PAR and UV-B light intensity decreased 28% and 53%, respectively, by the end of the smoke period compared to pre-smoke conditions (Figures 3c and 3d). PAR and UV-B values by August 1st and during the remaining smoke period of 2018 were significantly lower ( $p < 0.01$ ) and outside the confidence interval of light values for years without smoke. The extinction coefficient of UV-B and PAR increased 20% and 18% respectively, by the end of the smoke period of 2018 compared to pre-smoke conditions. The extinction coefficient of UV-B (starting on August 9th) and PAR (starting on 15<sup>th</sup>) by mid-August and during the remaining smoke period of 2018 were significantly higher ( $p < 0.01$ ) and outside the confidence interval for years without smoke. The observed differences in extinction coefficients between the smoke and non-smoke years continued beyond the smoke conditions, which ceased on September 10th. During smoke cover periods of 2018, we observed no change in water temperature at all sites ( $p < 0.93$ ; Figure 3b).

#### 3.3. Metabolism Habitat Variability

Volumetric rates of GPP, R, and NEP from littoral sites during the smoke period in 2018 did not differ statistically from non-smoke years ( $p > 0.3$ ; Figure 4; Table S1 in Supporting Information S1). In contrast, GPP and NEP from the epi-pelagic habitat were higher ( $p < 0.05$ ), while R remained similar ( $p = 0.07$ ) in 2018, compared to the non-smoke years (Figure 4; Table S1 in Supporting Information S1). GPP and NEP in the epi-pelagic habitat remained high in 2018 even when the smoke ceased in late September (Figure 4). During the smoke year of 2018, the total magnitude of epi-pelagic GPP ( $15 \times 10^7 \text{ mmol O}_2$ ) was higher than non-smoke years ( $11 \times 10^7 \pm 1 \times 10^7 \text{ mmol O}_2$ ; Figure S1 in Supporting Information S1). The relative contribution of epi-pelagic to whole-lake epilimnetic production was 5%–14% higher during the smoke year in comparison to all but the wettest year (Figure S1 in Supporting Information S1), which had an exceptionally late ice-off (Scordo et al., 2022).

The Littoral 1 habitat had significantly higher GPP ( $p < 0.01$ ) and R ( $p < 0.01$ ) rates than the epi-pelagic (Figure 4; Table S2 in Supporting Information S1). The Littoral 1 site had higher GPP ( $p = 0.03$ ) and R ( $p = 0.02$ ) rates

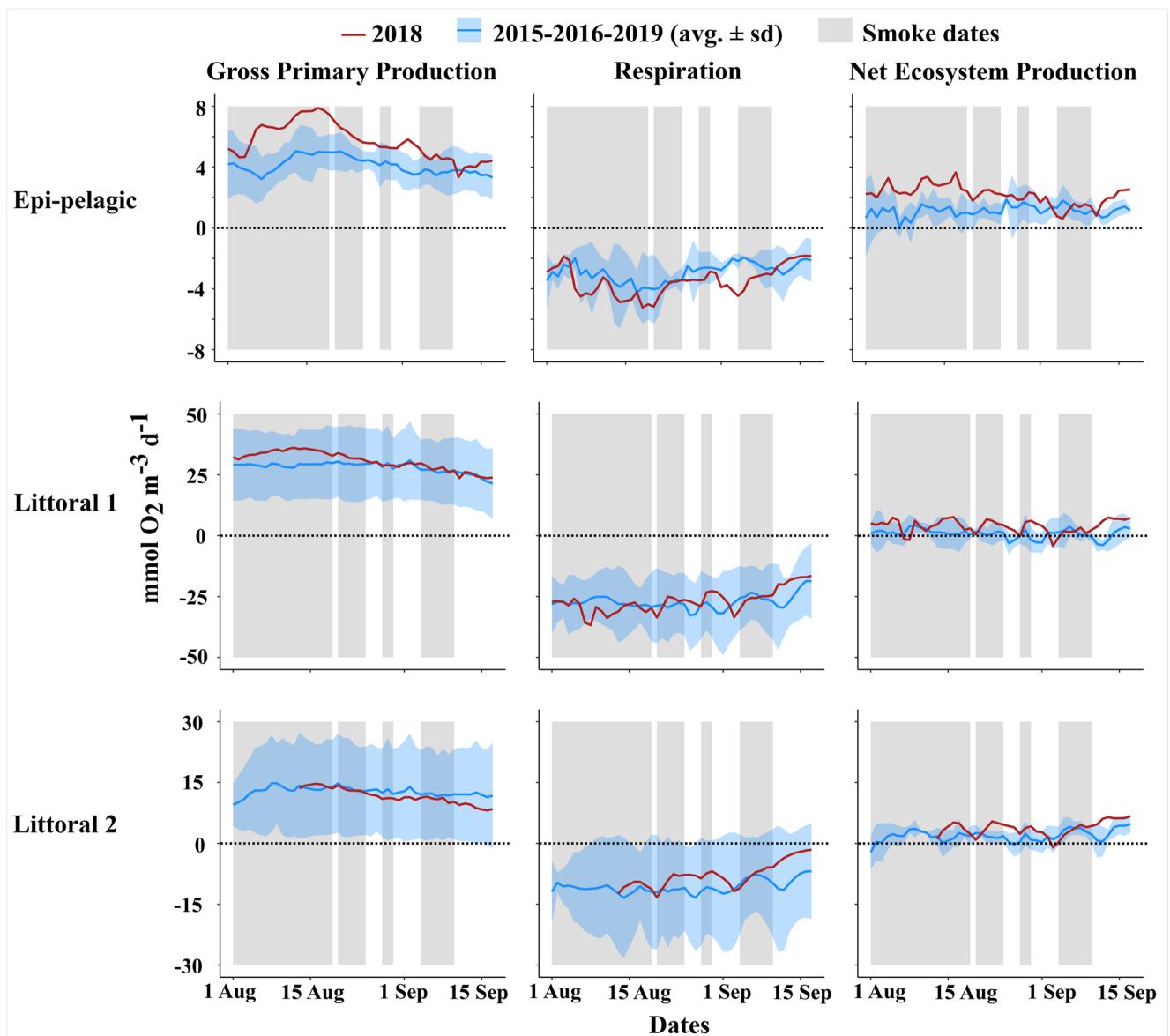


**Figure 3.** Summer seasonal pattern of environmental variables of the 2018 year with smoke (red) and the mean ( $\pm 95\%$  confidence interval in blue) for non-smoke years 2015, 2016, and 2019 (blue). Concentration of  $\text{PM}_{2.5}$  in the air (a), water temperature at 3 m depth in each site (b), incident UV-B (c) and PAR (d) at the surface of the lake, and extinction coefficients of UV-B (e) and PAR (f). Gray background represents days with smoke in 2018.

than the Littoral 2 site (Figure 4; Table S2 in Supporting Information S1). Despite the differences in metabolism rates at the two littoral sites, neither of these sites presented detectable metabolism rate changes during the smoke period of 2018.

#### 4. Discussion

Wildfire smoke significantly increased epi-pelagic primary productivity but not littoral productivity in Castle Lake, causing the relative contribution of epi-pelagic habitats to whole-lake production to be higher in comparison to the years with average or lower ice-cover. We suggest that these patterns result from reduced radiative inputs (specially UV-B) in the water column, alleviating photoinhibition. The higher light adaptation of littoral primary producers (Karsten & Garcia-Pichel, 1996; Vinebrooke & Leavitt, 1999) may reduce the stimulatory effect of smoke on primary producers in these habitats. In contrast, we note that in the pelagic habitat the parameter of maximum production rate increased in the smoke year, reflecting a possible reduction in photoinhibition (as per Staehr et al., 2016; Figure S2 in Supporting Information S1). We posit that the reduction in photoinhibition increased the biomass-specific photosynthetic rates, as there was no change in epi-pelagic biomass (measured as chlorophyll-*a*; Scordo et al., 2021). The maximum production rate at the two littoral habitats occurred within the variability of non-smoke years, indicating the reduction in light did not enhance productivity in the littoral and/or the continued influence of light saturation despite a reduction in PAR.



**Figure 4.** Metabolism at the epi-pelagic and the littoral-benthic sites of Castle Lake in 2018 with smoke (red) and the non-smoke years of 2015, 2016, and 2019 (mean  $\pm$  95% confidence interval in blue). Gray background represents days with smoke in 2018.

The increase in the GPP in the epi-pelagic habitat during the smoke period was likely due to reduced photoinhibition. We operationally define photoinhibition as the reduction of photosynthetic capacity induced through prolonged or excessive exposure to solar radiation along a continuum of wavelengths, including PAR and UV. Response to photoinhibition can vary with taxa, cell size, habitats, and prior exposure (Campbell & Serôdio, 2020; Long et al., 1994). Phytoplankton and algae are affected through physiological mechanisms associated with photosynthesis or cellular repair that have been long studied and well described (Campbell & Serôdio, 2020; Häder et al., 2011; Long et al., 1994; Wu et al., 2012). Previous research from Castle Lake indicates light inhibits production in the shallow pelagic waters (Huovinen et al., 1999); other clear lakes have similar observations, specifically between 11 a.m. and 2 p.m. (Staehr et al., 2016; Vadeboncoeur et al., 2014). UV-B light inhibits productivity down to three meters at Castle Lake (Scordo et al., 2021), and the decline in UV-B during the smoke period likely lessened photoinhibition and allowed primary producers to photosynthesize at their maximum rate for a larger proportion of daylight hours (Falkowski & Raven, 2007). Scordo et al. (2021) showed Castle Lake pelagic productivity at 0, 1 and 3 m depths increased after wildfire smoke reduced UV-B light in 2018. In our

study, even when smoke reduced PAR, the midday light intensity at depth remained between 650 and 850  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; these intensities can cause photoinhibition in the epi-pelagic of clear lakes (Staehr et al., 2016; Vadeboncoeur et al., 2014), suggesting observed differences in GPP were primarily the result of changes in UV-B.

Littoral habitat GPP did not increase despite smoke-induced UV-B light reduction. Littoral primary producers, through adaptation and complex habitat, are less affected by high UV-B radiation than epi-pelagic algae (Karsten & Garcia-Pichel, 1996; Vinebrooke & Leavitt, 1999). Vadeboncoeur et al. (2014) showed periphyton productivity plateaued at the highest field light intensities, and photoinhibition was never evident in seven clear North American lakes. Experiments from Castle Lake that removed UV radiation by 99% using filters did not find a change in periphyton biomass despite altered species composition (Higley et al., 2001), suggesting that changes in the community composition of the periphyton moderates UV-B radiation effects on productivity.

The magnitude of decrease in PAR due to smoke was not large enough to reduce productivity in either of the habitats. Even during the smoke periods of 2018, midday maximum PAR intensity in both the littoral and epi-pelagic habitats reached values above 700  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , values that are optima for photosynthesis in Castle Lake (Goldman et al., 1973), and other clear lakes (Staehr et al., 2016; Vadeboncoeur et al., 2014). However, we recognize that our study only covered the epilimnetic zone of the lake, and that PAR reduction could have lessened productivity at greater depths or caused a shift in the depth of the euphotic zone. Scordo et al. (2021) found that after smoke reduced PAR at depth (12.5 m and lower) in Castle Lake, the deep chlorophyll-*a* and productivity maximum (15–20 m) did not develop. Giling et al. (2017) showed that metalimnetic contribution to whole-lake metabolism can be highly variable. Therefore, studies that analyzed whole water column metabolism are needed to understand how wildfire smoke affects the pelagic habitats of lakes.

Epi-pelagic NEP increased because GPP increased more than R during the smoke period. A lack of a corresponding increase in respiration was surprising as they are coupled ecosystem processes (Sadro, Nelson, & Melack, 2011), but may reflect the reduced metabolic costs associated with a decrease in photoinhibition (Häder et al., 2011). Our results indicate that on short time scales (weeks to months), smoke can increase the assimilation of carbon in the ecosystem. However, further research is needed to establish the mechanisms involved and determine the fate of the net increase in carbon within the ecosystem.

Future explorations will help us understand how wildfire smoke affects the community of producers related to metabolic changes in lakes. We speculate based on studies that examine the influences of UV-B light on planktonic community structure, that photoinhibition has a differential impact on picophytoplankton than phytoplankton (Häder et al., 2011). A shift to picoplankton effectively increases productivity (Banse, 1976). Also, nutrients contributed by ash deposition may stimulate productivity. Scordo et al. (2021) did not find a change in macronutrient limitation at Castle Lake under the smoke conditions of 2018. However, ash deposition may contribute trace metals to waterbodies (Tang et al., 2021), which can increase productivity despite no changes in macronutrient concentration (Goldman et al., 1990). Indeed, deposition of smoke in the Southern Ocean fueled a phytoplankton bloom because of trace metal fertilization (Tang et al., 2021).

## 5. Conclusions

We show differential responses in the productivity of lake habitats due to wildfire smoke, with an increase in the epi-pelagic GPP. These findings underscore the need to untangle our understanding of how lake processes within lake habitats are affected by wildfire smoke. While we present a new conceptual understanding of habitat-specific responses to wildfire smoke (Figure 1), there are limitations from single-site studies and many of the mechanisms we identified need to be tested across lake types to explore the generalities of our conceptual model.

Four broad areas of research questions may help advance our understanding of smoke effects on lakes. (a) How does variation within littoral-bottom habitats (rock, sand, plant) and community architecture mediate the effect of smoke on ecosystem metabolic rates? (b) How do responses to smoke vary across lake types (e.g., trophic status, morphological characteristics like depth, watershed-to-area ratios)? (c) How do the quantity and quality (e.g., elemental composition and bioavailability of particles) of smoke affect aquatic ecosystems? (d) What scale of time associated impacts from smoke will lead to changes in ecological interactions in the lake? As wildfire occurrences increase globally, designing monitoring programs and field experiments to understand the impacts of smoke will be important.

## Data Availability Statement

Data and metadata are available at Scordo, F., Chandra, S. (2022), "Particulate material in the air (PM2.5), light (UV-B and PAR), littoral and pelagic metabolism estimates in Castle Lake (California, USA) 2015, 2016, 2019 and 2018", [Dataset]. Mendeley Data, V2, <https://doi.org/10.17632/7bs4htfy4b.2>.

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