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Hydroclimate Variability Affects Habitat-Specific (Open Water and Littoral) Lake Metabolism

Key Points:

- Within-lake habitats do not have equivalent responses to climate forcing
- Primary production and respiration of the littoral habitat shows greater sensitivity to hydroclimate changes than the open water habitat
- Littoral net ecosystem production can change from autotrophic under dry conditions to heterotrophic under wet conditions

Facundo Scordo^{1,2} , Noah R. Lottig³ , Juan E. Fiorenza^{4,5} , Joshua Culpepper^{1,6} , James Simmons¹ , Carina Seitz^{1,2} , Edward M. Krynak^{1,7} , Erin Suenaga¹, and Sudeep Chandra¹

¹Global Water Center and the Department of Biology, University of Nevada, Reno, NV, USA, ²Instituto Argentino de Oceanografía (IADO-CONICET-UNS), Bahía Blanca, Argentina, ³University of Wisconsin Center for Limnology, Wisconsin University, Madison, WI, USA, ⁴CONICET, Universidad de Buenos Aires (UBA), Instituto de Investigaciones Fisiológicas y Ecológicas Vinculadas a la Agricultura, (IFEVA), Buenos Aires, Argentina, ⁵Universidad de Buenos Aires, Facultad de Agronomía, Departamento de Métodos Cuantitativos y Sistemas de Información, Buenos Aires, Argentina, ⁶Division of Hydrologic Sciences at the Desert Research Institute and the Graduate Program in Hydrologic Sciences at the University of Nevada, Reno, NV, USA, ⁷Now at StrEAMS Lab, Department of Biology, University of Waterloo, Waterloo, ON, Canada

Supporting Information:

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

Correspondence to:

F. Scordo,
scordo@agro.uba.ar

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Author Contributions:

Conceptualization: Facundo Scordo, Noah R. Lottig, Joshua Culpepper, James Simmons, Carina Seitz, Edward M. Krynak, Erin Suenaga, Sudeep Chandra
Data curation: Facundo Scordo, Juan E. Fiorenza, Joshua Culpepper, Carina Seitz
Formal analysis: Facundo Scordo, Juan E. Fiorenza, Sudeep Chandra
Funding acquisition: Sudeep Chandra
Investigation: Facundo Scordo, Carina Seitz, Erin Suenaga, Sudeep Chandra
Methodology: Facundo Scordo, Noah R. Lottig, Juan E. Fiorenza, Joshua Culpepper, James Simmons, Edward M. Krynak, Erin Suenaga, Sudeep Chandra

Abstract Lakes integrate the signals of changing hydroclimate in their surrounding basin, which substantially influence gross primary production (GPP), respiration (R), and net ecosystem production (NEP). Most research focuses only on the changes to the open water habitat despite the littoral habitat's importance to lakes and its sensitivity to hydroclimatic variability. We analyze how years with different ice-out dates and snow water equivalent (SWE) triggered different metabolism responses in the open water and littoral habitats of a subalpine lake. The dry (early ice-out date and low SWE) and wet (late ice-out date and high SWE) years had lower GPP and R rates in both habitats compared to the average hydroclimatic year. Furthermore, consumer biomass decreased during dry and wet years. GPP and R reduced the most in the littoral habitat. Consequently, the relative contribution to total lake GPP and R of the littoral habitat decreased, and the contribution of the open water habitat increased during the dry and wet years. We demonstrate that hydroclimatic conditions affect productivity and consumer biomass and show that within-lake habitats do not experience equivalent responses to climate forcing. Our study has implications for how ecosystem scientists and managers quantify the absolute and relative contributions of the littoral habitat to whole lake production in the context of climate variation.

Plain Language Summary Lakes integrate climate variability at the catchment scale. These large-scale changes influence the food production and consumption (i.e., metabolism) of lake habitats both at the nearshore and open water. While the shallow nearshore habitat is recognized as an important site for food production, the offshore habitat remains the focus of many lake studies. We analyzed how years with different climatic conditions (dry and wet) affected metabolism in the nearshore and offshore habitats of a mountain lake. During dry and wet years, the food production and consumption in both habitats was lower compared to a year with average climatic conditions. Furthermore, animal biomass decreased during dry and wet years and the nearshore bottom habitat was more sensitive to changes with a large reduction in food production. We demonstrate that climatic conditions lead to differential impacts within-lake habitats. Thus, lake management may be deficient if only one habitat is studied.

1. Introduction

As sentinel ecosystems, lakes integrate the loading and environmental processes from their surrounding landscapes, reflecting the hydroclimatic contributions from precipitation and temperature (Adrian et al., 2009; Williamson et al., 2008, 2009). In addition, more frequent extreme weather events (e.g., severe and prolonged droughts to intense precipitation in a short period of time) can influence the hydroclimatic exposure of lakes (Melillo, et al., 2014; Williamson et al., 2016). Lakes exhibit complex responses to these extreme weather events, which influence the supply of nutrients to the planktonic ecosystem or alter food web connections (Adrian et al., 2009; Shimoda et al., 2011). For example, warming conditions and changes in precipitation increases lake primary and secondary productivity by increasing lake heat content while at the same time reducing accessibility to productive lake habitats by fishes, which are sensitive to warming waters (Caldwell et al., 2020).

Lakes are spatially heterogeneous ecosystems with nearshore littoral and open water habitats providing different metabolic pathways for autochthonous energy sources (Devlin et al., 2016; Vadeboncoeur et al., 2003; Vander

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Project Administration: Facundo Scordo, Sudeep Chandra
Resources: Sudeep Chandra
Software: Noah R. Lottig
Supervision: Facundo Scordo, Sudeep Chandra
Validation: Juan E. Fiorenza, Edward M. Krynak
Visualization: Facundo Scordo, Juan E. Fiorenza
Writing – original draft: Facundo Scordo, Noah R. Lottig, Juan E. Fiorenza, Joshua Culpepper, James Simmons, Carina Seitz, Edward M. Krynak, Erin Suenaga, Sudeep Chandra
Writing – review & editing: Facundo Scordo, Noah R. Lottig, Juan E. Fiorenza, Joshua Culpepper, James Simmons, Carina Seitz, Edward M. Krynak, Erin Suenaga, Sudeep Chandra

Zanden & Vadeboncoeur, 2020). The littoral habitat gross primary production (GPP) and ecosystem respiration (R) can be seven times higher compared to the open water habitat (Van de Bogert et al., 2007, 2012) and represent up to 50% of the total lake production in large lakes (Brothers et al., 2016). However, the littoral habitats in lakes show lower resilience to changes in hydroclimatic conditions, as they are proximate to the land's edge and have shorter retention times of water, nutrients, and detritus than open water habitats (Jeppesen et al., 2014; Peters & Lodge, 2009). The nearshore littoral habitats are also important for fishes as the benthic macroinvertebrates production is generally higher and more efficiently passed to fish than zooplankton production (Vander Zanden et al., 2007, 2011). Despite the importance of lake littoral habitats and their sensitivity to hydroclimatic variability, most monitoring programs and research continues to focus on the open water habitat (Cantonati & Lowe, 2014; Vadeboncoeur et al., 2014, 2021).

Hydroclimatic conditions modify the balance between GPP and R in lakes (Ask, et al., 2012; Sadro & Melack, 2012), which affects whether an ecosystem serves as a source or sink for atmospheric carbon dioxide (Dodds & Cole, 2007; Engel et al., 2018; McCullough et al., 2018; Tranvik et al., 2018). For example, in temperate oligo-mesotrophic lakes, increasing run-off due to intense precipitation shifts lakes to negative net ecosystem production (NEP; quantified as GPP-R) during the summer when GPP is expected to dominate (Ask et al., 2012; Sadro & Melack, 2012). Greater run-off increases allochthonous organic compounds entering the lake, which stimulates heterotrophic bacterioplankton activity (Ask et al., 2012; Karlsson et al., 2007; McCallister & Del Giorgio, 2008). At the same time, suspended particles reduce light penetration and decrease benthic periphyton GPP (Ask et al., 2009, 2012; Vadeboncoeur et al., 2014). Increasing water temperature enhances GPP at the beginning of the growing season while providing higher potential growth rates for the zooplankton and benthic macroinvertebrates communities, which in turn, reduces GPP by the end of the summer season (Caldwell et al., 2020; Park et al., 2004). Therefore, understanding the role of lakes in processing carbon and whether they serve as net carbon sinks or sources to the atmosphere relies on understanding the drivers of a lake's metabolic processes and how those drivers vary under different hydroclimatic conditions (Staehr et al., 2012; Tranvik et al., 2018).

Climate and ecoregion characterize the influence of hydroclimate on open water productivity. Ice out and snow water equivalent (SWE) influence important drivers of carbon processing (i.e., water temperature, nutrient and light availability, biomass, and community composition of consumers) in western mountain lakes of the United States (Melack et al., 2020; Sadro et al., 2018). Accumulated SWE at the start of ice break-up functions as a surrogate for lake inflow during the spring (Goldman et al., 1989). Ice-out date and SWE at the start of ice break-up have been shown to affect inter-annual open water productivity, including the amount and timing of peak GPP and R (Goldman et al., 1989; Jassby et al., 1990; Park et al., 2004; Strub et al., 1985). When the ice break-up period starts, water influx flushes nutrients and algae from the lake, altering the initial conditions for summer production (Goldman et al., 1989). Higher accumulated SWE results in a stronger flush (Goldman et al., 1989; Melack et al., 2020). Late ice-out date lowers heat content during the summer and shortens recovery time for primary producers, resulting in lower open water productivity (Goldman et al., 1989; Park et al., 2004; Strub et al., 1985). Early ice-out allows producers more recovery time and the lake has more time to incorporate heat, resulting in higher metabolic rates (Goldman et al., 1989; Park et al., 2004; Strub et al., 1985). However, a long ice-free season may result in nutrient depletion and a high consumer grazing rate (Carter & Schindler, 2012; Jassby et al., 1990; Park et al., 2004), which will affect the open water pelagic primary producers, causing metabolic rates to decrease. Comparatively, little is known about the effects of variable hydroclimatic regimes on the littoral habitats within lakes or how yearly variability in hydroclimate may affect the relative contribution of the littoral habitat compared to the open water from a standpoint of GPP, R, and NEP.

Lake metabolism provides a framework for understanding the balance of carbon fixation (GPP) and oxidation (R) in lake ecosystems. There is a long history of quantifying metabolism in lakes to understand the spatial and temporal variation within and among lakes, drivers of metabolism at different spatial scales (Alfonso et al., 2018; Hanson et al., 2008; Idrizaj et al., 2016; Staehr et al., 2012; Stefanidis & Elias, 2019). However, quantifying how years with different hydroclimatic conditions influence metabolism in littoral and open water lake habitats has not been addressed to date despite the relatively larger contribution of littoral habitats to whole lake function. With changes to hydroclimate due to anthropogenically driven climate change and the repeated observation that littoral production contributes to whole ecosystem function, studies are warranted that describe hydroclimatic

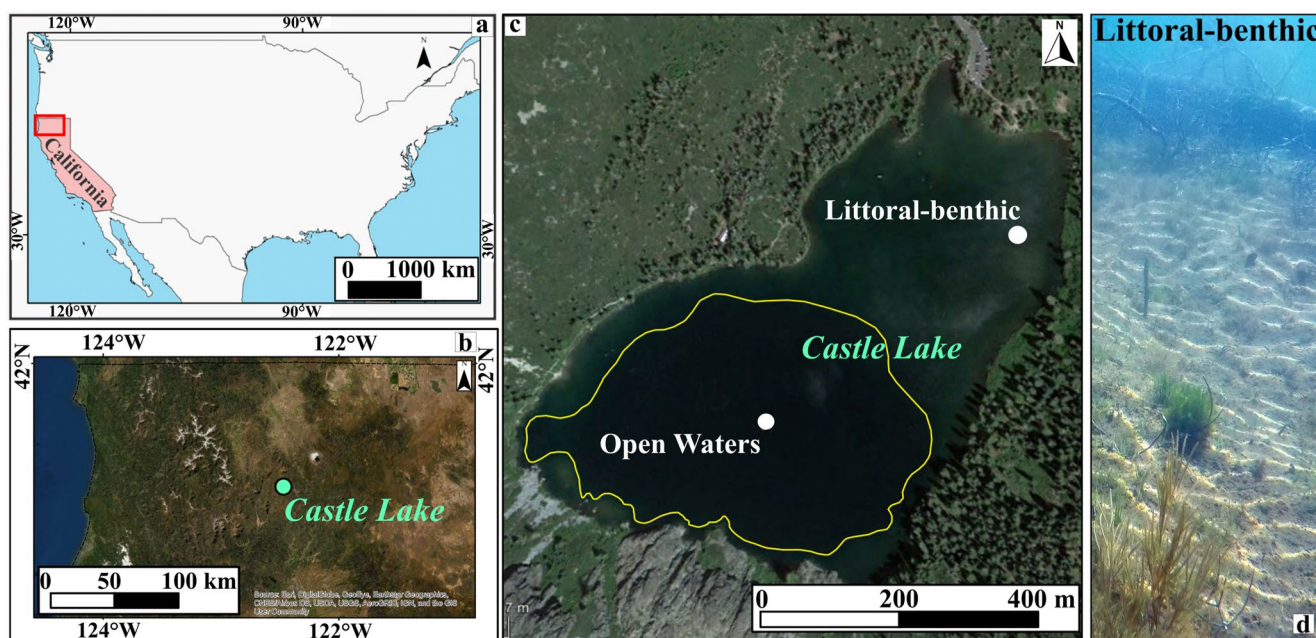


Figure 1. (a) Location of the study area in the state of California (USA). (b) Location of Castle Lake in northern California. (c) Location of the sensors (white dots) within the littoral and open water habitats where metabolism was calculated at Castle Lake. (d) Photo of the water column at the littoral habitat dominated by fine-organic sediments, regular terrestrial leaf inputs and inputs from groundwater seepage.

connections to these habitats, and how changing metabolic rates affect energy flow to consumers (Caldwell et al., 2020; Rüegg et al., 2021).

In this study, we analyze how years with different hydroclimates, specifically ice-out dates and SWE, triggered different metabolism responses in the open water and habitats of a subalpine lake. This paper (a) quantifies the absolute and relative metabolic rates in the littoral and open water habitats in years characterized by dry, average, and wet hydroclimates; (b) identifies if littoral and open water habitat-specific metabolism have differential responses to different hydroclimate conditions; (c) discusses the influence of metabolic changes on the invertebrate community and their potential feedbacks to our metabolic calculations, and (d) provides a conceptual model that incorporates our findings which can be tested in other lake ecosystems.

2. Methods

2.1. Study Sites

We carried out the study at Castle Lake, a meso-oligotrophic, dimictic, subalpine lake (1,646 m.a.s.l., surface area of 0.2 km², max depth = 35 m, and mean depth = 11.4 m) located in northern California, USA (41°13' N, 122°22' W; Figures 1a and 1b). Castle Lake is seasonally ice-covered (typically end of November to May), with an ice-free summer season that averages 135 days. We calculated metabolism (GPP, R, and NEP) during August and September (summer) because productivity reaches its peak in Castle Lake during this period.

We quantified metabolism in a nearshore littoral habitat and in the epilimnion of the open water habitat at an index station at the deepest point of the lake (Figure 1c). The index station is part of a long-term monitoring program whereas the littoral collections have only started in the last half decade. The nearshore littoral habitat depth ranges from 0 to 6 m, and its extension from the coast varies between 10 meters (southwest of the lake) and 100 meters (northeast of the lake). The lake littoral metabolism was measured at the north-east region of the lake at 30 meters from the coast. The littoral habitat contains some submerged macrophytes, woody debris, and sediments composed of clay-silt with 13% organic matter. Alder trees (*Alnus tenuifolia* Nutt.), the predominant vegetation near this site, provide the lake with nitrogen (Goldman, 1961), which is the main nutrient limiting open water phytoplankton production in this lake (Axler & Goldman, 1981; Axler et al., 1981).

Table 1
Hydroclimatic Differences in the Dry (2015), Average (2016), and Wet (2019) Years Included in the Study

Hydroclimatic variables	2015 (dry)	2016 (average)	2019 (wet)
Ice out date (ordinal date)	February 20 (51)	April 20 (111)	June 1 (152)
Snow water equivalent by the date ice-out started	4 mm	743 mm	1,047 mm

We quantified the influence of different hydroclimatic years (dry 2015; wet 2019; average 2016), on summer metabolic rates. We defined the hydroclimate conditions of dry, wet, and average based on the ice-out date and the snow water equivalent (SWE) at the time of ice-out each year (Table 1). We defined the early, average, and late ice-out date based on Castle Lake's 58-year ice-out date data, which ranged from February 20 to June 27, with a mean ice-out date on May 9. Daily time lapse photographs were used to determine the ice-out (80% of the surface free of ice) date each year. SWE (<https://nsidc.org/data/g02158>) was recorded when ice break-up started based on the above photographic time lapse records, which typically started one month prior to the lake being completely ice free.

2.2. Metabolism Model Data Sampling

The metabolism model used in this study is based on high-frequency measurements of dissolved oxygen (mg L^{-1}), water temperature ($^{\circ}\text{C}$), photosynthetically active radiation (PAR; $\mu\text{mol m}^{-2} \text{s}^{-1}$), wind speed (m s^{-1}), and barometric pressure (mbar). Dissolved oxygen and water temperature were measured every 10 min at a depth of 3 m at both the sites using an optical oxygen probe (PME miniDOT Logger). Wind speed and PAR were measured hourly at a weather station (Weatherhawk) on the shore of Castle Lake located 4 m above ground level. Light (PAR; 400–700 nm) and temperature profiles (every 0.5 m) were obtained weekly using a Biospherical Instruments 2104P radiometer at an index station in the open water at the deepest part of the lake. The raw, high-frequency time series of dissolved oxygen and water temperature were filtered to remove outliers by excluding values that were greater than 3 and 5 standard deviations respectively from a 7-day running average (Supporting Information S1). Finally, we averaged the 10-min measurements to an hourly scale to match the data resolution of the weather station.

Epilimnetic depth (m) was calculated from water temperature profile using rLakeAnalyzer (Winslow et al., 2019). At the littoral sites, we set epilimnetic depth as a fixed value corresponding to the maximum depth of this habitat (3 m) when epilimnetic depth was larger than 3 m. Light extinction coefficients (m^{-1}) were calculated from light profiles (Wetzel, 2009). Epilimnetic depth and extinction coefficients were linearly interpolated at hourly time steps and combined with PAR to estimate the average light levels within the epilimnion of the lake (Phillips, 2020; Staehr et al., 2012). We estimated gas exchange with the atmosphere (m hr^{-1}) using the LakeMetabolizer R package (Vachon & Prairie, 2013; Winslow et al., 2016).

We implemented a time-varying ecosystem metabolism model (Lottig et al., 2021; Phillips, 2020) to generate daily estimates ($\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$) of gross primary production (GPP), respiration (R), and net ecosystem production (NEP; $\text{NEP} = \text{GPP} - \text{R}$), using the data previously described. This model differs from many other models (e.g., LakeMetabolizer R package) in that instead of fitting each day individually, this model uses the entire time series to generate daily metabolism estimates. Model parameters are also constrained to ecologically feasible ranges (i.e., GPP and R must be positive and negative respectively).

The model (Lottig et al., 2021), uses a photoinhibition P-I curve (Steele, 1962) to describe the relationship between GPP and light:

$$P_I = P_{\max} \frac{I}{I_{\text{opt}}} \exp \left(1 - \frac{I}{I_{\text{opt}}} \right) \quad (1)$$

where P_I is the production rate at light intensity I , $P_{\max}$ is the maximum production rate, and I_{opt} is the optimal light intensity. This photoinhibition model was chosen because recent work by Staehr et al. (2016) found that photoinhibition often occurred in lakes and in situ ^{14}C production estimates in Castle Lake show evidence of photoinhibition as well (Huovinen et al., 1999). We used the Steele (1962) formulation because it is a simple (two-parameter) model, which increased the ease of fitting over more complex models with a greater number of

parameters. It is often difficult to identify statistical differences among different model formulations when fit to real data (Aalderink & Jovin, 1997) suggesting that the simple model will perform similarly to its more complex counterparts. We allowed $P_{\max}$, I_{opt} , and the respiration coefficient (see Phillips, 2020 for model formulation) to vary through time at a daily time scale. The degree of autocorrelation in the parameters through time was constrained by hierarchical variance parameters in the random walk components of the model. The random walk variances were selected manually such that the model converged while producing meaningful temporal smoothing in the parameters of the photoinhibition curve (Lottig et al., 2021).

Observed dissolved oxygen time series were fit to all years (2015, 2016, and 2019) simultaneously. The model was fit via Stan (Stan Development Team, 2020) run in *R* (R Core Team, 2020) using the *rstan* package as described in Phillips (2020), and Lottig et al. (2021). Posterior median values were used for daily GPP, *R*, and NEP values. Model fits were validated by checking effective sample size, $\hat{R}$, tree depth, energy Bayesian Fraction of Missing Information, and divergence (Betancourt, 2007).

Metabolic rate offered an avenue to calculate total quantities of whole-lake, epilimnetic metabolism ($\text{mmol O}_2 \text{ d}^{-1}$). We calculated the product of the metabolic rates ($\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$) and the volume (m^3) in each habitat (i.e., littoral and open water) separately, and then summed the littoral and open water values. From the bathymetric map of Castle Lake, the littoral (depth ≤ 6 m) and the open water (depth > 6 m) fraction each makes up 50% of the lake area ($107,000 \text{ m}^2$) (Vander Zanden et al., 2007). We assume that the areal extent of the habitats does not change throughout the period of the study. We used a hypsographic curve of Castle Lake to determine the total water volume of the littoral and open water epilimnetic habitats. We multiplied the area of the littoral-bottom and open water habitats with a time series of the mixed depth, which provided a volume for a given mixed depth. The daily volumetric rates obtained from the model at both sites were multiplied by the volume of each habitat to obtain total habitat metabolism. Here, we present the proportion of total GPP, *R*, and NEP contributed by each site during the study period (August to September) by summing the daily values of total littoral and open water metabolism.

2.3. Physical Variables

We analyzed the daily mean water temperature at the depth the dissolved oxygen sensors were placed (3 m) and epilimnetic PAR to study the relationship of these variables on metabolism estimates. Night values ($0 \mu\text{mol m}^{-2} \text{ s}^{-1}$) were excluded when calculating the daily light values.

2.4. Zooplankton and Benthic Macroinvertebrates

Zooplankton were collected biweekly from July to September, in mid-day and after dark, using a 12 L Schindler trap from the epilimnion of the open water site. Since zooplankton in Castle Lake express a strong diel vertical migration (Redfield & Goldman, 1978), mean estimates are obtained from the day and night collections. Zooplankton were identified to genus, and biomass ($\mu\text{g L}^{-1}$) was estimated using density-dry mass regressions determined previously for Castle Lake zooplankton (Redfield & Goldman, 1978). Community composition was determined as the proportion of group-specific biomass (*Daphnia* sp., *Bosmina* sp., *Holopedium* sp., *Diacyclops* sp., *Diaptomus* sp.).

Benthic macroinvertebrates were collected once per month in July and September at the littoral site (Figures 1c and 1d). Three subsamples using an Ekman grab sampler (0.023 m^2) were combined into one sample. Results from monthly samples were integrated by summation in each year and treated as a single sample. Benthic macroinvertebrate individuals were identified to the family, except for Oligochaeta and Hirudinea, which were identified to class and subclass, respectively (Thorpe & Covich, 2010), and measured to the nearest 0.1 mm. Benthic macroinvertebrate biomass (mg m^{-2}) was estimated as the product of species average dry mass and population density (Craig et al., 2015; Vander Zanden et al., 2007). Dry mass was estimated from published length to dry mass ratios (Baumgärtner & Rothhaupt, 2003; Benke et al., 1999; Edwards et al., 2009). We classified the taxa into five functional feeding groups (FFG; predators, collector/gatherers, collector/filterers, shredders, and grazers) and analyzed the proportion of each FFG in the total biomass (Merritt et al., 2007). The taxa included in each FFG were: Predators (*Aeshnidae*, *Coenagrionidae*, *Ceratopogonidae*, *Sialidae*, *Libellulidae*, *Rhyacophilidae*, and *Hirudinea*); collector/gatherers (*Baetidae*, *Caenidae*, *Chironomidae*, *Ephemerellidae*, *Leptoceridae*,

Leptophlebiidae, Oligochaeta); collector/filterers (*Pisidiidae*); shredders (*Lepidostomatidae*, *Limnephilidae*, *Sericostomatidae*); and grazers (*Psephenidae*, *Planorbidae*, and *Physidae*).

2.5. Statistical Analyses

Differences among hydroclimatic years in air and water temperature, incident PAR and PAR at 3 m depth, wind intensity, GPP, R, and zooplankton biomass were quantified using linear mixed-effects models (LMM), with year modeled as a fixed effect. We considered the specific covariance structure for repeated-measures data in each model, and when models did not meet the assumption of homoscedasticity, we modeled the variance. Tests for significance of the effects of the years in the models were performed via the Wald statistic (Zuur et al., 2009) using the `glS` function, in the `nlme` R package (Pinheiro et al., 2020). Multiple comparisons among years were performed with Tukey's HSD post hoc test (`emmeans` R package; Lenth, 2021). We analyzed the relative contribution of each site to overall GPP, R, and NEP, by summing the daily values of the two sites (hereafter "whole-lake GPP, R or NEP") during the entire study period and calculating the percentage that each of the sites contributed to the total. Permutational analysis of variance (PERMANOVA) using the `adonis` function, in the `vegan` R package (Anderson, 2017; Oksanen et al., 2019) was used to compare the zooplankton community composition data. All the analyses were performed in the statistical software R (R Core Team, 2020). Data and metadata for this study are available at Scordo et al. (2021).

3. Results

3.1. Hydroclimatic Conditions

We classified three hydroclimatic year conditions during the study period: dry, average, and wet years (Table 1; Figure 2). The dry year (2015) had an early ice-out (February 20) and low SWE (4 mm). The average year (2016) had a mean ice-out date (April 20), and SWE (743 mm). The wet year (2019) had a late ice-out date (June 1) and high SWE (1,047 mm).

3.2. Water Temperature and PAR at Depth

The water temperature was higher during the average hydroclimate year than in either the dry or wet years (Figure 3a). During 2016, mean water temperature ($20.6^{\circ}\text{C} \pm 0.2^{\circ}\text{C}$) was significantly higher ($p < 0.01$) than in the dry ($19.3^{\circ}\text{C} \pm 0.2^{\circ}\text{C}$) or wet year ($19.5^{\circ}\text{C} \pm 0.2^{\circ}\text{C}$) (Figure 3a). Epilimnetic PAR presents no significant differences between years ($p = 0.1$) (Figure 3b). During 2015, mean PAR ($541 \pm 31 \mu\text{mol m}^{-2} \text{s}^{-1}$) was similar to the dry ($530 \pm 31 \mu\text{mol m}^{-2} \text{s}^{-1}$) and the wet year ($566 \pm 31 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Figure 3b).

3.3. Metabolic Rates

The littoral habitat has substantially higher metabolism (GPP and R) rates than the open water habitat, resulting in a strong relative contribution to whole-lake production (Figure 4, Table 2, Supporting Information S1). In the average hydroclimatic year, the littoral habitat has significantly higher GPP and R rates than the open water habitat ($p < 0.01$). GPP ranged from 46.9 to 26.1 $\text{mmol O}_2 \text{m}^{-3} \text{d}^{-1}$ in the littoral habitat, and 6.8 to 3.9 $\text{mmol O}_2 \text{m}^{-3} \text{d}^{-1}$ in the open water habitat (Table 2). Values of R ranged from 49.6 to 30.2 $\text{mmol O}_2 \text{m}^{-3} \text{d}^{-1}$ at the littoral habitat, and 6.7–1.3 $\text{mmol O}_2 \text{m}^{-3} \text{d}^{-1}$ in the open water habitat (Table 2). NEP did not differ significantly between habitats ($p = 0.7$); however, the littoral site showed more variability (Figure 4 left panels, Table 2). Values of NEP range from 10.5 to $-8.1 \text{ mmol O}_2 \text{m}^{-3} \text{d}^{-1}$ in the littoral habitat, and from 3.4 to $-1.0 \text{ mmol O}_2 \text{m}^{-3} \text{d}^{-1}$ in the open water habitat (Table 2).

Compared to the average hydroclimatic year, the dry and wet years had lower GPP and R rates in both habitats ($p < 0.01$) (Figure 4 left panels; Table 2, Supporting Information S1). GPP and R reduced the most in the littoral habitat (Figure 4 left panels; Table 2).

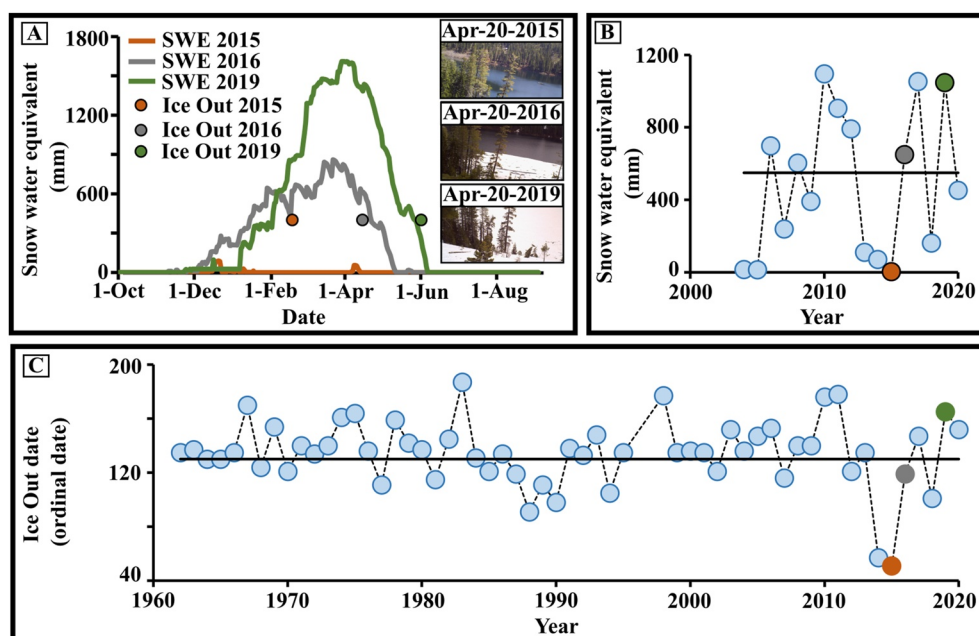


Figure 2. (a) Hydroclimate conditions for each year during this study. The year 2016 (gray) had a mean ice-out date (April 20) and average snow water equivalent (SWE). The year 2015 (orange) had an early ice-out date (February 20) and was dry (low SWE). The year 2019 (green) had a late ice-out date (June 1) and was wet (high SWE). The photos on the right show Castle Lake on April 20 for each of the study years. The lake was completely ice-free in 2015, was half covered in 2016, and was completely ice-covered in 2019. (b) We show the variability of SWE in 2015, 2016, and 2019 compared to the last 17 years before the lake was completely ice-free. (c) Ice-out date in 2015, 2016, and 2019 compared to the previous six decades. Panel (b and c) reaffirmed 2015, 2016, and 2019 were dry, average, and wet years, respectively, in the context of Castle Lake's long-term data.

3.4. Total Habitat Metabolism

When scaled to the volume of open water and littoral habitats, during the study period of the average hydroclimatic year the relative contribution to total GPP was 80% (693×10^6 mmol O_2) and 20% (175×10^6 mmol O_2) in the littoral and open water habitats, respectively (Figure 4 right panels; Table 3). In an average year, the relative contribution to total R was 85% (659×10^6 mmol O_2), and 15% (120×10^6 mmol O_2) in the littoral and open water habitats, respectively (Figure 4 right panels; Table 3). In the average hydroclimatic year, positive NEP values (GPP higher than R) represented 86% of total NEP (Figure 4 right panels). Negative NEP values represented 14% of total lake NEP and they occurred only in the littoral habitat.

The relative contribution to total lake GPP and R of the littoral habitat decreased, and the contribution of the open water habitat increased during the dry and wet years (Table 3). The relative contribution to whole lake GPP of the littoral habitat decreased by 5% (dry year) and 16% (wet year), while the relative contribution to whole lake R of the littoral habitat decreased by 7% (dry year) and 9% (wet year) (Figure 4 right panels).

Whole lake NEP behavior differs markedly depending on hydroclimate year (dry vs. wet). During the dry year, positive NEP values represented 96% of total NEP, implying an increase in the relative contribution of GPP to NEP compared to an average year (Figure 4 right panels). During the wet year, positive NEP values represented 61% of total NEP, implying an increase in the relative contribution of R to NEP compared to an average year (Figure 4 right panels). The littoral habitat had mostly negative NEP values, resulting in a high proportion of negative NEP values during the wet year (Figure 4 right panels, Supporting Information S1).

3.5. Zooplankton and Benthic Macroinvertebrates

In the average hydroclimatic year of 2016, total zooplankton biomass (98 ± 35 mg m^{-3}) was higher ($p < 0.01$) than in the dry (53 ± 46 mg m^{-3}) and wet (58 ± 21 mg m^{-3}) years (Figure 5c). The mean biomass decreased

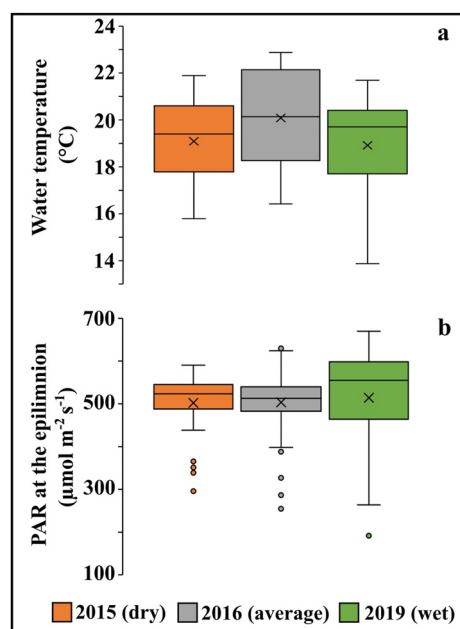


Figure 3. Water temperature (a) at sensor depth and epilimnetic photosynthetically active radiation (PAR) light (b) for the months of August and September during dry (2015), average (2016), and wet (2019) years in the open water habitat. Water temperature was higher during the average year, while PAR was similar between years. Water temperature in the littoral habitat was similar to the open water site in all the years ($p > 0.5$)

by 46% during the dry year and 40% during the wet year compared to the average year. Community composition remained similar between the average and wet years (Figure 5d; PERMANOVA, $p = 0.34$) but differed during the dry year (Figure 5d; PERMANOVA, $p = 0.02$). *Daphnia* accounted for 82% and 68% of the total zooplankton biomass in the average and the wet years, respectively. In the dry year by contrast, *Daphnia* represented 42% of the total zooplankton biomass, and the proportion of the copepod *Diacyclops* increased substantially. During the dry year, *Diacyclops* accounted for 30% of the total zooplankton biomass compared to 4% during the average year.

Total benthic macroinvertebrates biomass was also higher in the average hydroclimatic year ($4,339 \text{ mg m}^{-2}$) than in the dry ($3,175 \text{ mg m}^{-2}$) and wet ($3,158 \text{ mg m}^{-2}$) years. The biomass decreased by 27% during the dry and wet years compared to the average year. The FFG composition of the benthic macroinvertebrates remained similar during the average and dry years but differed during the wet year (Figure 5e). During the dry and average years, collector/gatherers, predators, and shredders dominate the community. Grazers were not present, and collector/filterers represent fewer than 4% of the community composition. In the wet year, collectors/gatherers still dominated the community composition (40%), but grazers (31%) were the second most abundant FFG (Figure 5c).

4. Discussion

While our findings agree with existing research that shows higher metabolism in the littoral habitat than the open water habitat, we show that the year's hydroclimate strongly influences metabolism (GPP, R, and NEP) in the littoral habitat. Furthermore, invertebrates experienced variation to both their

biomass and community structure depending on hydroclimate. Our study has implications for how ecosystem scientists and managers quantify the absolute and relative contributions of the littoral habitat to whole lake production. GPP and R decreased in both the dry and wet years and the open water habitat varied less than the littoral habitat. The difference between littoral and open water response indicates that processes in the bottom of lakes show greater sensitivity to the year's hydroclimate. The relative contribution of the open water habitat to overall GPP and R increased during wet and dry hydroclimatic conditions. While both the dry and wet conditions triggered a reduction in GPP and R, the effect of these hydroclimatic conditions on NEP was substantially different. The dry year tended toward autotrophic metabolism, while the wet year tended toward heterotrophic metabolism, particularly in the littoral habitat. We also observed a reduction in zooplankton and benthic macroinvertebrate biomass during the dry and wet year.

Hydroclimate accounts for changes in GPP and R in both open water and littoral habitats; however, the littoral habitat responds more dynamically than the open water to different hydroclimates. We suggest that metabolism varies less in the open water habitat due to having longer retention times of water, nutrients, and detritus than the littoral zone (Peters & Lodge, 2009). We developed a conceptual model to indicate the factors and magnitude of changes to different components of metabolism in the open water and the littoral habitat of the lake during the dry, average, and wet years (Figure 6). The ecological characteristics of each habitat likely dictate the differences in metabolism (Figure 6). Interannual variations in metabolism in all habitats conformed with the observed changes in water temperature, ice-out date, and snow water equivalent (SWE) accumulated by the beginning of ice break-up (Figure 6). Other studies quantifying metabolism from lakes indicate that changes in light dynamics influence GPP and R (Phillips, 2020; Sadro et al., 2011; Staehr et al., 2016). Metabolic rate differences between years does not seem to be sensitive to light considering light measured in the epilimnion was similar across years and throughout the study period. However, we were not able to measure light at the littoral sites and there could be subtle variations in light dynamics at these sites. During the wet year, loading of terrestrial particulate material into the lake after snow melt may have reduced the light penetration, in the littoral habitat, resulting in decreased benthic productivity.

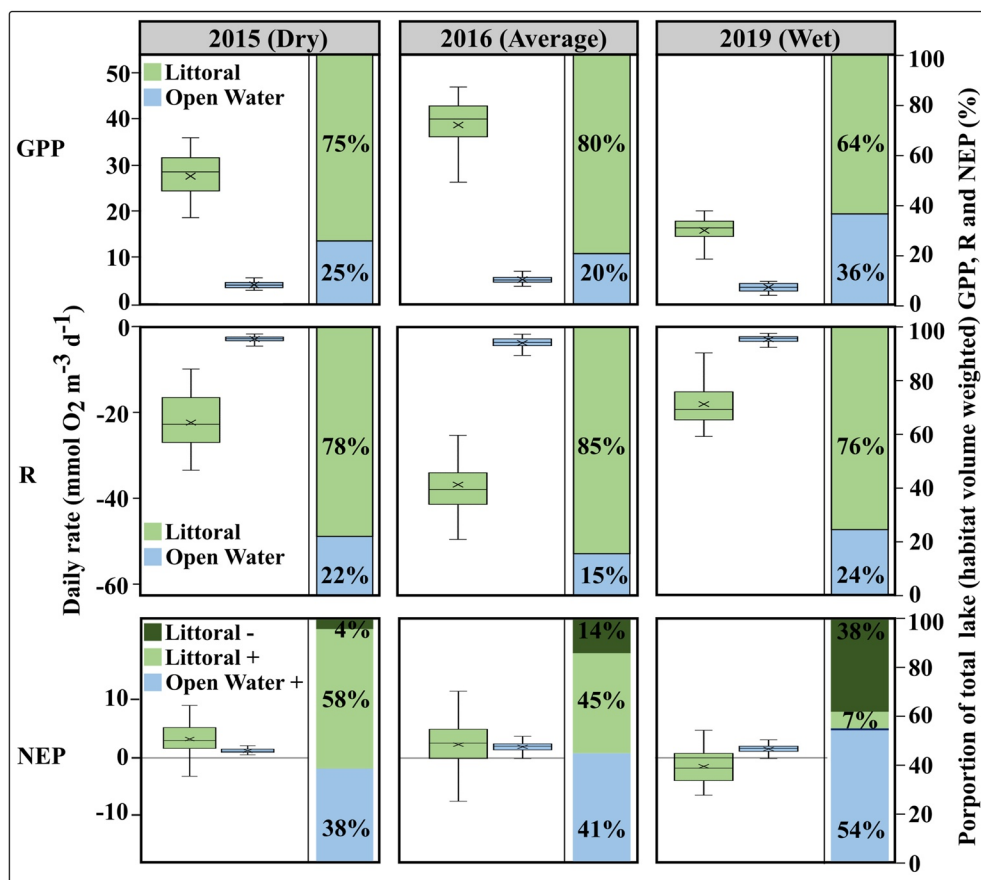


Figure 4. On the left panel of each figure, Castle Lake August to September, daily rates of gross primary production (GPP), R, and net ecosystem production (NEP) at the littoral (green), and open water (light blue) in the dry, average, and wet years. On the right panel of each figure, proportion of total GPP, R, and NEP contributed by each habitat (volume weighted) during the study period (dark green indicates that NEP was negative at the littoral site).

As expected, we observed higher volumetric rates of GPP and R at the littoral habitat compared to the open water habitat. In deep meso- and oligotrophic lakes, the nearshore littoral habitats are usually more productive than the offshore (Peters & Lodge, 2009). Littoral metabolic rates are high due to the accumulation of nutrients and detritus in this part of the lake and because algae grow faster when attached to a substrate (Peters & Lodge, 2009). In Castle Lake, the alder trees growing on the shore of the lake are among the main sources of nitrogen and

Table 2

Metabolic Rates (mmol O₂ m⁻³ d⁻¹) at the Littoral and Open Water Habitats

Lake habitat		2015 (dry)	2016 (average)	2019 (wet)
Littoral	GPP	25.8 (32.7; 16.9)*	40.4 (46.9; 29.1)	16.6 (20.; 8.5)**
	Open water	3.5 (4.9; 2.4)*	5.2 (6.8; 3.9)	3.6 (4.7; 1.9)**
Littoral	R	-22.8 (-33.4; -9.6)**	-39.0(-49.6; -30.2)	-18.9 (-25.2; -9.2)**
	Open water	-2.5 (-5.3; -1.4)*	-3.7 (-6.7; -1.3)	-2.4 (-4.9; -1.3)*
Littoral	NEP	3.0 (8.7; -3.5)	1.3 (10.5; -8.1)	-2.3 (3.4; -6.6)
	Open water	0.9 (1.8; 0.2)	1.5 (3.4; -1.0)	1.0 (2.9; -0.8)

Note. Mean (maximum; minimum) values of gross primary production (GPP), ecosystem respiration (R), and net ecosystem production (NEP) for August through September during dry (2015), average (2016) and wet (2019) years. GPP and R in both sites were significantly different during the dry and wet years than the average year (Wald statistic $p < 0.01$). Significant differences among years are shown in the table as * ($p < 0.05$) and ** ($p < 0.01$) (Tukey's HSD post hoc test).

Table 3

Relative Contribution (%) of the Littoral and Open Water Habitat (Volume Weighted; mmol O₂) to Lake Total Gross Primary Production (GPP), R, and Net Ecosystem Production (NEP), During the Study Period in the Dry, Average, and Wet Years

Lake habitat		2015 (dry)	2016 (average)	2019 (wet)
Littoral	GPP (%)	75	80	64
Open water		25	20	36
Littoral	R (%)	78	85	76
Open water		22	15	24

organic matter for the lake (Goldman, 1961). Soil under alder trees accumulates nitrogen through leaf fall, which is then transported by spring water into the lake (Goldman, 1961). In an experiment, Goldman (1961) showed that productivity doubled after spring water addition that traveled through alder humus.

The observed changes in water temperature and SWE during wet and dry years explain the reduction in R and GPP in both habitats. The water temperature decreased (on average by 1°C–1.2°C) in both the dry and wet years compared to the average hydroclimate year. Temperature variation influences both GPP and R (Solomon et al., 2013; Song et al., 2018) due to the relationship between enzyme kinetics and thermal regimes (Phillips, 2020). Blue-green algae dominate littoral and epilimnetic phytoplankton communities at Castle Lake during August and September (Axler et al., 1981; Higley

et al., 2001; Huovinen et al., 1999). The metabolic rates of blue-green algae substantially decrease with even a 1°C drop when water temperatures reach ~20°C (Wetzel, 2009; Carey, et al., 2011; Visser et al., 2016). The large amount of SWE and the late ice-out date likely caused the low water temperature in the wet year. Snowpack and lake temperature are strongly correlated in Castle Lake (Caldwell et al., 2020; Goldman et al., 1989; Park et al., 2004; Strub et al., 1985) and mountain lakes in general (Melack et al., 2020; Sadro et al., 2018; Smits et al., 2020). Previous research at Castle Lake demonstrated that water temperature tends to be higher during dry years, resulting in higher primary productivity (Caldwell et al., 2020; Park et al., 2004). However, in our study, water temperature in the dry year was lower than in the average year. While the differences were marginal, mean daily wind velocity increased and solar radiation decreased in the dry year. Both variables could have reduced water temperature (Supporting Information S1). The dry year had similar air temperature to the average year (Supporting Information S1) and lower snowmelt inputs, making them unlikely culprits to lower water temperatures during the dry year.

Variations in SWE likely constrained metabolic rates by reducing the input of nutrients and organic matter during the dry year (low SWE), and by flushing algae and nutrients from the lake and cooling the water during the wet year (high SWE) (Figure 6). The effect of SWE on Castle Lake's primary productivity depends on the amount of SWE and ice-out timing (Goldman et al., 1989; Park et al., 2004; Strub et al., 1985). Low SWE limits the amount of nutrients delivered to the lake from the surrounding watershed. In Castle Lake, low SWE combined with an early ice-out, such as in the dry year of our study, leads to nutrient depletion earlier in the open water season (Elser et al., 1995; Goldman et al., 1989; Huovinen et al., 1999). Therefore, the shallow primary productivity by August and September was likely nutrient-limited. In contrast, high SWE delivers more nutrients and organic matter to the lake, but the greater influx of snowmelt flushes primary producers from the lake (Goldman et al., 1989). In the wet year of our study, high SWE combined with late ice-out, in this scenario, incident light and water temperature had already begun to decrease by the time the primary producer community started to recover, which constrained metabolic rates. Moreover, high SWE reduces the lake's water temperature, making it more difficult for the algae community to recover (Goldman et al., 1989; Park et al., 2004; Strub et al., 1985).

Wet hydroclimatic conditions favored heterotrophic metabolism (especially within the littoral habitat), while drier conditions favored autotrophic metabolism. During the wet year, NEP decreased at both sites, and became predominantly negative at the littoral habitat. Sadro and Melack (2012) found a shift in NEP toward heterotrophy in alpine Emerald Lake after a large inflow of water that flushed primary producers and increased the amount of allochthonous organic carbon. We suspect that the increase in NEP during the dry year compared to the average hydroclimatic year is due to less allochthonous (out of system) material available for heterotrophic bacteria. These results show that the internal process of organic carbon in Castle Lake varies between habitats and under different hydroclimatic conditions. Therefore, research that focuses on lakes as sources or sinks of organic carbon would benefit from incorporating within-lake spatial and temporal variability.

We detected reciprocal relationships between consumers and GPP in Castle Lake (Figures 5a–5c and 5d). Decreased GPP in the dry and wet years coincided with reduced consumer biomass. We also observed changes in consumer community composition that may have contributed to reducing GPP. We saw no discernable change in zooplankton community composition during the wet year, but the proportion of the copepod *Diacyclops* increased while *Daphnia* decreased during the dry year. *Diacyclops* have a longer period of juvenile development than

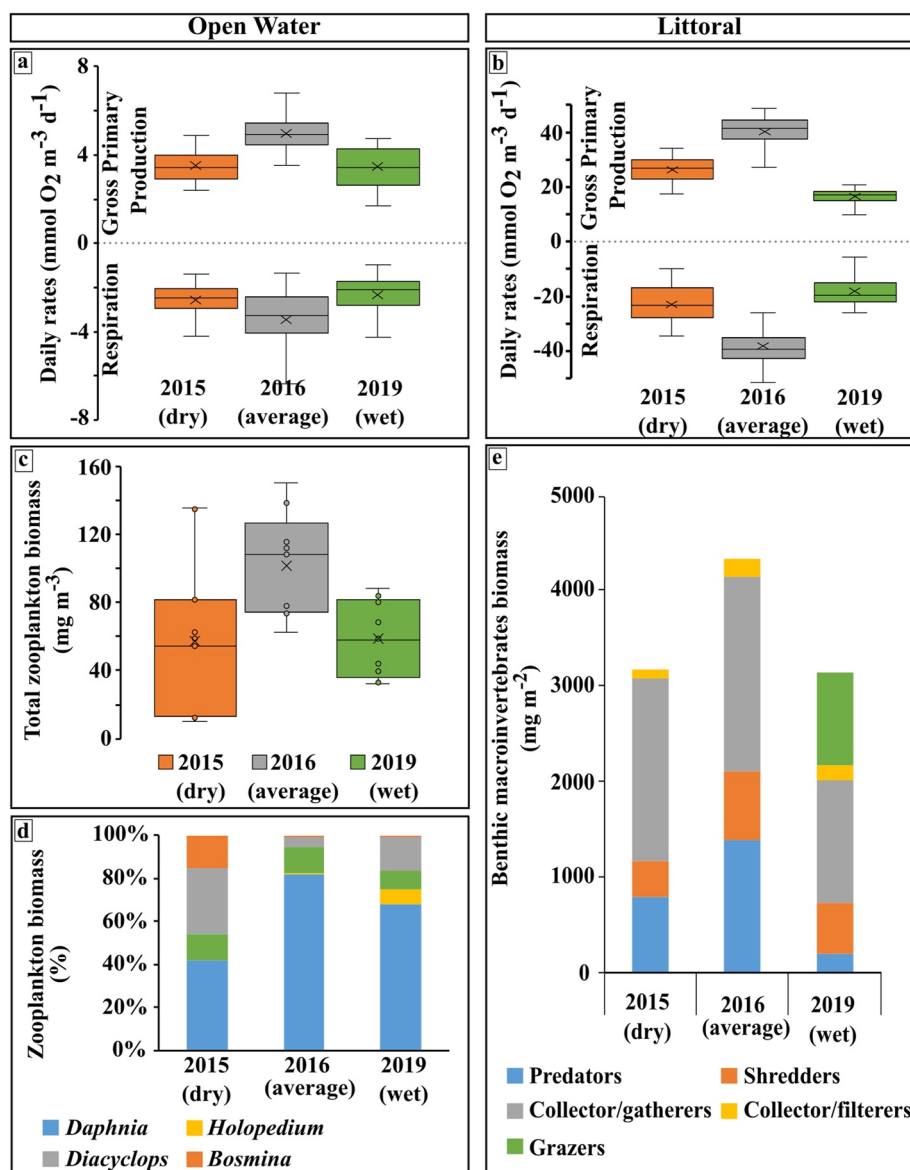


Figure 5. Daily rates of gross primary production (GPP), R, and net ecosystem production (NEP) at the open water (a), and littoral (b) in the dry, average, and wet years and its relation with consumer biomass and community composition. Comparison between a dry (2015), average year (2016), and wet (2019) years of zooplankton total biomass (c), and community composition (d) in the open water habitat, and benthic macroinvertebrates total biomass of each functional feeding group (e) in the littoral habitat

Daphnia (Horne & Goldman, 1994). Therefore, it is more likely that the relative number of *Diacyclops* would increase in a year with earlier ice-out rather than a year with average or late ice-out (Horne & Goldman, 1994). We suggest that an indirect effect related to nutrient recycling favors a reduction in primary productivity when the proportion of *Diacyclops* increases and the proportion of *Daphnia* decreases. At Castle Lake, *Daphnia* plays an important role in regenerating nitrogen (Brett et al., 1994; Elser et al., 1995), which is the main nutrient that limits shallow GPP in the lake (Axler et al., 1981; Axler & Goldman, 1981). *Daphnia* recycle nitrogen from the hypolimnion to the epilimnion due to its strong diel vertical migration (Elser et al., 1995). In contrast, *Diacyclops* do not modify the water nutrient composition at Castle Lake (Brett et al., 1994). *Diacyclops* are generally considered carnivores rather than grazers; they consume food with elemental ratios similar to their own and excrete few nutrients (Brett et al., 1994). Limited nutrient cycling from increased *Diacyclops* helps explain nitrogen-limitation for open water algae and the decreased GPP during the dry year of our study.

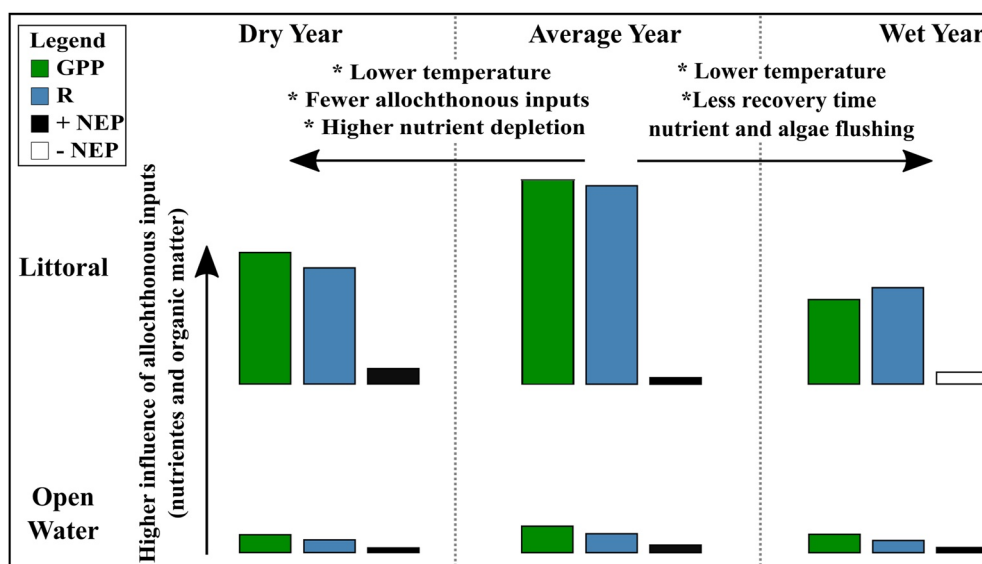


Figure 6. Conceptual model of late summer (August–September) gross primary production (GPP; green), ecosystem respiration (R; blue), and net ecosystem production (+NEP: black when positive; –NEP: white when negative) in littoral and open water habitats during dry, wet, and average years. The littoral habitat has the highest values of GPP and R due to receiving the highest loads of allochthonous inputs (nutrients and organic matter) and is the only site to shift to a negative NEP (during the wet year) due to R of allochthonous organic matter, despite GPP being low. The open water habitat presents the lower values of GPP, R, and NEP and the lowest variability within years, implying a high resilience. The height of the bars corresponds to the mean daily rates of GPP, R, and NEP in each habitat

The FFG shifts in the benthic macroinvertebrates that we observed in the littoral habitat may have contributed to reduced GPP during the wet year. Grazers constituted 31% of benthic invertebrate biomass during the wet year in the littoral habitat yet they were absent from our samples during the dry and average years. Previous studies at Castle Lake demonstrate that secondary invertebrate consumers can reduce or enhance productivity, depending on the animal biomass and the community composition (Elser, 1992). However, in this study, we did not evaluate the relative role of consumers in regulating metabolism. Therefore, while we suggest that hydroclimatic year influences metabolism and the production of secondary consumers, future work that elucidates the connections across the algae-herbivore interface and energy flow into the food web will build on our findings.

5. Conclusion

Our study demonstrates that the metabolism of the littoral habitat at Castle Lake, particularly GPP and R, shows greater sensitivity to hydroclimate changes than the open water habitat. We also showed that the site-specific NEP can change from autotrophic to heterotrophic, depending on hydroclimate conditions. This study must be understood in the context of climate variation (Dai, 2013; Min, et al., 2011) and its complex interaction with ecosystems. Not only do ecosystems respond to variations in climate forcing, but within-lake habitats do not have equivalent responses. The complex interactions between climate forcing and ecosystem and habitat-specific responses extends to habitat and resource use by consumers (Caldwell et al., 2020; Rosenblatt & Schmitz, 2016; Rüegg et al., 2021).

Our research amplifies the need for studies across multiple years with a similar hydroclimate to test the consistency of our findings. We recognize other concerns such as lake-specific differences in the littoral habitat composition. Castle Lake's woody debris-dominated habitat may have a different response when compared to metabolism changes in rock- or macrophyte-dominated littoral habitats under different hydroclimate conditions. An integration of such studies across lakes to test effects based on trophic conditions (ultraoligotrophic to eutrophic) would add valuable context to our findings from a subalpine lake. Additionally, many top consumers are non-open water fish, which rely on littoral resources in lakes (Vander Zanden et al., 2011). It would be interesting to analyze the coupling and decoupling effect that climate-driven changes produce across the different trophic levels and habitats of lakes.

Data Availability Statement

Data and metadata are available at Scordo, F., Chandra, S., Lottig, N.R. (2021), "Hydroclimate variability affects habitat-specific (open water and littoral) lake metabolism (Repository)." Mendeley Data, V1, <https://data.mendeley.com/datasets/tgbdcfgw2/1>.

Acknowledgments

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References

- Aalderink, R., & Jovin, R. (1997). Estimation of the photosynthesis/irradiance (P/I) curve parameters from light and dark bottle experiments. *Journal of Plankton Research*, 19, 1713–1742. <https://doi.org/10.1093/plankt/19.11.1713>
- Adrian, R., O'Reilly, C. M., Zagarese, H., Baines, S. B., Hessen, D. O., Keller, W., et al. (2009). Lakes as sentinels of climate change. *Limnology & Oceanography*, 54(62), 2283–2297. https://doi.org/10.4319/lo.2009.54.6_part_2.2283
- Alfonso, M. B., Brendel, A., Vitale, A. J., Seitz, C., Piccolo, M., & Perillo, G. (2018). Drivers of ecosystem metabolism in two managed shallow lakes with different salinity and trophic conditions: The Sauce Grande and La Salada Lakes (Argentina). *Water*, 10, 1136. <https://doi.org/10.3390/w10091136>
- Anderson, M. J. (2017). Permutational multivariate analysis of variance (PERMANOVA). *Wiley StatsRef: Statistics reference online* (pp. 1–15). <https://doi.org/10.1002/9781118445112.stat07841>
- Ask, J., Karlsson, J., & Jansson, M. (2012). Net ecosystem production in clear-water and brown-water lakes. *Global Biogeochemical Cycles*, 26(1), 1–7. <https://doi.org/10.1029/2010GB003951>
- Ask, J., Karlsson, J., Persson, L., Ask, P., Byström, P., & Jansson, M. (2009). Terrestrial organic matter and light penetration: Effects on bacterial and primary production in lakes. *Limnology & Oceanography*, 54(6), 2034–2040. <https://doi.org/10.4319/lo.2009.54.6.2034>
- Axler, R. P., & Goldman, C. R. (1981). Isotope tracer methods for investigations of nitrogen deficiency in Castle Lake, California. *Water Research*, 15(5), 627–632. [https://doi.org/10.1016/0043-1354\(81\)90027-0](https://doi.org/10.1016/0043-1354(81)90027-0)
- Axler, R. P., Redfield, G. W., & Goldman, C. R. (1981). The importance of regenerated nitrogen to phytoplankton productivity to phytoplankton productivity in a subalpine lake. *Ecology*, 62(2), 345–354. <https://doi.org/10.2307/1936709>
- Baumgärtner, D., & Rothhaupt, K. O. (2003). Predictive length-dry mass regressions for freshwater invertebrates in a pre-alpine lake littoral. *International Review of Hydrobiology*, 88(5), 453–463. <https://doi.org/10.1002/iroh.200310632>
- Benke, A. C., Huryn, A. D., Smock, L. A., & Wallace, J. B. (1999). Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society*, 18(3), 308–343. <https://doi.org/10.2307/1468447>
- Betancourt, M. (2007). *Robust statistical workflow with RStan*. Retrieved from https://betanalpha.github.io/assets/case_studies/rstan_workflow.html
- Brett, M. T., Wiackowski, K., Lubnow, F. S., Mueller-Solger, A., Elser, J. J., & Goldman, R. (1994). Species-dependent effects of zooplankton on planktonic ecosystem processes in Castle, California. *Ecology*, 75(8), 2243–2254. <https://doi.org/10.2307/1940880>
- Brothers, S., Vadeboncoeur, Y., & Sibley, P. (2016). Benthic algae compensate for phytoplankton losses in large aquatic ecosystems. *Global Change Biology*, 22(12), 3865–3873. <https://doi.org/10.1111/gcb.13306>
- Caldwell, T. J., Chandra, S., Feher, K., Simmons, J. B., & Hogan, Z. (2020). Ecosystem response to earlier ice break-up date: Climate-driven changes to water temperature, lake-habitat-specific production, and trout habitat and resource use. *Global Change Biology*, 26(10), 5475–5491. <https://doi.org/10.1111/gcb.15258>
- Cantonati, M., & Lowe, R. L. (2014). Lake benthic algae: Toward an understanding of their ecology. *Freshwater Science*, 33(2), 475–486. <https://doi.org/10.1086/676140>
- Carey, C. C., Ibelings, B. W., Hoffmann, E. P., Hamilton, D. P., & Brookes, J. D. (2011). Eco-physiological adaptations that favour freshwater cyanobacteria in a changing climate. *Water Research*, 46(5), 1394–1407. <https://doi.org/10.1016/j.watres.2011.12.016>
- Carter, J. L., & Schindler, D. E. (2012). Responses of zooplankton populations to four decades of climate warming in lakes of southwestern Alaska. *Ecosystems*, 15(6), 1010–1026. <https://doi.org/10.1007/s10021-012-9560-0>
- Craig, N., Jones, S. E., Weidel, B. C., & Solomon, C. T. (2015). Habitat, not resource availability, limits consumer production in lake ecosystems. *Limnology & Oceanography*, 60(6), 2079–2089. <https://doi.org/10.1002/lno.10153>
- Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature Climate Change*, 3(1), 52–58. <https://doi.org/10.1038/nclimate1633>
- Devlin, S. P., Vander Zanden, M. J., & Vadeboncoeur, Y. (2016). Littoral-benthic primary production estimates: Sensitivity to simplifications with respect to periphyton productivity and basin morphometry. *Limnology and Oceanography: Methods*, 14(2), 138–149. <https://doi.org/10.1002/lom3.10080>
- Dodds, W. K., & Cole, J. J. (2007). Expanding the concept of trophic state in aquatic ecosystems: It's not just the autotrophs. *Aquatic Sciences*, 69(4), 427–439. <https://doi.org/10.1007/s00027-007-0922-1>
- Edwards, F. K., Lauridsen, R. B., Armand, L., Vincent, H. M., & Jones, J. I. (2009). The relationship between length, mass and preservation time for three species of freshwater leeches (Hirudinea). *Fundamental and Applied Limnology*, 173(4), 321–327. <https://doi.org/10.1127/1863-9135/2009/0173-0321>
- Elser, J. J. (1992). Phytoplankton dynamics and the role of grazers in Castle Lake, California. *Ecology*, 73(3), 887–902. <https://doi.org/10.2307/1940166>
- Elser, J. J., Lubnow, F. S., Marzolf, E. R., Brett, M. T., Dion, G., & Goldman, C. R. (1995). Factors associated with interannual and intraannual variation in nutrient limitation of phytoplankton growth in Castle Lake, California. *Canadian Journal of Fisheries and Aquatic Sciences*, 52, 93–104. <https://doi.org/10.1139/f95-009>
- Engel, F., Farrell, K. J., McCullough, I. M., Scordo, F., Denfeld, B. A., Dugan, H. A., et al. (2018). A lake classification concept for a more accurate global estimate of the dissolved inorganic carbon export from terrestrial ecosystems to inland waters. *Naturwissenschaften*, 105(3–4), 25. <https://doi.org/10.1007/s00114-018-1547-z>
- Goldman, C. R. (1961). The contribution of alder trees (*Alnus tenuifolia*) to the primary productivity of Castle Lake, California. *Ecology*, 42(2), 282–288. <https://doi.org/10.2307/1932080>
- Goldman, C. R., Jassby, A., & Powell, T. (1989). Interannual fluctuations in primary production: Meteorological forcing at two subalpine lakes. *Limnology & Oceanography*, 34(2), 310–323. <https://doi.org/10.4319/lo.1989.34.2.0310>

- Hanson, P. C., Carpenter, S. R., Kimura, N., Wu, C., Cornelius, S. P., & Kratz, T. K. (2008). Evaluation of metabolism models for free-water dissolved oxygen methods in lakes. *Limnology and Oceanography: Methods*, 6. <https://doi.org/10.4319/lom.2008.6.454>
- Higley, B., Carrick, H. J., Brett, M. T., Luecke, C., & Goldman, C. R. (2001). The effects of ultraviolet radiation and nutrient additions on periphyton biomass and composition in a sub-alpine lake (Castle Lake, USA). *International Review of Hydrobiology*, 86(2), 147–163. [https://doi.org/10.1002/1522-2632\(200104\)86:2<147::AID-IROH147>3.0.CO;2-Y](https://doi.org/10.1002/1522-2632(200104)86:2<147::AID-IROH147>3.0.CO;2-Y)
- Horne, J. A., & Goldman, C. R. (1994). Zooplankton and zoobenthos. In *Limnology* (pp. 265–298). McGraw-Hill Inc.
- Huovinen, P. S., Brett, M. T., & Goldman, C. R. (1999). Temporal and vertical dynamics of phytoplankton net growth in Castle Lake, California. *Journal of Plankton Research*, 21(2), 373–385. <https://doi.org/10.1093/plankt/21.2.373>
- Idrizaj, A., Laas, A., Anijalg, U., & Nöges, P. (2016). Horizontal differences in ecosystem metabolism of a large shallow lake. *Journal of Hydrology*, 535, 93–100. <https://doi.org/10.1016/j.jhydrol.2016.01.037>
- Jassby, A. D., Powell, T. M., & Goldman, C. R. (1990). Interannual fluctuations in primary production: Direct physical effects and the trophic cascade at Castle Lake, California. *Limnology & Oceanography*, 35(5), 1021–1038. <https://doi.org/10.4319/lom.1990.35.5.1021>
- Jeppesen, E., Meerhoff, M., Davidson, T. A., Trolle, D., Søndergaard, M., Lauridsen, T. L., et al. (2014). Climate change impacts on lakes: An integrated ecological perspective based on a multi-faceted approach, with special focus on shallow lakes. *Journal of Limnology*, 73, 88–111. <https://doi.org/10.4081/jlimnol.2014.844>
- Karlsson, J., Jansson, M., & Jonsson, A. (2007). Respiration of allochthonous organic carbon in unproductive forest lakes determined by the Keeling plot method. *Limnology & Oceanography*, 52(2), 603–608. <https://doi.org/10.4319/lom.2007.52.2.0603>
- Lenth, R. V. (2021). *emmeans: Estimated marginal means, aka least-squares means*. Retrieved from <https://cran.r-project.org/package=emmeans>
- Lottig, N. R., Phillips, J., Batt, R. D., Scordo, F., Williamson, J. T., Carpenter, S. R., et al. (2021). Estimating primary production in lakes: Comparison of ¹⁴C incubation and free-water O₂ approaches. *Limnology and Oceanography: Methods*. <https://doi.org/10.1002/lom3.10471>
- McCallister, S. L., & Del Giorgio, P. A. (2008). Direct measurement of the δ¹³C signature of carbon respired by bacteria in lakes: Linkages to potential carbon sources, ecosystem baseline metabolism, and CO₂ fluxes. *Limnology & Oceanography*, 53(4), 1204–1216. <https://doi.org/10.4319/lom.2008.53.4.1204>
- McCullough, I. M., Dugan, H. A., Farrell, K. J., Morales-Williams, A. M., Ouyang, Z., Roberts, D., et al. (2018). Dynamic modeling of organic carbon fates in lake ecosystems. *Ecological Modelling*, 386(June), 71–82. <https://doi.org/10.1016/j.ecolmodel.2018.08.009>
- Melack, J. M., Sadro, S., Sickman, S., & Dozier, J. (2020). *Lakes and watersheds in the Sierra Nevada of California: Responses to environmental change* (1st ed.). <https://doi.org/10.2307/j.ctv17hm9sr>
- Melillo, J. M., Richmond, T., & Yohe, G. (2014). Climate change impacts in the United States: Great plains. In *Climate change impacts in the United States: The third national climate assessment*. <https://doi.org/10.7930/J0Z31WJ2>
- Merritt, R. W., Cummins, K. W., & Berg, M. B. (2007). *An introduction to the aquatic insects of North America*. Kendall/Hunt Publishing Company.
- Min, S. K., Zhang, X., Zwiers, F. W., & Hegerl, G. C. (2011). Human contribution to more-intense precipitation extremes. *Nature*, 470(7334), 378–381. <https://doi.org/10.1038/nature09763>
- Oksanen, J. F., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. (2019). *vegan: Community ecology package*. Retrieved from <https://cran.r-project.org/package=vegan%0A>
- Park, S., Brett, M. T., Müller-Solger, A., & Goldman, C. R. (2004). Climatic forcing and primary productivity in a subalpine lake: Interannual variability as a natural experiment. *Limnology & Oceanography*, 49(2), 614–619. <https://doi.org/10.4319/lom.2004.49.2.0614>
- Peters, J. A., & Lodge, D. M. (2009). Littoral zone. *Encyclopedia of inland waters* (pp. 79–87). <https://doi.org/10.1016/B978-012370626-3.00218-0>
- Phillips, J. S. (2020). Time-varying responses of lake metabolism to light and temperature. *Limnology & Oceanography*, 65(3), 652–666. <https://doi.org/10.1002/lno.11333>
- Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D., & R Core Team. (2020). *nlme: Linear and nonlinear mixed effects models*. Retrieved from <https://cran.r-project.org/package=nlme>
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Redfield, G. W., & Goldman, C. R. (1978). Diel vertical migration and dynamics of zooplankton biomass in the epilimnion of Castle Lake, California. *Verhandlungen Des Internationalen Verein Limnologie*, 20, 381–387. <https://doi.org/10.1080/03680770.1977.11896536>
- Rosenblatt, A. E., & Schmitz, O. J. (2016). Climate change, nutrition, and bottom-up and top-down food web processes. *Trends in Ecology & Evolution*, 31(12), 965–975. <https://doi.org/10.1016/j.tree.2016.09.009>
- Rüegg, J., Conn, C. C., Anderson, E. P., Battin, T. J., Bernhardt, E. S., Boix Canadell, M., et al. (2021). Thinking like a consumer: Linking aquatic basal metabolism and consumer dynamics. *Limnology and Oceanography Letters*, 6, 1–17. <https://doi.org/10.1002/lol2.10172>
- Sadro, S., & Melack, J. (2012). The effect of an extreme rain event on the biogeochemistry and ecosystem metabolism of an oligotrophic high-elevation lake. *Arctic Antarctic and Alpine Research*, 44(2), 222–231. <https://doi.org/10.1657/1938-4246-44.2.222>
- Sadro, S., Nelson, C. E., & Melack, J. M. (2011). Linking diel patterns in community respiration to bacterioplankton in an oligotrophic high-elevation lake. *Limnology & Oceanography*, 56(2), 540–550. <https://doi.org/10.4319/lom.2011.56.2.0540>
- Sadro, S., Sickman, J. O., Melack, J. M., & Skeen, K. (2018). Effects of climate variability on snowmelt and implications for organic matter in a high-elevation lake. *Water Resources Research*, 54(7), 4563–4578. <https://doi.org/10.1029/2017WR022163>
- Scordo, F., Chandra, S., & Lottig, N. R. (2021). “Hydroclimate variability affects habitat-specific (open water and littoral) lake metabolism (Repository).” *Mendeley Data, V1*. <https://data.mendeley.com/datasets/tgbdcfwgwx2/1>
- Shimoda, Y., Azim, M. E., Perhar, G., Ramin, M., Kenney, M. A., Sadraddini, S., et al. (2011). Our current understanding of lake ecosystem response to climate change: What have we really learned from the north temperate deep lakes? *Journal of Great Lakes Research*, 37(1), 173–193. <https://doi.org/10.1016/j.jglr.2010.10.004>
- Smits, A. P., MacIntyre, S., & Sadro, S. (2020). Snowpack determines relative importance of climate factors driving summer lake warming. *Limnology and Oceanography Letters*, 5(3), 271–279. <https://doi.org/10.1002/lol2.10147>
- Solomon, C. T., Bruesewitz, D. A., Richardson, D. C., Rose, K. C., Van de Bogert, M. C., Hanson, P. C., et al. (2013). Ecosystem respiration: Drivers of daily variability and background respiration in lakes around the globe. *Limnology & Oceanography*, 58(3), 849–866. <https://doi.org/10.4319/lom.2013.58.3.0849>
- Song, C., Dodds, W. K., Rüegg, J., Argerich, A., Baker, C. L., Bowden, W. B., et al. (2018). Continental-scale decrease in net primary productivity in streams due to climate warming. *Nature Geoscience*, 11(6), 415–420. <https://doi.org/10.1038/s41561-018-0125-5>
- Staehr, P. A., Baastrop-Spohr, L., Sand-Jensen, K., & Stedmon, C. (2012). Lake metabolism scales with lake morphometry and catchment conditions. *Aquatic Sciences*, 74(1), 155–169. <https://doi.org/10.1007/s00027-011-0207-6>
- Staehr, P. A., Brighenti, L. S., Honti, M., Christensen, J., & Rose, K. C. (2016). Global patterns of light saturation and photoinhibition of lake primary production. *Inland Waters*, 6(4), 593–607. <https://doi.org/10.1080/iw-6.4.888>
- Stan Development Team. (2020). *RStan: the R interface to Stan. R package version 2.21.2*. Retrieved from <http://mc-stan.org>

- Steele, J. H. (1962). Environmental control of photosynthesis in the sea. *Limnology & Oceanography*, 7, 137–150. <https://doi.org/10.4319/lo.1962.7.2.0137>
- Stefanidis, K., & Elias, D. (2019). Differentiation in aquatic metabolism between littoral habitats with floating-leaved and submerged macrophyte growth forms in a shallow eutrophic lake. *Water*, 11, 287. <https://doi.org/10.3390/w11020287>
- Strub, P. T., Powell, T., & Goldman, C. R. (1985). Climatic forcing: Effects of El Niño on a small, temperate lake. *Science*, 227(4682), 55–57. <https://doi.org/10.1126/science.227.4682.55>
- Thorpe, J. H., & Covich, A. P. (2010). *Ecology and classification of North American freshwater invertebrates* (4th ed.). Academic Press.
- Tranvik, L. J., Cole, J. J., & Prairie, Y. T. (2018). The study of carbon in inland waters—from isolated ecosystems to players in the global carbon cycle. *Limnology and Oceanography Letters*, 3(3), 41–48. <https://doi.org/10.1002/lol2.10068>
- Vachon, D., & Prairie, Y. T. (2013). The ecosystem size and shape dependence of gas transfer velocity versus wind speed relationships in lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 70(12), 1757–1764. <https://doi.org/10.1139/cjfas-2013-0241>
- Vadeboncoeur, Y., Devlin, S. P., McIntyre, P. B., & Zanden, M. J. V. (2014). Is there light after depth? Distribution of periphyton chlorophyll and productivity in lake littoral zones. *Freshwater Science*, 33(2), 524–536. <https://doi.org/10.1086/676315>
- Vadeboncoeur, Y., Jeppesen, E., Vander Zanden, M. J., Schierup, H. H., Christoffersen, K., & Lodge, D. M. (2003). From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. *Limnology & Oceanography*, 48(4), 1408–1418. <https://doi.org/10.4319/lo.2003.48.4.1408>
- Vadeboncoeur, Y., Moore, M. V., Stewart, S. D., Chandra, S., Atkins, K. S., Baron, J. S., et al. (2021). Green bottoms: Benthic filamentous algal blooms are an emerging threat to clear lakes worldwide. *BioScience*, 71. <https://doi.org/10.1093/biosci/biab049>
- Van de Bogert, M. C., Bade, D. L., Carpenter, S. R., Cole, J. J., Pace, M. L., Hanson, P. C., & Langman, O. C. (2012). Spatial heterogeneity strongly affects estimates of ecosystem metabolism in two north temperate lakes. *Limnology & Oceanography*, 57(6), 1689–1700. <https://doi.org/10.4319/lo.2012.57.6.1689>
- Van de Bogert, M. C., Carpenter, S. R., Cole, J. J., & Pace, M. L. (2007). *OCEANOGRAPHY: METHODS assessing pelagic and benthic metabolism using free water measurements* (pp. 145–155). <https://doi.org/10.4319/lom.2007.5.145>
- Vander Zanden, M. J., Chandra, S., Park, S.-K., Vadeboncoeur, Y., & Goldman, C. R. (2007). Efficiencies of benthic and pelagic trophic pathways in a subalpine lake. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(12), 2608–2620. <https://doi.org/10.1139/f06-148>
- Vander Zanden, M. J., & Vadeboncoeur, Y. (2020). Putting the lake back together 20 years later: What in the benthos have we learned about habitat linkages in lakes? *Inland Waters*, 10(3), 305–321. <https://doi.org/10.1080/20442041.2020.1712953>
- Vander Zanden, M. J., Vadeboncoeur, Y., & Chandra, S. (2011). Fish reliance on littoral-benthic resources and the distribution of primary production in lakes. *Ecosystems*, 14(6), 894–903. <https://doi.org/10.1007/s10021-011-9454-6>
- Visser, P. M., Verspagen, J. M. H., Sandrini, G., Stal, L. J., Matthijs, H. C. P., Davis, T. W., et al. (2016). How rising CO₂ and global warming may stimulate harmful cyanobacterial blooms. *Harmful Algae*, 54, 145–159. <https://doi.org/10.1016/j.hal.2015.12.006>
- Wetzel, R. G. (2009). Limnology. In *Low temperature physics*. <https://doi.org/10.1063/1.3224729>
- Williamson, C. E., Dodds, W., Kratz, T. K., & Palmer, M. A. (2008). Lakes and streams as sentinels of environmental change in terrestrial and atmospheric processes. *Frontiers in Ecology and the Environment*, 6(5), 247–254. <https://doi.org/10.1890/070140>
- Williamson, C. E., Overholt, E. P., Brenttrup, J. A., Pilla, R. M., Leach, T. H., Schladow, S. G., et al. (2016). Sentinel responses to droughts, wildfires, and floods: Effects of UV radiation on lakes and their ecosystem services. *Frontiers in Ecology and the Environment*, 14(2), 102–109. <https://doi.org/10.1002/fee.1228>
- Williamson, C. E., Saros, J. E., Vincent, W. F., & Smol, J. P. (2009). Lakes and reservoirs as sentinels, integrators, and regulators of climate change. *Limnology & Oceanography*, 54(62), 2273–2282. https://doi.org/10.4319/lo.2009.54.6_part_2.2273
- Winslow, L., Read, J., Woolway, R., Brenttrup, J., Zwart, J., Albers, S., & Collinge, D. (2019). Package ‘rLakeAnalyzer’. *Lake physics tools*. Retrieved from <https://cran.r-project.org/package=rLakeAnalyzer>
- Winslow, M. L., Winslow, A. L., Zwart, J., Batt, R., Corman, J., Dugan, H., et al. (2016). Package ‘LakeMetabolizer’.
- Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer.