LIMNOLOGY
and
OCEANOGRAPHY

Limnol. Oceanogr. 9999, 2025, 1–15

doi: 10.1002/lno.70157

RESEARCH ARTICLE

The influence of mountain streamflow on nearshore ecosystem metabolism in a large, oligotrophic lake across a drought and a wet year

Kelly Loria[1*], **Heili Lowman**[1,2], **Jasmine Krause**[1,3], **Leon Katona**[1,4], **Ramon Naranjo**[5], **Facundo Scordo**[6,7,8], **Adrian Harpold**[1], **Sudeep Chandra**[8], **Joanna R. Blaszczak**[1]

[1]Department of Natural Resources & Environmental Science and Global Water Center, University of Nevada, Reno, Nevada, USA; [2]Department of Biology, Duke University, Durham, North Carolina, USA; [3]Department of Biological & Ecological Engineering, Oregon State University, Corvallis, Oregon, USA; [4]U.S. Geological Survey Upper Midwest Water Science Center, Lansing, Michigan, USA; [5]U.S. Geological Survey Nevada Water Science Center, Carson City, Nevada, USA; [6]Instituto Argentino de Oceanografía, Universidad Nacional del Sur (UNS)-CONICET, Bahía Blanca, Provincia de Buenos Aires, Argentina; [7]Departamento de Geografía y Turismo, Universidad Nacional del Sur, Bahía Blanca, Provincia de Buenos Aires, Argentina; [8]Biology Department and Global Water Center, University of Nevada, Reno, Nevada, USA

Abstract

The influence of streamflow can be highly heterogeneous around lake edges, making it challenging to predict how benthic productivity in the littoral zone responds to hydroclimatic change. The degree to which streamflow affects nearshore productivity varies as a function of catchment characteristics, internal lake morphometry, and processes. This study investigates the relative influence of streamflow on nearshore metabolism (e.g., gross primary productivity [GPP], ecosystem respiration [ER], and net ecosystem productivity [NEP]) for shores with large, small, or no stream inflows (four locations across two shores) during two contrasting water years (one drought and one wet) in Lake Tahoe (Nevada/California, USA). Using Bayesian structural equation modeling, we found streamflow decreased water temperature, benthic light, and GPP across both years. Compared to the drought year, the subsequent wet year had 54% higher annual streamflow, 37% less light, and lower NEP at locations with large or small inflows (39% Δ -0.32 mmol O_2 m^{-3} $d^{-1\%}$ and 49% Δ -1.19 mmol O_2 m^{-3} d^{-1}, respectively). During the wet year, we observed a 68% increase in the negative association between streamflow and nearshore GPP at the large inflow and a 62% decrease in the positive association between streamflow and GPP at the small inflow. This work demonstrates how oligotrophic littoral productivity varies across shorelines and in response to hydrological conditions, with streamflow and precipitation exerting contrasting effects depending on the proximity to inflowing streams. Our results suggest future lake responses to climate volatility depend on spatial and temporal hydrologic connectivity to catchments and upland processes.

Lakes integrate environmental processes from their surrounding water and airsheds, reflecting seasonal patterns of material transport, precipitation, and evapotranspiration (Adrian et al. 2009; Williamson et al. 2009). Within lakes, the nearshore, or littoral zone, plays a key role in biogeochemical cycling and supporting biodiversity (Vadeboncoeur et al. 2003; Devlin et al. 2016; Vander Zanden and Vadeboncoeur 2020). The nearshore is characterized by greater substrate-surface water interactions which can elevate ecosystem productivity relative to the limnetic zone but can also be highly heterogeneous around a lake's perimeter (Vadeboncoeur et al. 2006; Cavalcanti et al. 2016; Scordo et al. 2022a, 2022b). This high spatial heterogeneity in nearshore habitat quality originates in part from variation in hydrologic connectivity with upland landscapes (Vander Zanden and Vadeboncoeur 2020). Relative to the limnetic

---

*Correspondence: kloria@unr.edu

Associate editor: Marie-Elodie Perga

Data Availability Statement: All originally generated data associated with this manuscript can be found on Environmental Data Initiative (Loria et al. 2025; https://doi.org/10.6073/pasta/dd1577416e9da88f29da80cef06e510c) all analysis can be found at (https://github.com/kellyloria/Tahoe-streamflow-and-nearshore-metabolism). Aggregated and transformed data from public domains (GLDAS, NLDAS, PRISM, SNOTEL, and USGS) is available upon request.

zone, nearshore lake habitats are expected to be more sensitive to interannual hydroclimatic variability because of their responsiveness to short-term environmental change (Hanson et al. 2015; Richardson et al. 2021; Ward et al. 2022). Climate change is projected to shift precipitation and drought patterns (Dettinger and Rajagopal 2023; Swain et al. 2025), thereby altering stream flow. It remains unclear how these changes in streamflow will alter the lake-catchment connectivity dynamics that regulate ecosystem processes in nearshore habitats (Williamson et al. 2009; Siirila-Woodburn et al. 2021).

Spatially heterogeneous stream-to-lake transition zones can create a combination of environmental conditions that make it challenging to predict where and when nearshore biogeochemical activity will be stimulated or suppressed (Johengen et al. 2008; Jones 2010; Bernhardt et al. 2017). Inflowing streams transport organic matter (OM) and nutrients from catchments to the nearshore of lakes (Scott and Wohl 2017). In snow-dominated ecosystems, winter precipitation can generate pulses of both nutrient-rich groundwater and shallow subsurface flow, which stimulate attached algae growth for shallow, cobble-dominated areas in oligotrophic mountain lakes (Naranjo et al. 2019; Domagalski et al. 2021), especially at the inflows of streams draining relatively large catchments (Coats et al. 2008; Domagalski et al. 2021). Yet, the degree to which nearshore ecosystem processes in lakes reflect changes in hydrologic connectivity with uplands relative to internal lake conditions (e.g., different dominant substrata, lake morphometry) and processes (e.g., water residence time and mixing, fine particulates suspension, and internal nutrient loading) is unclear (Dodds et al. 2019; Vander Zanden and Vadeboncoeur 2020). Hydroclimatic conditions can influence nearshore habitats through lake level rise and fall (Hofmann et al. 2008; Scordo et al. 2022a), groundwater intrusion (Rosenberry et al. 2015; Naranjo et al. 2019), and variation in streamflow paths (Langlois et al. 2005; Miller et al. 2005). Despite our knowledge of the importance of these mechanisms, it is still challenging to anticipate how ecosystem processes, such as the global phenomenon of increasing benthic filamentous algal blooms in oligotrophic lakes (Vadeboncoeur et al. 2021), vary along the perimeter of lakes.

Aquatic ecosystem metabolism is an ecosystem process increasingly used to assess freshwater ecosystem responses to environmental change (Hoellein et al. 2013; Jankowski et al. 2021). Metabolism is comprised of gross primary productivity (GPP) and ecosystem respiration (ER), which are estimated on a daily time step from diel changes in dissolved oxygen (DO) concentrations driven by oxygen generation by photosynthesis, oxygen consumption by respiration by benthic and pelagic organisms, and gas exchange with the atmosphere (Odum 1956; Winslow et al. 2019; Lottig et al. 2022). For many lakes, nearshore GPP is a large fraction of whole lake GPP fluxes relative to open water (i.e., pelagic) habitats (Devlin et al. 2016; Staehr et al. 2018; Ward et al. 2022). Despite the potential impact of nearshore metabolism on whole-lake carbon cycling, much of past limnological theory and current monitoring efforts often rely on extrapolations from single, open water stations or pelagic energetic models, neglecting within-lake heterogeneity and variation in watershed contributions. This oversight can lead to substantial bias in whole lake metabolism estimates depending on the characteristics of the lake. Capturing the relative contribution of inflowing streams in the nearshore can reduce spatial bias in whole lake metabolism estimates (Hotchkiss et al. 2018; Ward et al. 2022).

This study investigates the relative influence of streams on nearshore metabolism by monitoring nearshore littoral environmental conditions and estimating ecosystem metabolism continuously near and far from stream inflows on two contrasting shores for a drought (2022) and a wet (2023) water year at Lake Tahoe (Nevada/California, USA). Specifically, we asked how stream inflow regulates littoral environmental conditions (e.g., nutrient availability, water temperature, and light availability) and nearshore metabolism between a drought water year vs. a wet water year? Our overarching objective was to quantify the relative importance of streams to nearshore metabolism over time and across distinct stream-to-lake transitional zones to provide a mechanistic understanding of how and when hydrologic connectivity with uplands drives nearshore productivity.

Methods

Site description

Lake Tahoe is a large, oligotrophic freshwater lake occupying 38% of its total watershed area (1313 km^2) in the Sierra Nevada mountains spanning both California and Nevada, United States of America (USA). We monitored three nearshore areas spanning a range in stream inflows (large, small, and none) to compare nearshore dynamics across a drought (September 2021 to September 2022) and a wet (September 2022 to September 2023), slightly offset water year to match our data availability (hereafter referred to as water year; Fig. 1). Following three of the consecutive driest water years on record for the state of California (2020–2022), 2023 ranked among the top five wettest years in terms of precipitation accumulation, exemplifying an extreme drought-to-wet whiplash event in the Sierra Nevada Mountains (California Department of Water Resources 2023; Swain et al. 2025). The large volume stream-to-lake transition zone was at the inflow of Blackwood creek (BW; large catchment, west shore, flow range 0.020–13.309 m^{3}s^{-1}), the small volume stream-to-lake transition zone was at the inflow of Glenbrook creek (GB; small catchment, east shore, flow range 0.001–0.852 m^{3}s^{-1}), and the no inflow location was at the Sunnyside marina (SS), approximately 2.8 km north of BW creek on the western shore of the lake (Fig. 1; Supporting Information Fig. S1; Supporting Information Table S1). These catchments represent hydroclimatic differences within the Lake Tahoe Basin, where the larger, western catchment, BW, can receive 35% more mean annual

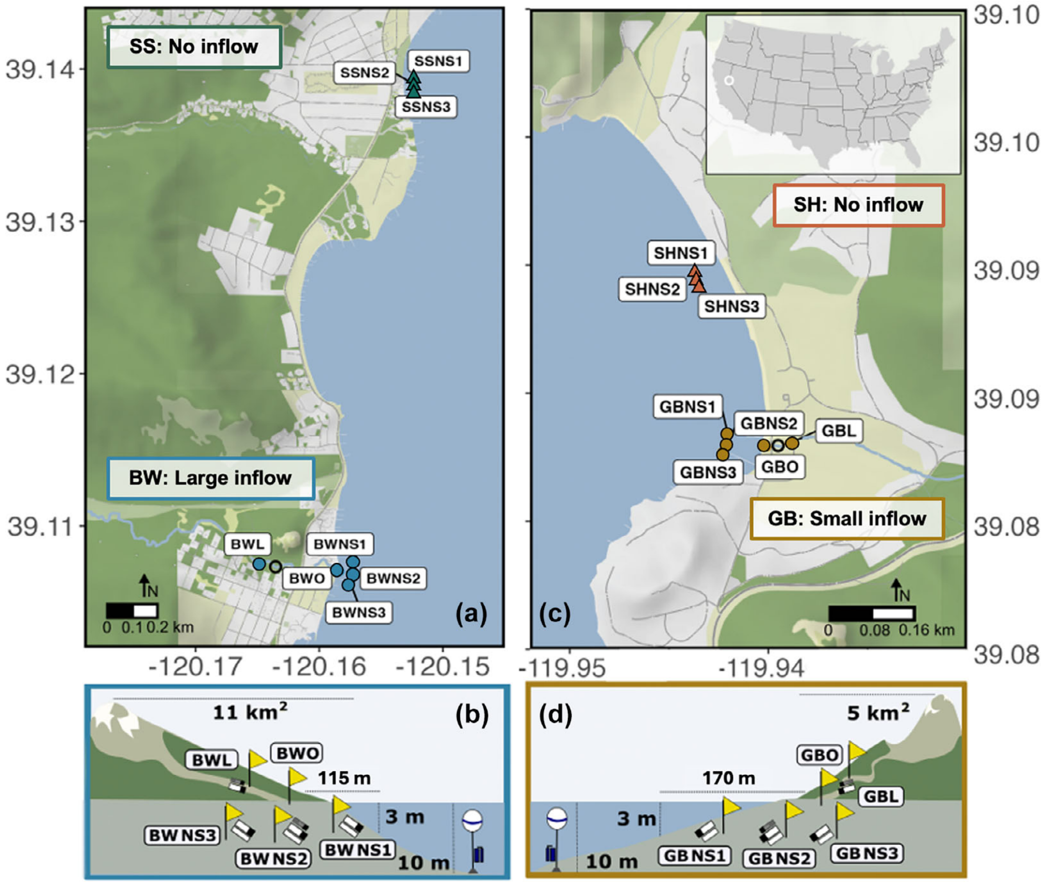

Fig. 1. Map of study locations (**a** and **c**) and conceptual diagram of instrumentation. The large stream inflow on the (a) west shore, Blackwood (BW), with sensor positions in the nearshore (NS), and the stream (L, O) in blue (panels a and **b**), as well as (c) the small stream in flow on the east shore, Glenbrook (GB), with sensor positions in the NS, L, and O, in gold (panels b and **d**), as well as the shore location isolated away from stream inflows on the west shore Sunnyside (SS in green triangles), and the east shore Slaughterhouse (SH in orange triangles). Nearshore locations represent the placement of dissolved oxygen (DO) sensors used to model metabolism at roughly three meters deep when initially deployed. L and O locations represent stream survey areas for sample collection at the lower (L), which was instrumented with a dissolved oxygen sensor, and outlet (O) reach segments of either BW or GB creeks. The conceptual diagrams (b and d) of sub-catchment morphology (lower panels), locations of instrumentation (DO, conductivity, and photosynthetically active radiation sensors), and sampling locations (yellow flags). Open black circles represent the location of U.S. Geological Survey stream gages.

precipitation relative to GB (Reuter and Miller 2000). Blackwood creek flows through a 29.9 km^2, largely undeveloped watershed underlain by volcanic and surficial deposits. Glenbrook creek integrates flow from a 10.6 km^2 watershed primarily comprised of decomposed granitic rock. To assess productivity and habitat quality differences between paired nearshore locations near and far from streams between the east and west sides of the lake, we added a fourth shore location at Slaughterhouse meadow (SH) 1.15 km north of the inflow of the GB creek location in February of 2023 (Supporting Information Section 1; Supporting Information Fig. S2).

Field instrumentation

To understand nearshore differences in metabolism and habitat quality among the shore locations (BW, GB, SH, and SS), we deployed three optical DO and temperature sensors (miniDOT, Precision Management Engineering, Vista California, USA) on cinder blocks (~ 0.25 m above the bed) in nearshore habitats adjacent to the large (BW) and small (GB) stream inflows, sunk to depths of ~ 3 m (Fig. 1; Supporting Information Fig. S2) in June 2021. To standardize deployment depth across sites with variable bathymetry, sensors were positioned 115 m (BW), 170 m (GB), 100 m (SS), and 140 m (SH) from shore (Supporting Information Fig. S3). At BW and GB, sensors were placed directly in front of the inflow and $\sim$ 50 m north and south to capture spatial variability in inflow morphometry. At non-inflow sites (SS, deployed August 2021; SH, deployed February 2023), sensors were spaced $\sim$ 50 m apart and aligned parallel to shore. All sensors recorded DO and temperature at 15-min intervals.

Benthic light was measured with a photosynthetic active radiation (PAR) sensor and wiper (Odyssey® Submersible PAR Loggers, Dataflow Systems Ltd, Christchurch New Zealand) secured vertically on benthic buoy lines at 9.5 m deep directly behind the central DO sensor at each stream mouth and recorded PAR every 15 min from October 2021 through September 2023. We maintained sensors via SCUBA approximately every 3–4 months, except in 2023, where sensors were cleaned every month from June to September 6th, 2023, after which all instrumentation was removed (Supporting Information Section 1).

In the uplands, we instrumented BW and GB creeks with DO and conductivity (Onset HOBO U24) sensors horizontally mounted to cinderblocks (to place sensors 0.1 m above the substrate) without wipers in the thalweg of each stream. We deployed the sensors at 0.75 km (BW) and 0.15 km (GB) upstream of the shoreline to monitor in-stream water quality from Spring 2021 to Fall 2023. We used 15-min observations of streamflow and water stage from USGS stream gaging stations for BW (gage: 10336660, 39.11°N, −120.16°W, and at 1900 m ASL, U.S. Geological Survey 2024) and GB (gage: 10336730, 39.09°N, −119.94°W, and 1901 m ASL, U.S. Geological Survey 2024) downloaded using the dataRetrieval package (DeCicco et al. 2024).

Data collection and sample processing

We paired sensor deployments with regular sampling of water and sediment adjacent to the sensors for analysis of nutrient concentrations (nitrate [NO_3^--N in mg L^{-1}], ammonium [NH_4^+-N in mg L^{-1}], orthophosphate as soluble reactive phosphorus [ortho-PO_4^{3-} in μg L^{-1}]), dissolved organic carbon [DOC in mg L^{-1}], and volumetric core samples of organic matter (OM in mg mL^{-1}, Supporting Information 1.2 and 1.3). Beginning in October 2021 for nearshore areas near inflowing streams (BW and GB), we sampled twice monthly May through September and once monthly October through April at each stream (BWL or GBL) and directly in front of the inflow (BWO or GBO) at a 0.5 m depth (Fig. 1). We measured water quality (DO [mg L^{-1}], temperature [°C], specific conductance [SPC, μS cm^{-1}], and pH) at these same sites using a YSI multiparameter sonde (YSI proPlus, Yellow Springs, OH, USA and Orion) and collected the top 5–10 mm of the sand or gravel using a standard metal cylinder (5.08 cm diameter). We sampled water just above the benthos and the sediment surrounding each of the three littoral DO sensors (NS1–NS3) for a given shore area (BW, GB, SH, and SS) at a 3 m depth. We composited, homogenized, and sieved (2 mm) substrate samples and took subsamples to measure OM, pore water, and sediment pH (Supporting Information Section 1.3).

We determined sediment organic matter by drying samples at 60°C for 48 h and combusting them at 500°C for 8 h. Sediment pH was measured with an Orion Star A211 Benchtop pH Meter (Thermo Fisher Scientific, Waltham, Massachusetts, USA; Carter and Gregorich 2007). We extracted pore water solutes from 3 ± 0.25 g of wet sediment mixed with 25 mL of deionized water (Blaszczak et al. 2018). We measured DOC using a total organic carbon (TOC) analyzer with a total nitrogen (TN) module (TOC-V CPH; Shimadzu, Kyoto, Japan). Ammonium (NH_3-N) with a detection limit of 0.002 mg N L^{-1} was converted to NH_4^+-N using pH and temperature (U.S. Environmental Protection Agency 1993a), orthophosphate (o-P with a detection limit of 0.402 μg P L^{-1}; 1993b), and nitrate (NO_3-N with a detection limit 0.003 mg N L^{-1}; U.S. Environmental Protection Agency. 1993c). were measured with a SEAL AQ400 discrete analyzer (SEAL Analytical, Mequon, Wisconsin, USA).

Climate data

We aggregated hourly data of surface light (shortwave radiation flux downwards [W m^{-2}]), interpolated 3-h wind speed (near surface wind [m s^{-1}]), and 3-h barometric surface pressure (Pa) at an eighth of a degree latitude and longitude from the North American Land Data Assimilation System (Xia et al. 2012; Beaudoing et al. 2020). We converted incoming shortwave radiation from W m^{-2} to surface irradiance in PAR (μmol m^{-2} s^{-1}) by multiplying it by 2.114 (Savoy et al. 2021). We used precipitation (mm) from PRISM (PRISM Climate Group 2024), as well as nearby Snow Telemetry (SNOTEL) station data from sites 848 on the west shore (Ward Creek 39.14°N, −120.22°W, and at 2056 m ASL) and 615 on the east shore (Marlette Lake 39.16°N, −119.9°W, and at 2403 m ASL) for precipitation events, accumulated precipitation, as well as snow water equivalent (SWE; Hufkens 2022).

Modeling nearshore-littoral habitat metabolism

We estimated daily nearshore metabolism (GPP and ER in mmol O_2 m^{-3} d^{-1}) using the methods in Lottig et al. (2022) and Scordo et al. (2022a) which allow for the possibility of photoinhibition on productivity (Staehr et al. 2016; *see* Supporting Information Section 3.2). This model fits each day individually, leveraging the entire time series of high-frequency (15-min) measurements of DO (in mg L^{-1}), water temperature (°C), benthic light (PAR; μmol m^{-2} s^{-1}), DO saturation given barometric pressure (mbar), and final gas transfer velocity (k in h^{-1}) given wind speed (m s^{-1}), to generate daily metabolism estimates and constrains model parameters to ecologically feasible ranges (i.e., GPP and ER must be positive and negative, respectively; Lottig et al. 2022). We calculated net ecosystem productivity (NEP) as the difference between GPP minus the absolute magnitude of ER.

We filtered DO data by excluding values that were either greater than three standard deviations from seven consecutive running observations or associated with an amplified signal pre-sensor cleaning that may have been indicative of biofouling (Supporting Information Fig. S4). To reduce atmospheric gas exchange driving DO dynamics in our observed data, we removed days with mean daily wind speeds greater than 5.9 m s^{-1} ($n = 21$) (k in h^{-1}; Supporting Information Table S2) and reduced the lake area to a third of Tahoe's size ($165.4\,\mathrm{km}^2$) to estimate k for a smaller nearshore zone. We used the photoinhibition photosynthesis-irradiance (P_I) curve (Steele 1962) to define the relationship between GPP and light based on Lottig et al. (2022) and Scordo et al. (2022a).

We fit each metabolism model to time series of filtered and post-deployment intercalibrated DO observations for each sensor via Stan (Stan Development Team 2024) in R (R Core Team 2024) using the RStan package as described in Phillips (2020) and Lottig et al. (2022; Supporting Information Section 3.2). We evaluated model performance through the effective sample size (ESS), potential scale reduction factor (PSRF), and the Gelman–Rubin statistic ($\widehat{R}$) of each parameter in the model and used only daily estimates of GPP or ER with appropriate model convergence (posterior median $\widehat{R} < 1.05$) for statistical inference (Scordo et al. 2022a; Supporting Information Section 4).

Statistical analyses

Quantifying differences between water years and paired shore locations

We first used Student's t-tests to evaluate how mean annual differences in nearshore metabolism (e.g., GPP, ER, and NEP), precipitation, light, and water temperature changed from drought (2022) to wet (2023) water years modified in length to match our data availability (2022: September 30th 2021 to September 6th 2022 and 2023: September 30th 2022 to September 6th 2023) at each of the shores (the large stream inflow—BW, the small stream inflow—GB, and the shore with no inflow—SS). We additionally used ANOVA to evaluate how daily GPP, $|\mathrm{ER}|$, and NEP varied across each of the shore locations (BW, GB, and SS) for overlapping observations from both the modified water years. We reported the percent change, F-statistics, and p-values for results with meaningful differences ($p < 0.05$). Lastly, we evaluated geographic differences in GPP, $|\mathrm{ER}|$, benthic light, water temperature, nutrients, and sediment organic matter between paired locations with and without stream inflows on the east (drier) or west (wetter) shore of the lake and reported the mean weekly differences (GB–SH or BW–SS) in those parameters from a subset of data from February 2nd 2023 to September 6th 2023.

Quantifying the influence of streamflow on nearshore metabolism

To examine the influence of streamflow relative to within-lake light and temperature conditions on daily gross primary production (GPP) and ecosystem respiration ($|\mathrm{ER}|$), we fit piecewise Bayesian structural equation models (SEMs; Lefcheck 2016; Brown et al. 2023) using the brms package in R (Bürkner 2021; Fig. 4a). Gross primary productivity and $|\mathrm{ER}|$ were modeled as a function of their lagged values (temporal autoregressive component), nearshore benthic light ($\mu\mathrm{mol\ m^{-2}\ s^{-1}}$), nearshore water temperature (°C), and catchment-normalized log transformed streamflow, using a hurdle lognormal distribution to account for the semi-continuous nature and zero-inflation of metabolic rates (Mullahy 1986; Bürkner 2021). To characterize the influence of streamflow and precipitation on within-lake light and temperature conditions, our final SEM structure included nested submodels for each intermediate variable. Specifically, water temperature and benthic light were each modeled as a function of streamflow and precipitation, while streamflow itself was modeled as a function of precipitation. These submodels were specified jointly, forming a hierarchical SEM structure. All continuous predictors were standardized (i.e., mean-centered and scaled) to allow for direct comparisons of path coefficient strength.

We fit separate SEMs for each shore (large stream inflow: BW, small stream inflow: GB, no stream inflow: SS) and water year (September 30th to September 6th; 2022 or 2023), including a random intercept for each replicate sensor location ($n = 3$, except SS with $n = 2$). We reported the median posterior estimate and 95% credible intervals for each parameter estimate with an $\widehat{R} < 1.05$, as well as the variance of the predicted values divided by the variance of the data as Bayesian R^2 values (Gelman et al. 2019; Vehtari et al. 2021; Supporting Information Section 4.2; Data Availability Statement).

Results

Differences in streamflow and precipitation across catchments from a drought to a wet year

Throughout the study, the larger west shore catchment, BW, accumulated 32% more SWE and generated 82% more streamflow relative to the smaller east shore catchment, GB. During the drought year, peak snowmelt occurred 27 d earlier in the larger west shore sub-catchment (BW) and 12 d earlier in the smaller east shore sub-catchment (GB) relative to the wet water year. We observed 65% more annual SWE accumulation and 56% higher surface water yield across both catchments in the wet year, which resulted in higher annual water yields to the lake (2022: $1.24 \times 10^6\ \mathrm{m^3\ year^{-1}}$ and 2023: $2.79 \times 10^6\ \mathrm{m^3\ year^{-1}}$). Similarly, mean annual specific discharge ($\mathrm{m^3\ s^{-1}\ km^{-1}}$) was 54% higher across both creeks (Fig. 2a; Supporting Information Fig. S5) and we observed twice as much precipitation at all locations (BW: $t = 13.95$, $\mathrm{df} = 2039$, $p < 0.001$, $\alpha = 0.05$; GB: $t = 12.42$, $\mathrm{df} = 2039$, $p < 0.001$, $\alpha = 0.05$; SS: $t = 11.25$, $\mathrm{df} = 1359$, $p < 0.001$, $\alpha = 0.05$) in the drought year relative to the wet water year.

Variation in littoral conditions between the drought and the wet water year

Benthic light availability at nearshore locations near inflowing streams declined in response to the different hydroclimatic conditions between the drought (2022) and the wet (2023) water years, while water temperature in the nearshore was relatively stable across years (Supporting Information Fig. S12). In the wet year, light attenuation increased in the

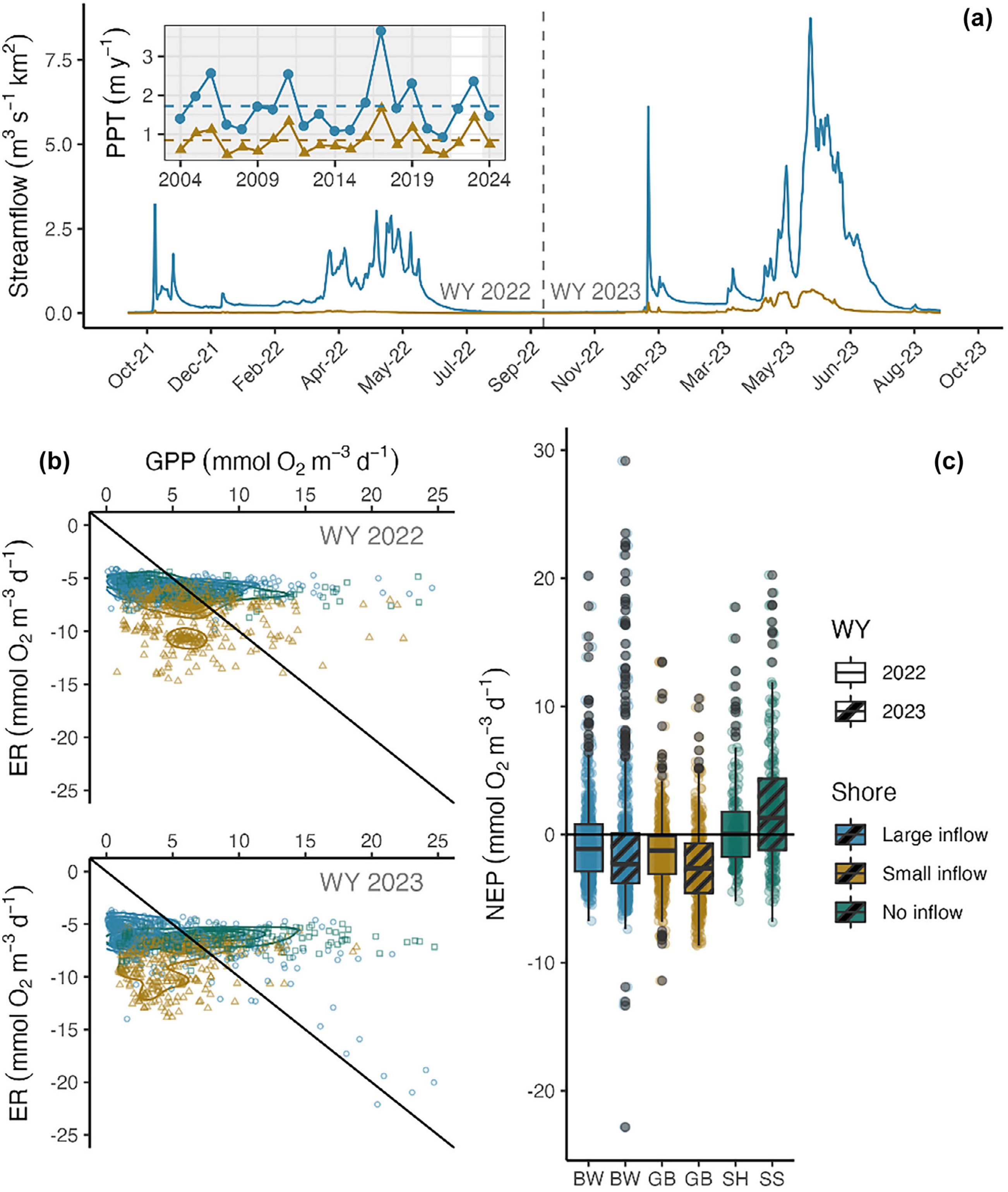

Fig. 2. (**a**) Daily specific stream flow in (m^3 s^{-1} km^{-1}) for the small inflowing creek (GB, gold, triangle) and the large inflowing creek (BW, blue circle) for the drought (2022) and wet (2023) water years (WY). The inset of mean annual precipitation accumulation in (m yr^{-1}) from WY 2004 to 2024. The dashed lines represent the 20-year mean and the white box highlights 2022 and 2023. (**b**) Plots of gross primary productivity (GPP in mmol O_2 m^{-3} d^{-1}) and ecosystem respiration (ER in mmol O_2 m^{-3} d^{-1}) for the drought year (WY 2022, upper) and the wet year (WY 2023, lower). Blackwood creek is represented by blue circles, GB is represented by gold triangle, and shore with no inflowing stream, (SS) is represented by green squares. (**c**) Box plots of net ecosystem productivity (NEP in O_2 m^{-3} d^{-1}) for BW, GB, and SS with pattern representing water year (drought with no pattern and wet with stripes).

nearshore at the inflows of the large stream (32% increase Δ +0.04 m at BW: $t = 4.05$, df = 2030, $p < 0.001$, $\alpha = 0.05$) and small stream (GB: $t = 3.35$, df = 2030, $p < 0.001$, $\alpha = 0.05$) but remained stable at the nearshore location isolated from stream inflows (Supporting Information Figs. S7, S8). In contrast, during the wet water year, mean annual benthic water temperatures increased marginally at the nearshore location with either stream inflow (BW: Δ +0.7°C and GB: Δ +0.1°C) and more strongly at the nearshore location isolated from stream inflows (SS: Δ +1.9°C).

Spatial differences in nearshore metabolism with large, small, and no inflowing streams

Mean nearshore NEP was greater at the location isolated from stream inflows (SS) than at either inflow location (BW or GB; Fig. 2), indicating that nearshore metabolism was more autotrophic in the absence of stream-derived inputs and increasingly heterotrophic near inflow zones. The shore location isolated from stream inflows (SS) had higher GPP (mean: 7.9 mmol O_2 m^{-3} d^{-1}) fluxes relative to the nearshore areas adjacent to inflowing streams (BW: 5.6 mmol O_2 m^{-3} d^{-1} or GB 5.8 mmol O_2 m^{-3} d^{-1}; $F_{2,2153}$: 24.43, $p < 0.001$; Fig. 2), while nearshore areas adjacent to inflowing streams (BW: −7.3 mmol O_2 m^{-3} d^{-1} or GB: −8.4 mmol O_2 m^{-3} d^{-1}) had higher ER fluxes relative to SS (−6.3 mmol O_2 m^{-3} d^{-1}; $F_{2,2164}$: 42.21, $p < 0.001$; Fig. 2b). We observed contrasting differences in GPP and ER from the drought (2022) to the wet (2023) water year at locations with and without stream inflows. We found a 24% decrease in mean annual GPP (Δ −1.61 mmol O_2 m^{-3} d^{-1}) at the location with the small inflowing stream (GB), but a 13% increase (Δ +0.74 mmol O_2 m^{-3} d^{-1}) at the location with the large inflowing stream (BW), and a 20% increase (Δ +1.69 mmol O_2 m^{-3} d^{-1}) at the location isolated from stream inflows (SS) in the wet year. |ER| increased by 30% (Δ +2.5 mmol O_2 m^{-3} d^{-1}) at the location with the large inflowing stream (BW), by 4% (Δ +0.2 mmol O_2 m^{-3} d^{-1}) at the location isolated from stream inflows (SS), and remained unchanged at the location with the small stream inflow (GB; Fig. 2). At both locations with stream inflows, NEP decreased from the drought to the wet water year (GB: 49% Δ −1.2 mmol O_2 m^{-3} d^{-1} and BW: 39% Δ −0.4 mmol O_2 m^{-3} d^{-1}), while NEP at the location isolated from stream inflows increased (SS: 62% Δ +1.4 mmol O_2 m^{-3} d^{-1}).

Spatial differences between east and west shore catchments with and without stream inflows

Comparing paired east and west shore locations with and without stream inflows from February to September 2023, we found that areas near streams had higher sediment organic matter, greater concentrations of inorganic nitrogen, and elevated ecosystem respiration (|ER|) fluxes compared to adjacent areas isolated from stream inflows. On the east shore (Fig. 3a; Supporting Information Table S5), GPP was lower (Δ −2.0 mmol O_2 m^{-3} d^{-1}), while |ER| (Δ +2.6 mmol O_2 m^{-3} d^{-1} $n = 23$) and SPC (Δ 7.4 μS cm^{-1}, $n = 14$) were higher near the stream inflow. On the west shore (Fig. 3b), |ER| was also higher near the stream inflow (Δ +3.9 mmol O_2 m^{-3} d^{-1}, $n = 16$), but water temperature (Δ −0.6°C, $n = 30$), benthic light (Δ −7.2 μmol m^{-2} s^{-1}, $n = 30$), and SPC (Δ −11.0 μS cm^{-1}, $n = 14$) were lower near the stream inflow, and GPP was not noticeably different. The east shore location with the small inflowing stream had the highest NO_3^--N (17.8 μg L^{-1}), NH_4^+-N (16.0 μg L^{-1}), and DOC (0.73 mg L^{-1}), while the west shore location isolated from stream inflows had the highest ortho-PO_4^{3-} (13.7 μg L^{-1}). Similarly, sediment organic matter was lower in the shore locations away from inflowing creeks (29% SH: 10.6 mg mL^{-1}, range: 5.6–70.0 mg $mL^{-1\%}$ and 32% SS mean: 21.0 mg m L^{-1}, range: 16.1–26.6 mg m L^{-1}) relative to the nearshore locations near inflowing creeks.

Streamflow influence on nearshore littoral metabolism across inflow size in drought and wet conditions

After accounting for temporal autocorrelation, the strength and direction of environmental drivers on nearshore metabolism varied by shore and between the dry (2022) and wet (2023) water years (Fig. 4b,c; Supporting Information Tables S6, S7). We observed a large range in the Bayesian R^2 values for both the GPP and |ER| models (R^2: 0.01–0.78), indicating that SEMs captured key drivers of daily metabolism at some shore areas. At the small inflow during the dry year, the SEM explained a large portion of the variance in GPP ($R^2 = 0.78$) and suggested a strong influence of modeled drivers on GPP. In contrast, other location-years showed limited explanatory power (e.g., $R^2 < 0.1$), likely reflecting weaker or more diffuse environmental controls on daily metabolism (Supporting Information Tables S6, S7). At nearshore locations with stream inflows (BW and GB), temperature had a positive effect on GPP at the large stream inflow during the wet year (BW: 0.38) and at the small inflow during the drought year (GB: 0.35). Similarly, temperature had a slight negative influence on |ER| at the large stream inflow (BW: −0.07), and a slight positive influence on |ER| at the small stream inflow during the wet year (GB: −0.03). At the nearshore isolated from stream inflows, temperature negatively influenced GPP (SS: −0.12) in both years and did not discernibly affect |ER| in either year. Direct effects of benthic light intensity generally suppressed GPP during both the dry (BW: −0.62 GB: −0.21, and SS: −0.28) and wet (BW: −0.20, GB: −0.16, and SS: −0.28) water years across all shore locations. Light intensity was also weakly associated with |ER|, but most posterior estimates centered on zero.

Streamflow exerted both direct and indirect influences on nearshore metabolism. At the shore adjacent to the large stream inflow, streamflow suppressed GPP during the drought year (BW: −0.07) and this negative relationship intensified under wet conditions (BW: −0.23). In contrast, near the small inflow, streamflow consistently enhanced both GPP and |ER| across years. During the drought year, GPP and |ER| increased

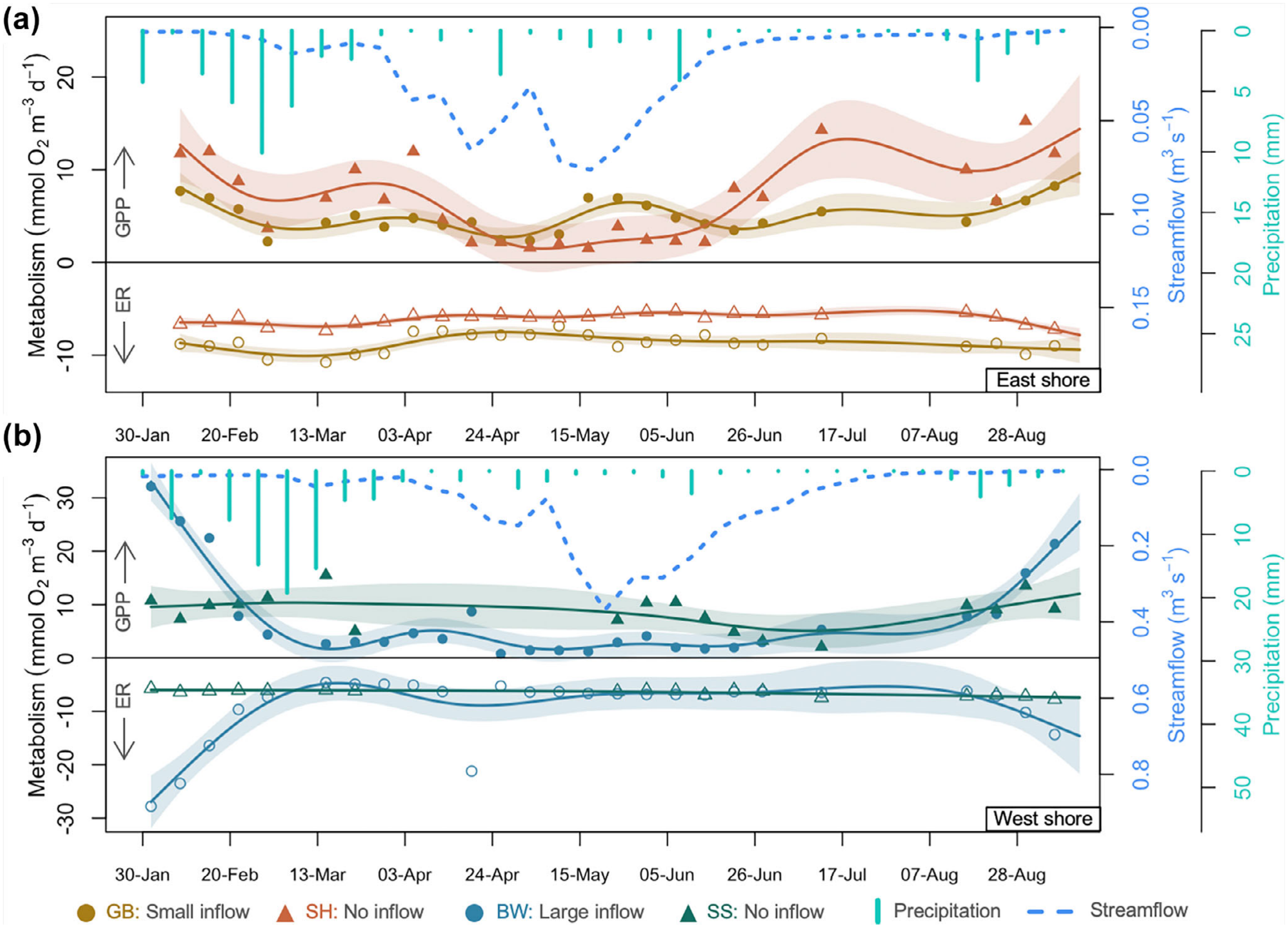

Fig. 3. Comparison of (**a**) east shore mean weekly metabolism dynamics at the small stream inflow (GB in gold circles), and the shore location isolated from stream inflows (SH in orange triangles) and (**b**) west shore mean weekly metabolism dynamics at the large stream inflow (BW in blue circles) and the shore location isolated from stream inflows (SS in green triangles) from February 2nd to September 6th, 2023. Filled in point shapes indicate metabolism as gross primary productivity (GPP) while open shapes correspond to ecosystem respiration (ER). The dashed blue line represented streamflow from (a) GB creek or (b) BW creek, and vertical teal bars represent precipitation events.

with flow (GPP at GB: 0.55 and |ER| at GB: 0.10). Although the magnitude of these effects declined in the wet year, they remained positive (GPP at GB: 0.21 and |ER| at GB: 0.01). Streamflow also exerted indirect effects on metabolism by modifying temperature and light conditions. During the drought year, streamflow strongly reduced benthic temperatures at the small stream inflow (GB: −1.16), whereas this cooling effect was considerably weaker during the wet year (0.12). In contrast, in the drought year, streamflow was positively associated with benthic light at the large inflow site (BW: 0.17) but negatively related at the small inflow site (GB: −0.28). During the wet year, this relationship reversed at GB, coinciding with a delayed peak in streamflow that more closely aligned with the spring increase in solar irradiance and flow observed at BW (Supporting Information Fig. S5). These positive associations between streamflow and benthic light during the wet year may reflect the seasonal synchrony of snowmelt-driven discharge and increasing daylength, rather than direct hydrologic effects on turbidity or light attenuation.

Precipitation primarily influenced metabolism via its effects on flow, light, and temperature. Mean daily precipitation increased streamflow during the dry year at both inflow sites (BW: 0.07 and GB: 0.10) and continued to do so near the small inflow during the wet year (GB: 0.06). Relative to streamflow, the effect of precipitation on reducing water temperature and benthic light availability increased by 45% and 60% during the wet year. Precipitation significantly cooled benthic waters during the wet year (BW: −0.12, GB: −0.22, and SS: −0.07). Across all locations and years, precipitation consistently reduced benthic light availability, with the strongest suppression occurring at the inflow locations (wet year BW: −0.33, GB: −0.34, SS: −0.24).

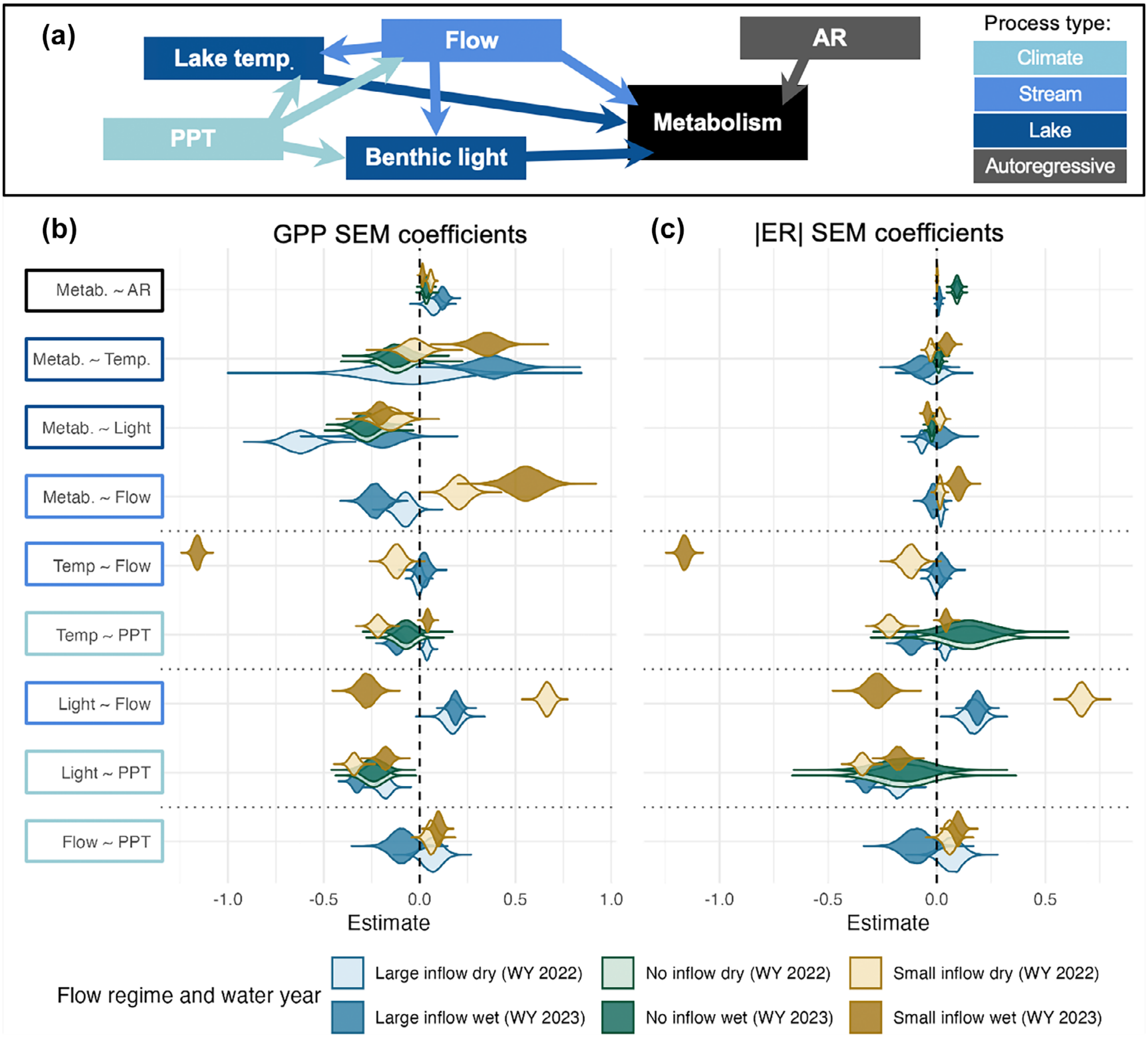

Fig. 4. (**a**) Path diagram representing the Piecewise Bayesian structural equation model (SEM) of how metabolism (metab., as either gross primary productivity [GPP] or ecosystem respiration [|ER|]) is a function of the day prior's metabolism (AR as GPP_{t-1} or $|\mathrm{ER}|_{t-1}$), benthic water temperature (temp.), benthic light, or streamflow (flow), while accounting for how benthic water temperature and benthic light could also be functions as both streamflow and precipitation (as PPT). The box color for each parameter represents the type of process associated with a given parameter (light blue for stream, dark blue for lake, teal for climate, and gray for autoregressive). (**b** and **c**) Posterior estimates of path coefficients from SEMs for (b) GPP (in $\mathrm{O_2\ m^{-3}\ d^{-1}}$) or (c) |ER| (in $\mathrm{O_2\ m^{-3}\ d^{-1}}$) at shore locations with either a large stream inflow (BW in blue), a small stream inflow, (GB in gold), or isolated from stream inflows (SS in green). Water year is represented by fill color transparent for drought (2022) or filled for wet (2023).

Discussion

This study demonstrates that variation in hydrologic connectivity at stream–lake transition zones shape nearshore metabolism and littoral habitat conditions in oligotrophic mountain lakes. Our monitoring period captured a dry-to-wet "hydroclimate whiplash event" in the Pacific Southwest (Swain et al. 2025), enabling us to evaluate how streamflow, precipitation, water temperature, and benthic light availability interact to shape nearshore ecological processes at both ends of the hydroclimatic extremes in Lake Tahoe. Our results showed how littoral productivity in oligotrophic lakes varies along shorelines and responds differently to streamflow and precipitation, depending on the proximity to streams inflows and hydroclimatic conditions. Nearshore areas adjacent to stream inflows had lower net ecosystem productivity (NEP) fluxes, with heterotrophic metabolism regimes. During the drought year, streamflow exhibited localized and relatively modest effects on gross primary production (GPP) and ecosystem respiration (ER). In contrast, the wet year intensified hydrologic connectivity, amplifying the effect of streamflow on metabolism; when we observed a 68% increase in the suppressive influence of streamflow on nearshore GPP at the large inflow site, and a 62% decrease in the strength of the positive association between streamflow and GPP at the small inflow. Concurrently, the role of precipitation in modifying physical habitat conditions (e.g., water temperature and benthic light) increased in the wet year. Precipitation-driven cooling of benthic waters increased by up to 83%, precipitation-based reduction in benthic light availability increased by up to 60%. This shift suggests that under wetter hydroclimatic conditions, precipitation may supersede streamflow as the dominant control on light and temperature regimes in the nearshore, thereby altering the spatial patterning of NEP—suppressing it near stream mouths while enhancing it at hydrologically isolated shores. These findings underscore the importance of accounting for both spatial heterogeneity and interannual variability in hydrologic forcing when evaluating lake–stream connectivity and its ecosystem-level consequences.

Effects of variation in precipitation on streamflow and nearshore littoral habitat conditions

Even within a single mountain lake basin, nearshore sites exhibited pronounced spatiotemporal variation in hydrologic dynamics across contrasting water years. Shifts from a drought year to a substantially wetter year altered the timing and magnitude of streamflow inputs affecting nearshore environmental conditions. All nearshore locations (with or without stream inflows) were subject to prolonged spring run-off conditions following the historic winter conditions observed in water year 2023 (Supporting Information Fig. S11), likely leading to elevated material transport as well as enhanced turbulent mixing (Langlois et al. 2005; Ohara et al. 2011). In the wetter year, both of our study catchments experienced marked increases in snowpack storage (65%) and surface water yield (56%) relative to the dry year. Mean daily precipitation was more strongly related to streamflow dynamics during the dry water year, especially in the smaller, drier catchment (GB), while the greater snowpack accumulation on the west shore of Lake Tahoe that supports larger inflowing streams, as well as the delayed timing of peak flow during the wet year, likely caused individual precipitation events to become less correlated to streamflow generation in the larger stream.

When comparing the relative importance of lake vs. stream-driven processes in regulating productivity at the stream–lake transition zone, we found that both the strength and direction of these influences varied with shore location and hydroclimatic context. During the drought year, GPP was negatively associated with streamflow at the large inflow but positively associated with streamflow at the small inflow, with both relationships intensifying in wet conditions. At the streamflow-isolated site (SS), GPP and ER were largely unresponsive to temperature and instead showed stronger temporal autocorrelation and a consistent negative association with light across both years. These results indicate that ER at sites with stream inflows is more responsive to hydrologic conditions during dry years, while in wetter years, light and legacy effects (e.g., lagged ER) become more dominant, particularly at less hydrologically connected locations. Together, these patterns suggest that nearshore metabolism is increasingly coupled to hydrologic forcing in areas with greater stream influence, while isolated shorelines remain more tightly associated with local light and temperature regimes.

Controls on oligotrophic mountain lake nearshore metabolic processes

Lake Tahoe is a large, high elevation lake renowned for its clarity; thus, it is likely that ultraviolet solar radiation in summertime suppresses GPP by limiting algal accrual and photosynthesis (Vinebrooke and Leavitt 1996; Huovinen and Goldman 2000; Tank et al. 2003). Streamflow effects on nearshore benthic light availability were dependent on the hydroclimatic context and reflected the differences in snowmelt-fed inputs. Within a year, streamflow magnitude and light were positively related at nearshore locations near inflowing streams, but this is likely driven by concurrent increases in day length, solar radiation, and thereby increased snowmelt contributions to streamflow during the spring (Ohara et al. 2011; Kirchner et al. 2020). Despite the positive relationship between streamflow and light, the amount of light reaching the benthic lake environment declined substantially. Similarly, light attenuation increased at the nearshore locations adjacent to inflowing streams in the wet year, especially compared to the nearshore location isolated from inflowing stream contributions. These increases in light attenuation at inflowing streams are likely because of increased fine particulate and sediment loading from the catchments which decrease lake clarity (Reuter and Miller 2000; Langlois et al. 2005; Coats et al. 2016).

In large oligotrophic mountain lakes, streamflow can exert a uniquely powerful influence on nearshore metabolic processes by delivering organic matter and nutrient inputs, alongside hydrologic flushing that can favor ER over GPP (Paul and Hall Jr 2002; Langlois et al. 2005; Roberts et al. 2018). In Lake Tahoe, we found nearshore areas with stream inflows tended to support higher ER, while areas away from stream inflows tended to support higher GPP and NEP. Large inflows in clear lakes draining temperate, snow-dominated forests can cause flushing around the stream-to-lake transition zone, which can decrease primary producer biomass, dilute nutrient concentrations, lower water temperature, and ultimately reduce GPP (Paul and Hall Jr 2002). We found that nearshore locations near inflowing streams had $\sim 70\%$ higher sediment organic matter concentrations relative to areas away from streams and higher fluxes of ER relative to GPP, suggesting more heterotrophic metabolism regimes. These dynamics were especially true for the larger stream, which had the highest degree of connectivity to the nearshore. While all nutrient concentrations in both surface and pore water samples were relatively low, the combinations of paired stream and non-stream locations on the east and west shores of the lake demonstrated that nearshore locations with stream inflows (BW and GB) had higher mean NO_3^--N and DOC concentrations relative to locations isolated from stream inflows (SS and SH; Supporting Information Table S4). Nutrient concentration variation in response to streamflow was notably stronger for the larger, wetter west shore sub-catchment (BW) as compared to the smaller, drier east shore sub-catchment (GB; Supporting Information Fig. S10).

These observations support similar work in mountain lakes where drier years favored higher GPP fluxes, while wetter hydroclimatic conditions favored higher ER fluxes, especially in the littoral areas closer to inflowing streams (Scordo et al. 2022a). Drier years in oligotrophic mountain lakes have been associated with greater algal productivity due to warmer water temperatures and enhanced contributions from nutrient-rich groundwater discharge (Périllon et al. 2017; Naranjo et al. 2019). Most mountainous regions in the United States are experiencing decreased snowpack persistence and earlier onset of melt (Musselman et al. 2021; Siirila-Woodburn et al. 2021; Hale et al. 2023), subsequently altering the timing and amount of surface water and solutes to lake ecosystems from year to year (Dodds et al. 2019; Oleksy et al. 2021a; Dettinger and Rajagopal 2023). Therefore, projected climate trends of greater hydroclimatic volatility (Swain et al. 2025) as well as warmer temperatures, lengthier droughts, lower streamflow, and enhanced groundwater nutrient delivery in mountain basins (Naranjo et al. 2019; Vadeboncoeur et al. 2021; Musselman et al. 2021) may facilitate more gross primary productivity in the nearshore of oligotrophic mountain lakes. Given the causal influences of streamflow on nearshore metabolism and water temperature, exploring other fine spatial scale processes (e.g., groundwater inflows, offshore circulation) would offer valuable insight into other key drivers of benthic metabolic regimes.

Conclusion

Mountain lakes are sentinels of environmental change (Moser et al. 2019). While internal lake processes modify whole-lake (i.e., both pelagic and benthic) responses to global change (Baron and Caine 2000), the nearshore (i.e., littoral) zone around the edges of mountain lakes may be more susceptible to changes brought on by increasing hydroclimatic volatility (Scordo et al. 2022a). In this study, we captured a dry-to-wet hydroclimate whiplash event in the Pacific Southwest (Swain et al. 2025) that substantially increased streamflow to the nearshore of Lake Tahoe. Streamflow dictates how materials enter aquatic ecosystems and can also directly facilitate or suppress benthic productivity. Streamflow responses to changing snow dynamics can be highly variable across small (e.g., sub-catchment) spatial scales despite similar regional precipitation patterns (Kirchner et al. 2020; Gordon et al. 2022). Our results highlighted how hydrologic variation in stream inflows can lead to variation in carbon cycling and primary productivity on sub-annual timescales (i.e., weeks to months). For example, algal productivity in the nearshore can respond more rapidly to hydrological changes relative to pelagic phytoplankton productivity (Scordo et al. 2022a), leading to shifts in the benthic community assembly that can alter nitrogen availability (Reuter et al. 1986; Oleksy et al. 2021b; Atkins et al. 2021).

While we acknowledge that some unexplained variation in the nearshore metabolism in this study may reflect unmeasured factors such as benthic grazing or lateral mixing, these findings advance our understanding of how benthic productivity in the nearshore varies with proximity to stream inflows across contrasting hydrologic regimes. We show that even low-order streams can measurably influence nearshore metabolic dynamics, and that the magnitude and direction of this influence can differ markedly among tributaries within a single lake. These results underscore the heterogeneity of nearshore ecosystem function and highlight the importance of considering fine-scale spatial variation along complex lake shorelines. Improved mechanistic understanding of these transition zones will be critical for forecasting changes in carbon cycling and primary production in freshwater systems increasingly shaped by hydroclimatic volatility.

Author Contributions

Kelly Loria is the lead and corresponding author; Conceptualization (equal); Funding Acquisition (supporting); Data Curation (equal); Methodology—sample acquisition (equal); Methodology—metabolism modeling (lead); Formal Analysis (lead); formal analysis (lead); writing; original draft (lead); writing—review and editing (equal). Heili Lowman: Conceptualization (equal); Funding Acquisition (supporting); Data Curation (equal); sample acquisition (equal); metabolism modeling (supporting); Formal Analysis (supporting); writing; original draft (supporting); writing—review and editing (equal). Jasmine Krause: Data Curation (equal); sample acquisition (equal); writing—review and editing (equal). Leon Katona: Conceptualization (supporting); Methodology—sample acquisition (equal); writing; original draft (supporting); writing—review and editing (equal). Ramon Naranjo: Conceptualization (supporting); writing—review and editing (equal). Facundo Scordo: Conceptualization (supporting); Methodology—metabolism modeling (equal); Formal Analysis (supporting); writing—review and editing (equal). Adrian Harpold: Conceptualization (supporting); Formal Analysis (supporting); writing—review and editing (equal). Sudeep Chandra: Conceptualization (equal); Funding Acquisition (supporting); writing—review and editing (equal). Joanna R. Blaszczak:

Conceptualization (equal); Funding Acquisition (lead); metabolism modeling (supporting); Formal Analysis (supporting); writing; original draft (supporting); writing—review and editing (equal).

Acknowledgments

We thank the Blaszczak laboratory members, Rob Miller, Meredith Brehob, Helen Lei, Taryn Elliott, Ian Halterman, Molly Ferro, Keenan Seto, Wubneh Belete Abebe, Rija Masroor, and Dillon Ragar, as well as winter divers Monique Rydel Fortner and Seth Jones from Marine Taxonomic Services, for their help in collecting and processing survey data. We thank the University of Nevada, Ren's Global Water Center and the Chandra Lab team, especially Emily Carlson, Erin Suenaga, Elizabeth Everest, and Zach Bess; the Tahoe Regional Planning Agency; Kris Morehead; Tahoe National Forest; and the residents of Glenbrook, Nevada, especially Gary and Susan Clemons, for their support and collaboration. We further thank David Smith and Kathi Jo Jankowski for their insightful feedback during the U.S. Geological Survey internal review, the three anonymous reviewers, and David Hambright at Limnology and Oceanography for comments that greatly improved this manuscript. This work was supported by the National Science Foundation (NSF) under award OIA-2019528 and by the Nevada Division of State Lands. Kelly Loria was supported by an NSF Graduate Research Fellowship (No. 2020000930863). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Conflicts of Interest

None declared.

References

Adrian, R., C. M. O'Reilly, H. Zagarese, et al. 2009. "Lakes as Sentinels of Climate Change." *Limnology and Oceanography* 54, no. 6part2: 2283–2297. https://doi.org/10.4319/lo.2009.54.6_part_2.2283.

Atkins, K. S., S. H. Hackley, B. C. Allen, S. Watanabe, J. E. Reuter, and S. G. Schladow. 2021. "Variability in Periphyton Community and Biomass Over 37 Years in Lake Tahoe (CA-NV)." *Hydrobiologia* 848: 1755–1772. https://doi.org/10.1007/s10750-021-04533-w.

Baron, J. S., and N. L. Caine. 2000. "Temporal Coherence of Two Alpine Lake Basins of the Colorado Front Range, USA." *Freshwater Biology* 43, no. 3: 463–476. https://doi.org/10.1046/j.1365-2427.2000.00517.x.

Beaudoing, H., M. Rodell, and NASA/GSFC/HSL. 2020. GLDAS Noah Land Surface Model L4 3 Hourly 0.25 × 0.25 Degree V2.1. Greenbelt, MD: Goddard Earth Sciences Data and Information Services Center (GES DISC). https://doi.org/10.5067/E7TYRXPJKWOQ.

Bernhardt, E. S., J. R. Blaszczak, C. D. Ficken, M. L. Fork, K. E. Kaiser, and E. C. Seybold. 2017. "Control Points in Ecosystems: Moving Beyond the Hot Spot Hot Moment Concept." *Ecosystems* 20: 665–682. https://doi.org/10.1007/s10021-016-0103-y.

Blaszczak, J. R., M. K. Steele, B. D. Badgley, et al. 2018. "Sediment Chemistry of Urban Stormwater Ponds and Controls on Denitrification." *Ecosphere* 9, no. 6: e02318. https://doi.org/10.1002/ecs2.2318.

Brown, C. J., C. Saint Ange, R. M. Connolly, et al. 2023. "Ecosystem Services in Connected Catchment to Coast Ecosystems: Monitoring to Detect Emerging Trends." *Science of the Total Environment* 869: 161670. https://doi.org/10.1016/j.scitotenv.2023.161670.

Bürkner, P. 2021. "Bayesian Item Response Modeling in R with Brms and Stan." *Journal of Statistical Software* 100, no. 5: 1–54. https://doi.org/10.18637/jss.v100.i05.

California Department of Water Resources. 2023. *Water Year 2023 Wrap-Up Brochure*. https://water.ca.gov/-/media/DWR-Website/Web-Pages/Water-Basics/Drought/Files/Publications-And-Reports/Water-Year-2023-wrap-up-brochure_01.pdf.

Carter, M. R., and E. G. Gregorich, eds. 2007. Soil Sampling and Methods of Analysis. Boca Raton: CRC Press. https://doi.org/10.3923/pjbs.2007.4391.4398.

Cavalcanti, J. R., D. da Motta-Marques, and C. R. Fragoso Jr. 2016. "Process-Based Modeling of Shallow Lake Metabolism: Spatio-Temporal Variability and Relative Importance of Individual Processes." *Ecological Modeling* 323: 28–40. https://doi.org/10.1016/j.ecolmodel.2015.11.010.

Coats, R., M. Larsen, A. Heyvaert, J. Thomas, M. Luck, and J. Reuter. 2008. "Nutrient and Sediment Production, Watershed Characteristics, and Land Use in the Tahoe Basin, California-Nevada 1." *JAWRA Journal of the American Water Resources Association* 44, no. 3: 754–770. https://doi.org/10.1111/j.1752-1688.2008.00203.x.

Coats, R., J. Lewis, N. Alvarez, and P. Arneson. 2016. "Temporal and Spatial Trends in Nutrient and Sediment Loading to Lake Tahoe, California-Nevada, USA." *JAWRA Journal of the American Water Resources Association* 52, no. 6: 1347–1365. https://doi.org/10.1111/1752-1688.12461.

DeCicco, L., R. Hirsch, D. Lorenz, D. Watkins, and M. Johnson. 2024. dataRetrieval: R Packages for Discovering and Retrieving Water Data Available from US Federal Hydrologic Web Services (Version 2.7.15). Reston, VA: US Geological Survey.

Dettinger, M., and S. Rajagopal. 2023. Simulated Hydrologic Responses to ClimateChange Projections for the Lake Tahoe Basin (Desert Research Institute Publication 41292). Nevada, USA: Zenodo. https://doi.org/10.5061/dryad.2v6wwpzrg.

Devlin, S. P., M. J. Vander Zanden, and Y. Vadeboncoeur. 2016. "Littoral-Benthic Primary Production Estimates:

Sensitivity to Simplifications with Respect to Periphyton Productivity and Basin Morphometry." *Limnology and Oceanography: Methods* 14, no. 2: 138–149. https://doi.org/10.1002/lom3.10080.

Dodds, W. K., L. Bruckerhoff, D. Batzer, et al. 2019. "The Freshwater Biome Gradient Framework: Predicting Macroscale Properties Based on Latitude, Altitude, and Precipitation." *Ecosphere* 10, no. 7: e02786. https://doi.org/10.1002/ecs2.2786.

Domagalski, J. L., E. Morway, N. L. Alvarez, J. Hutchins, M. R. Rosen, and R. Coats. 2021. "Trends in Nitrogen, Phosphorus, and Sediment Concentrations and Loads in Streams Draining to Lake Tahoe, California, Nevada, USA." *Science of the Total Environment* 752: 141815. https://doi.org/10.1016/j.scitotenv.2020.141815.

Gelman, A., B. Goodrich, J. Gabry, and A. Vehtari. 2019. "R-Squared for Bayesian Regression Models." *The American Statistician* 73: 307–309. https://doi.org/10.1080/00031305.2018.1549100.

Gordon, B. L., P. D. Brooks, S. A. Krogh, et al. 2022. "Why Does Snowmelt-Driven Streamflow Response to Warming Vary? A Data-Driven Review and Predictive Framework." *Environmental Research Letters* 17, no. 5: 053004. https://doi.org/10.1088/1748-9326/ac64b4.

Hale, K. E., K. S. Jennings, K. N. Musselman, B. Livneh, and N. P. Molotch. 2023. "Recent Decreases in Snow Water Storage in Western North America." *Communications Earth & Environment* 4, no. 1: 170. https://doi.org/10.1038/s43247-023-00751-3.

Hanson, P. C., M. L. Pace, S. R. Carpenter, J. J. Cole, and E. H. Stanley. 2015. "Integrating Landscape Carbon Cycling: Research Needs for Resolving Organic Carbon Budgets of Lakes." *Ecosystems* 18: 363–375. https://doi.org/10.1007/s10021-014-9826-9.

Hoellein, T. J., D. A. Bruesewitz, and D. C. Richardson. 2013. "Revisiting Odum (1956): A Synthesis of Aquatic Ecosystem Metabolism." *Limnology and Oceanography* 58, no. 6: 2089–2100. https://doi.org/10.4319/lo.2013.58.6.2089.

Hofmann, H., A. Lorke, and F. Peeters. 2008. Temporal Scales of Water-Level Fluctuations in Lakes and their Ecological Implications, 85–96. Netherlands: Springer. https://doi.org/10.1007/s10750-008-9474-1.

Hotchkiss, E. R., S. Sadro, and P. C. Hanson. 2018. "Toward a More Integrative Perspective on Carbon Metabolism Across Lentic and Lotic Inland Waters." *Limnology and Oceanography Letters* 3, no. 3: 57–63. https://doi.org/10.1002/lol2.10081.

Hufkens, K. 2022. *snotelr: A Toolbox to Facilitate Easy SNOTEL Data Exploration and Downloads in R* https://doi.org/10.5281/zenodo.7012728.

Huovinen, P. S., and C. R. Goldman. 2000. "Inhibition of Phytoplankton Production by UV-B Radiation in Clear Subalpine Lake Tahoe, California-Nevada." *SIL Proceedings, 1922–2010* 27, no. 1: 157–160. https://doi.org/10.1080/03680770.1998.11901217.

Jankowski, K. J., F. H. Mejia, J. R. Blaszczak, and G. W. Holtgrieve. 2021. "Aquatic Ecosystem Metabolism as a Tool in Environmental Management." *WIREs Water* 8, no. 4: e1521. https://doi.org/10.1002/wat2.1521.

Johengen, T. H., B. A. Biddanda, and J. B. Cotner. 2008. "Stimulation of Lake Michigan Plankton Metabolism by Sediment Resuspension and River Runoff." *Journal of Great Lakes Research* 34, no. 2: 213–227. https://doi.org/10.3394/0380-1330(2008)34[213:SOLMPM]2.0.CO;2.

Jones, N. E. 2010. "Incorporating Lakes Within the River Discontinuum: Longitudinal Changes in Ecological Characteristics in Stream–Lake Networks." *Canadian Journal of Fisheries and Aquatic Sciences* 67, no. 8: 1350–1362. https://doi.org/10.1139/F10-069.

Kirchner, J. W., S. E. Godsey, M. Solomon, R. Osterhuber, J. R. McConnell, and D. Penna. 2020. "The Pulse of a Montane Ecosystem: Coupling Between Daily Cycles in Solar Flux, Snowmelt, Transpiration, Groundwater, and Streamflow at Sagehen Creek and Independence Creek, Sierra Nevada, USA." *Hydrology and Earth System Sciences* 24, no. 11: 5095–5123. https://doi.org/10.5194/hess-24-5095-2020.

Langlois, J. L., D. W. Johnson, and G. R. Mehuys. 2005. "Suspended Sediment Dynamics Associated With Snowmelt Runoff in a Small Mountain Stream of Lake Tahoe (Nevada)." *Hydrological Processes* 19, no. 18: 3569–3580. https://doi.org/10.1002/hyp.5844.

Lefcheck, J. S. 2016. "piecewiseSEM: Piecewise Structural Equation Modeling in R for Ecology, Evolution, and Systematics." *Methods in Ecology and Evolution* 7, no. 5: 573–579. https://doi.org/10.1111/2041-210X.12512.

Loria, K., H. Lowman, J. Blaszczak, and J. Krause. 2025. Nearshore High-Frequency Temporal Water Quality Observations and Process-Based Modeling of Aquatic Ecosystem Metabolism in Lake Tahoe Completed by Members of the Blaszczak Lab at the University of Nevada Reno, 2021–2023 (Version 1). Environmental Data Initiative. https://doi.org/10.6073/pasta/dd1577416e9da88f29da80cef06e510c.

Lottig, N. R., J. S. Phillips, R. D. Batt, et al. 2022. "Estimating Pelagic Primary Production in Lakes: Comparison of ^{14}C Incubation and Free-Water O_2 Approaches." *Limnology and Oceanography: Methods* 20, no. 1: 34–45. https://doi.org/10.1002/lom3.10471.

Miller, W. W., D. W. Johnson, C. Denton, P. S. J. Verburg, G. L. Dana, and R. F. Walker. 2005. "Inconspicuous Nutrient Laden Surface Runoff From Mature Forest Sierran Watersheds." *Water, Air, and Soil Pollution* 163: 3–17. https://doi.org/10.1007/s11270-005-7473-7.

Moser, K. A., J. S. Baron, J. Brahney, et al. 2019. "Mountain Lakes: Eyes on Global Environmental Change." *Global and Planetary Change* 178: 77–95. https://doi.org/10.1016/j.gloplacha.2019.04.001.

Mullahy, J. 1986. "Specification and Testing of Some Modified Count Data Models." *Journal of Econometrics* 33, no. 3: 341–365. https://doi.org/10.1016/0304-4076(86)90002-3.

Musselman, K. N., N. Addor, J. A. Vano, and N. P. Molotch. 2021. "Winter Melt Trends Portend Widespread Declines in Snow Water Resources." *Nature Climate Change* 11, no. 5: 418–424. https://doi.org/10.1038/s41558-021-01014-9.

Naranjo, R. C., R. G. Niswonger, D. Smith, D. Rosenberry, and S. Chandra. 2019. "Linkages Between Hydrology and Seasonal Variations of Nutrients and Periphyton in a Large Oligotrophic Subalpine Lake." *Journal of Hydrology* 568: 877–890. https://doi.org/10.1016/j.jhydrol.2018.11.033.

Odum, H. T. 1956. "Primary Production in Flowing Waters 1." *Limnology and Oceanography* 1, no. 2: 102–117. https://doi.org/10.4319/lo.1956.1.2.0102.

Ohara, N., M. L. Kavvas, D. Easton, E. C. Dogrul, J. Y. Yoon, and Z. Q. Chen. 2011. "Role of Snow in Runoff Processes in a Subalpine Hillslope: Field Study in the Ward Creek Watershed, Lake Tahoe, California, During 2000 and 2001 Water Years." *Journal of Hydrologic Engineering* 16, no. 6: 521–533. https://doi.org/10.1061/(ASCE)HE.1943-5584.0000348.

Oleksy, I. A., S. E. Jones, and C. T. Solomon. 2021*a*. "Hydrologic Setting Dictates the Sensitivity of Ecosystem Metabolism to Climate Variability in Lakes." *Ecosystems* 25: 1–1345. https://doi.org/10.1007/s10021-021-00718-5.

Oleksy, I. A., J. S. Baron, and W. S. Beck. 2021*b*. "Nutrients and Warming Alter Mountain Lake Benthic Algal Structure and Function." *Freshwater Science* 40, no. 1: 88–102. https://doi-org.unr.idm.oclc.org/10.1086/713068.

Paul, M. J., and R. O. Hall Jr. 2002. "Particle Transport and Transient Storage along a Stream-Size Gradient in the Hubbard Brook Experimental Forest." *Journal of the North American Benthological Society* 21, no. 2: 195–205. https://doi.org/10.2307/1468409.

Périllon, C., F. Pöschke, J. Lewandowski, M. Hupfer, and S. Hilt. 2017. "Stimulation of Epiphyton Growth by Lacustrine Groundwater Discharge to an Oligo-Mesotrophic Hard-Water Lake." *Freshwater Science* 36, no. 3: 555–570. https://doi.org/10.1086/692832.

Phillips, J. S. 2020. "Time-Varying Responses of Lake Metabolism to Light and Temperature." *Limnology and Oceanography* 65, no. 3: 652–666. https://doi.org/10.1002/lno.11333.

PRISM Climate Group. 2024. PRISM Climate Data: 30-Year Normals (Version 4.2). Oregon State University, Oregon USA. https://prism.oregonstate.edu/.

R Core Team. 2024. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. https://www.R-project.org/.

Reuter, J. E., S. L. Loeb, and C. R. Goldman. 1986. "Inorganic Nitrogen Uptake by Epilithic Periphyton in a N-Deficient Lake 1." *Limnology and Oceanography* 31, no. 1: 149–160. https://doi.org/10.4319/lo.1986.31.1.0149.

Reuter, J. E., and W. W. Miller. 2000. "Aquatic Resources, Water Quality, and Limnology of Lake Tahoe and its Upland Watershed." In Lake Tahoe Watershed Assessment, vol. 1, 215–399.

Reuter, J. E., and W. W. Miller. 2000. "Aquatic resources, water quality, and limnology of Lake Tahoe and its upland watershed, in Lake Tahoe Watershed Assessment: Volume 1", Gen. Tech. Rep. PSW-GTR-175, edited by D. D. Murphy, and C. M. Knopp, 215–399 pp., Pac. Southwest Res. Stn., For. Serv., U.S. Dep. of Agric., Albany, Calif.

Richardson, J. S., T. Michalski, and M. Becu. 2021. "Stream Inflows to Lake Deltas: A Tributary Junction that Provides a Unique Habitat in Lakes." *Freshwater Biology* 66, no. 11: 2021–2029. https://doi.org/10.1111/fwb.13816.

Roberts, D. C., A. L. Forrest, G. B. Sahoo, S. J. Hook, and S. G. Schladow. 2018. "Snowmelt Timing as a Determinant of Lake Inflow Mixing." *Water Resources Research* 54, no. 2: 1237–1251. https://doi.org/10.1002/2017WR021977.

Rosenberry, D. O., J. Lewandowski, K. Meinikmann, and G. Nützmann. 2015. "Groundwater—The Disregarded Component in Lake Water and Nutrient Budgets. Part 1: Effects of Groundwater on Hydrology." *Hydrological Processes* 29, no. 13: 2895–2921. https://doi.org/10.1002/hyp.10403.

Savoy, P., E. Bernhardt, L. Kirk, M. J. Cohen, and J. B. Heffernan. 2021. "A Seasonally Dynamic Model of Light at the Stream Surface." *Freshwater Science* 40, no. 2: 286–301. https://doi.org/10.1086/714270.

Scordo, F., N. R. Lottig, J. E. Fiorenza, et al. 2022*a*. "Hydroclimate Variability Affects Habitat-Specific (Open Water and Littoral) Lake Metabolism." *Water Resources Research* 58, https://doi.org/10.1029/2021WR031094.

Scordo, F., S. Sadro, J. Culpepper, C. Seitz, and S. Chandra. 2022*b*. "Wildfire Smoke Effects on Lake-Habitat Specific Metabolism: Toward a Conceptual Understanding." *Geophysical Research Letters* 49: e2021GL097057. https://doi.org/10.1029/2021GL097057.

Scott, D. N., and E. E. Wohl. 2017. "Evaluating Carbon Storage on Subalpine Lake Deltas." *Earth Surface Processes and Landforms* 42, no. 10: 1472–1481. https://doi.org/10.1002/esp.4110.

Siirila-Woodburn, E. R., A. M. Rhoades, B. J. Hatchett, et al. 2021. "A Low-To-No Snow Future and Its Impacts on Water Resources in the Western United States." *Nature Reviews Earth and Environment* 2, no. 11: 800–819. https://doi.org/10.1038/s43017-021-00219-y.

Staehr, P. A., E. Asmala, J. Carstensen, D. Krause-Jensen, and H. Reader. 2018. "Ecosystem Metabolism of Benthic and Pelagic Zones of a Shallow Productive Estuary: Spatio-Temporal Variability." *Marine Ecology Progress Series* 601: 15–32. https://doi.org/10.3354/meps12697.

Staehr, P. A., L. S. Brighenti, M. Honti, J. Christensen, and K. C. Rose. 2016. "Global Patterns of Light Saturation and Photoinhibition of Lake Primary Production." *Inland Waters* 6, no. 4: 593–607.https://doi.org/10.1080/IW-6.4.888

Stan Development Team. 2024. *RStan: The R interface to Stan* (Version 2.32.6) [R Package]. https://mc-stan.org/.

Steele, J. H. 1962. "Environmental Control of Photosynthesis in the Sea." *Limnology and Oceanography* 7, no. 2: 137–150. https://doi.org/10.4319/lo.1962.7.2.0137.

Swain, D. L., A. F. Prein, J. T. Abatzoglou, et al. 2025. "Hydroclimate Volatility on a Warming Earth." *Nature Reviews Earth and Environment* 6, no. 1: 35–50. https://doi.org/10.1038/s43017-024-00624-z.

Tank, S. E., D. W. Schindler, and M. T. Arts. 2003. "Direct and Indirect Effects of UV Radiation on Benthic Communities: Epilithic Food Quality and Invertebrate Growth in Four Montane Lakes." *Oikos* 103, no. 3: 651–667. https://doi.org/10.1034/j.1600-0706.2003.12198.x.

U.S. Environmental Protection Agency. 1993*a*. "Method 350.1: Nitrogen, Ammonia (Colorimetric, Automated Phenate)." Revision 2.0. Cincinnati, OH USA.

U.S. Environmental Protection Agency. 1993*b*. "Method 365.1: Determination of phosphorus by semi-automated colorimetry." Revision 2.0. Cinicinnati, OH USA.

U.S. Environmental Protection Agency. 1993*c*. "Method 353.2: Determination of Nitrate-Nitrite Nitrogen by Automated Colorimetry." Revision 2.0. Cincinnati, OH USA.

U.S. Geological Survey. 2024. *USGS Water Data for the Nation: U.S. Geological Survey National Water Information System Database* https://doi.org/10.5066/F7P55KJN.

Vadeboncoeur, Y., E. Jeppesen, M. J. V. Zanden, H. H. Schierup, K. Christoffersen, and D. M. Lodge. 2003. "From Greenland to Green Lakes: Cultural Eutrophication and the Loss of Benthic Pathways in Lakes." *Limnology and Oceanography* 48, no. 4: 1408–1418. https://doi.org/10.4319/lo.2003.48.4.1408.

Vadeboncoeur, Y., J. Kalff, K. Christoffersen, and E. Jeppesen. 2006. "Substratum as a Driver of Variation in Periphyton Chlorophyll and Productivity in Lakes." *Journal of the North American Benthological Society* 25, no. 2: 379–392. https://doi.org/10.1899/0887-3593(2006)25[379:SAADOV]2.0.CO;2.

Vadeboncoeur, Y., M. V. Moore, S. D. Stewart, et al. 2021. "Blue Waters, Green Bottoms: Benthic Filamentous Algal Blooms Are an Emerging Threat to Clear Lakes Worldwide." *Bioscience* 71, no. 10: 1011–1027. https://doi.org/10.1093/biosci/biab049.

Vander Zanden, M. J., and Y. Vadeboncoeur. 2020. "Putting the Lake Back Together 20 Years Later: What in the Benthos Have We Learned about Habitat Linkages in Lakes?" *Inland Waters* 10, no. 3: 305–321. https://doi.org/10.1080/20442041.2020.1712953.

Vehtari, A., A. Gelman, D. Simpson, B. Carpenter, and P. C. Bürkner. 2021. "Rank-Normalization, Folding, and Localization: An Improved $\widehat{R}$ for Assessing Convergence of MCMC (With Discussion)." *Bayesian Analysis* 16, no. 2: 667–718. https://doi.org/10.1214/20-BA1221.

Vinebrooke, R. D., and P. R. Leavitt. 1996. "Effects of Ultraviolet Radiation on Periphyton in an Alpine Lake." *Limnology and Oceanography* 41, no. 5: 1035–1040. https://doi.org/10.4319/lo.1996.41.5.1035.

Ward, N. K., J. A. Brentrup, D. C. Richardson, et al. 2022. "Dynamics of the Stream–Lake Transitional Zone Affect Littoral Lake Metabolism." *Aquatic Sciences* 84, no. 3: 31. https://doi.org/10.1007/s00027-022-00854-7.

Williamson, C. E., J. E. Saros, W. F. Vincent, and J. P. Smol. 2009. "Lakes and Reservoirs as Sentinels, Integrators, and Regulators of Climate Change." *Limnology and Oceanography* 54, no. 6part2: 2273–2282. https://doi.org/10.4319/lo.2009.54.6_part_2.2273.

Winslow, L., J. Read, R. Woolway, et al. 2019. *rLakeAnalyzer: Lake Physics Tools* (R Package Version 1.11.4). https://CRAN.R-project.org/package=rLakeAnalyzer.

Xia, Y., K. Mitchell, M. Ek, et al. 2012. "Continental-Scale Water and Energy Flux Analysis and Validation for the North American Land Data Assimilation System Project Phase 2 (NLDAS-2): 1. Intercomparison and Application of Model Products." *Journal of Geophysical Research: Atmospheres* 117, no. D3: 2011JD016048. https://doi.org/10.1029/2011JD016048.

Supporting Information

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

Submitted 20 January 2025
Revised 10 June 2025
Accepted 18 July 2025