

UNIVERSITY OF CALIFORNIA, SAN DIEGO

Effects of food web interactions and climate on the partial pressure of
carbon dioxide in San Diego reservoirs

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Master of Science

in

Biology

by

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Chair

University of California, San Diego

2014

DEDICATION

I would like to dedicate this thesis to my aunt, Christine Lwe, who has proven time after time that cherishing every moment in life and keeping one's spirits high are the best ways to be happy. Her strength and positive outlook encouraged me to keep pushing forward even when I just wanted to drop it all; she has showed me that it is possible to remain hopeful even in one's weakest moments. For that, I am forever grateful. I miss her immensely and hope that she is enjoying her journey throughout the Pacific Ocean and the waters of worlds beyond.

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LIST OF ABBREVIATIONS

chl- <i>a</i>chlorophyll- <i>a</i> ($\mu\text{g L}^{-1}$)
DAPI4',6-diamidino-2-phenylindole
DIdeionized
DOdissolved oxygen (mg L^{-1})
DOCdissolved organic carbon (mg C L^{-1})
GHGgreenhouse gas
PBSphosphate buffered saline
POCparticulate organic carbon (mg C L^{-1})
POMparticulate organic matter
PONparticulate organic nitrogen (mg N L^{-1})
pptparts per thousand
psipounds per square inch
TAtotal alkalinity (ppm)
TNtotal nitrogen (mg N L^{-1})
TPtotal phosphorous (mg P L^{-1})

LIST OF SYMBOLS

C	carbon
°C	degrees centigrade
CH ₄	methane
cm	centimeter
CO ₂	carbon dioxide
Hg	mercury
km	kilometer
L	liter
m	meter
mg	milligram
mL	milliliter
mm	millimeter
μ	micro
N	nitrogen
P	phosphorus
<i>p</i>	p-value
pCO ₂	partial pressure of carbon dioxide
S	siemens
\bar{X}	mean

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ABSTRACT OF THE THESIS

Effects of food web interactions and climate on the partial pressure of carbon dioxide in San Diego reservoirs

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Man-made reservoirs around the world contribute to cycling of carbon dioxide (CO₂) with the atmosphere, but there is little information on how ecosystem processes determine the absorption or emission of CO₂. It is essential to determine if reservoirs sequester or release CO₂ to understand how water impoundments impact global carbon cycling. We sampled three reservoirs throughout San Diego, California, all of which receive most of their water from Northern California and the Colorado River, weekly for one year. We measured seasonal variation in the abundances of bacteria, pelagic fungi,

phytoplankton, and zooplankton, as well as abiotic factors such as water chemistry (pH, nutrients, conductivity, ions, dissolved organic carbon [DOC], and partial pressure of CO₂ [pCO₂]). We found that San Diego reservoirs are most often undersaturated with CO₂ with respect to the atmosphere and vary seasonally in both different trophic level abundances and pCO₂. pCO₂ was highest in the winter and lower in the summer, indicating seasonal shifts in the magnitudes of photosynthesis and respiration. Microbes (bacteria and fungi) showed peak abundances in the winter, while phytoplankton, nutrients, and DOC were all relatively uncorrelated with pCO₂. Our data indicate that San Diego reservoirs are consistently net photosynthetic and therefore function mainly as sinks of carbon from the atmosphere. pCO₂ was mainly related to seasonal variation in system respiration but not to the abundances of pelagic producers or consumers.

INTRODUCTION

Role of freshwater systems in global C cycle: Why are lakes usually sources?

Feedbacks between ecosystems and the atmosphere determine the fate of anthropogenic CO₂ and the potential for biological sequestration. The physical and biological processes that occur within lakes determine the metabolic balance between respiration and photosynthesis, and therefore whether they sequester or emit CO₂ (Schindler et al. 1997). Since lakes are generally at low positions on the landscape, they receive large quantities of terrestrial detritus, which are either respired, generating CO₂ that escapes to the atmosphere, or stored in the sediments. Lakes with high concentrations of allochthonous dissolved organic carbon (DOC) are therefore often net sources of CO₂ (Prairie et al. 2002; Sobek et al. 2003; Lapierre et al. 2013). However, processes that affect *in situ* primary productivity may affect the rate of biological CO₂ uptake by autotrophs. The supply of inorganic nutrients and rate of grazing by heterotrophic consumers are two factors that play a large role in carbon exchange. Eutrophic lakes with very high productivity are often CO₂ depleted (Larmola et al. 2003). In addition, predators can indirectly control primary production through trophic cascades, resulting in greater CO₂ uptake when herbivores are under strong top-down control (Schindler et al. 1997; Atwood et al. 2013). The relative roles of local ecological interactions vs. processes in the watershed that determine the supply of allochthonous organic material are poorly understood.

Role of reservoirs: Why are they different from lakes and rivers?

Manmade reservoirs contribute about 37% of the global efflux of CO₂ to the atmosphere from all freshwater ecosystems, including lakes, rivers, streams, groundwater, and brackish ecosystems such as wetlands and estuaries (Cole et al. 2007). When a landscape is flooded to create a reservoir, terrestrial plant communities are inundated and organic carbon may either accumulate in sediments or decompose, releasing CO₂ (Molot and Dillon 1996). The decrease in terrestrial photosynthesis and assimilation of CO₂ may result in the loss of an atmospheric CO₂ sink (Kelly et al. 1997). The sequestration of organic carbon in inland water sediments is estimated to exceed the global burial of organic carbon on the ocean floor (Tranvik et al. 2009). Additionally, the global annual amount of organic carbon buried in the sediments of reservoirs and natural lakes combined is three times higher than that in ocean sediments (Dean and Gorham 1998). It is estimated that artificial reservoirs emit twice the quantity of CO₂ compared to natural lakes (St. Louis et al. 2000; Cole et al. 2007). Studies have shown that after a natural area is purposely flooded to create a reservoir, greenhouse gas (GHG) emissions, including CO₂ and CH₄, generally increase rapidly within a period of 10 years, after which emission rates decrease and become equivalent to those normally found in natural lakes (Tremblay et al. 2005). Metabolism of organic carbon compounds by aquatic bacteria in reservoirs can exceed autotroph photosynthesis, resulting in a net source of CO₂ to the atmosphere (Tranvik 1988; del Giorgio et al. 1997). The effect of impoundment on GHG fluxes is the difference between the fluxes of those emissions before and after flooding (St. Louis et al. 2000). The role of reservoirs in the global carbon cycle is therefore uncertain but potentially significant.

Reservoirs in semi-arid environments: History and environment of San Diego reservoirs.

Reservoirs for water storage have been extensively constructed throughout the arid southwest of North America, and represent the largest area of freshwater ecosystems. In San Diego County, most of freshwater for human use is imported. From 2009 to 2013, the five-year average imported water supplies for San Diego County included 63% from the Colorado River, 20% from the Sacramento and San Joaquin rivers, and the last 17% from local supplies including runoff from seven watersheds, groundwater, and recycled waste water (Figure 1) (San Diego County Water Authority 2014a). 24 major reservoirs in the county (Figure 2) store water for human consumption (San Diego County Water Authority 2014b) and are used for recreational activities such as boating and fishing.

There are no known data on how these reservoirs affect regional CO₂ budgets. Additionally, no studies have investigated how the transport of water over great distances and its eventual storage in San Diego affects the carbon cycle in Southern California. With the enactment of California's Assembly Bill 32 in 2006, many counties have been taking steps to reduce GHG emissions, including investigating the impacts of reservoirs on CO₂ and CH₄, such as Lake Oroville in Butte County (Anderson 2009). As water demand increases with continued human population growth, resulting in more construction of dams, it is important to understand the impact of creating and maintaining reservoirs on the global carbon cycle.

Although tropical and temperate reservoirs function mainly as net sources of CO₂ to the atmosphere (Lazzarino et al. 2009; Roehm et al. 2009), studies of the carbon balance of western United States reservoirs have reached contradictory conclusions. Therrien et al. (2005) found that 46 water reservoirs in semi-arid ecosystems throughout

the southwestern U.S. are super-saturated with CO₂ and emit a similar amount of CO₂ per unit area as boreal lakes. In contrast, a study on GHG emissions from six reservoirs throughout Northern California, Washington, Oregon, and Idaho showed that four of the six reservoirs studied were sinks for atmospheric CO₂ (Soumis et al. 2004). Neither of these studies examined temporal variation in net CO₂ flux in reservoirs or its relationship to biological or physical processes. Thus, spatial and temporal variation in the carbon balance of reservoirs, and their relationship to ecosystem structure, remain in question.

Ecological control of pCO₂: DOC, primary production (nutrients and consumers).

Net CO₂ flux between aquatic ecosystems and the atmosphere is determined by the physical processes that regulate gas exchange and biological processes that determine *in situ* rates of photosynthesis and respiration. Wind, water temperature, vertical stratification and concentrations of solutes all affect gas exchange. Dissolved organic carbon (DOC) can also drive high rates of respiration by providing substrate for the growth of aquatic heterotrophic bacteria (Tranvik 1988; Jansson et al. 2000; Sobek et al. 2005). CO₂ supersaturation in lakes and its emission to the atmosphere has been shown to be a result of allochthonous DOC, which drives net heterotrophy and bacteria metabolism (del Giorgio and Peters 1994; Cole et al. 2000; Jansson et al. 2000). Finally, conditions that favor increased autotrophic production, including high nutrient supply or reduced top-down control by grazers, can increase CO₂ uptake and sequestration (Schindler et al. 1997, del Giorgio et al. 1999). The balance of these processes in reservoirs of the semi-arid south west of North America, their seasonal variability and relationship to food web processes, are all poorly understood.

In this study, we estimated seasonal variation in $p\text{CO}_2$ in three San Diego reservoirs along with physical, chemical, and biological factors that may affect rates of ecosystem production and decomposition.

The goal of this study was to elucidate how seasonal changes in food web structure determine the net balance of CO_2 flux between reservoirs and the atmosphere, and addressed two main questions: (1) Do reservoirs in semi-arid ecosystems similar to that of San Diego County sequester or emit atmospheric CO_2 ? (2) How do ecosystem processes regulate CO_2 flux/ $p\text{CO}_2$ in these reservoirs, both spatially and temporally? To explore these questions, we sought to identify the key biotic and abiotic drivers for variation among reservoirs and over time in $p\text{CO}_2$. We sampled three reservoirs in San Diego (Murray, Miramar, and Poway) weekly for the partial pressure of CO_2 , water chemistry, vertical stratification, and the abundances of phytoplankton, bacteria, aquatic fungi and zooplankton in the water column. Our data allowed us to determine how seasonal variation in ecological processes and species interactions influence absorption of atmospheric carbon.

METHODS AND MATERIALS

We sampled three reservoirs in San Diego County: Lake Murray (32.7861⁰ N, 117.0442⁰ W), Lake Miramar (32.9154⁰ N, 117.0988⁰ W), and Lake Poway (33.0069⁰ N, 117.0099⁰W) on a weekly basis a total of 50 times between June 2013 and June 2014. All of the reservoirs contained piscivorous fish, primarily bass, trout, and catfish introduced for sport fisheries. We sampled zooplankton, phytoplankton, bacteria, chytrid fungi, and measured total alkalinity, concentrations of total phosphorous and nitrogen, water and air temperature, pH, salinity, conductivity, partial pressure of CO₂, dissolved oxygen, dissolved organic carbon, particulate organic matter, and C/N ratios. Reservoirs were sampled at the deepest point from a small boat.

Water Chemistry and Organism Collection

A YSI® multiparameter sonde (Xylem Inc.: Professional Plus) was used to measure vertical profiles of water and air temperature (°C), dissolved oxygen (% saturation), dissolved oxygen (mg L⁻¹), barometric pressure (mm Hg), conductivity (µS cm⁻¹), salinity (ppt), pH. The data were recorded throughout the water column every 4 m up to a maximum depth of 20 m. The pH and conductivity probes were calibrated with standard solutions before sampling. When the YSI® was not available for use, a HOBO Pendant® Temperature/Light Data Logger (Onset®: 8K – UA-002-08) was used to measure water and air temperature (°C) and water was collected from a depth of 1 m to analyze pH, conductivity, and salinity in the lab. Conductivity and pH were measured using a VWR® SympHony™ SB80PC Benchtop Meter and salinity was converted from conductivity according to the methods of Eaton et al. (1998).

Surface water samples were collected for measuring phytoplankton (chlorophyll-*a*) biomass, total nitrogen and phosphorus concentrations, abundances of bacteria and chytrid fungi, alkalinity, and particulate organic matter (POM) with a 1m integrated tube sampler. Water samples were filtered through a 63 μ m mesh to remove any zooplankton from the sample, and sample bottles were pre-rinsed with lake water. pCO₂ was determined by running salinity, water temperature, total alkalinity, pH, and total phosphorus values from each reservoir through CO2calc 1.2.0 (Robbins et al. 2010). CO2calc preferences for certain parameters were as follows: salinity was 0 ppt for freshwater; the constants K1 and K2 were from Millero 1979, the acid dissociation constant of bisulfate ion was from Dickson 1990, and pH was used on a NBS scale (mol kg⁻¹ water).

Phytoplankton (chlorophyll-a) biomass

In vivo chlorophyll-*a* (chl-*a*) concentration was measured using a Trilogy® Laboratory Turner Fluorometer as an indicator of phytoplankton biomass. We also compared *in vivo* with extracted chlorophyll by filtering water through a Whatman® 25 mm (0.7 μ m porosity) GF/F which had been pre-combusted in a drying oven at 500 °C for at least four hours. The filter was wrapped in foil and frozen at -20.5 °C until analysis. We analyzed phytoplankton by extracting chl-*a* using methanol and analyzing the sample by fluorometry with a module for extracted chlorophyll.

Total Nitrogen and Phosphorous

Water collected for total nitrogen and phosphorus analysis was preserved in 20 mL scintillation vials, which were rinsed three times with each respective reservoir water before being filled. For the first 25 sampling dates, nutrient samples were preserved with 400 μL sulfuric acid, but after the 25th date, the acidity was reduced to 40 μL sulfuric acid since the lowered acidity was found to provide more accurate nutrient analysis results. With a lowered acidity, there were higher concentrations of TN and TP. The samples were frozen at $-26.5\text{ }^{\circ}\text{C}$ until analysis. To measure total nitrogen and phosphorous concentrations, the QuikChem® Method 10-107-04-4-C and QuikChem® Method 10-115-01-4-C were used respectively on a QuikChem® 8500 Series 2 Flow Injection Analysis System (Lachat Instruments). The data were analyzed using Omnion 3.0 software (Lachat: Hach 2007).

Bacteria and Chytrid Fungi abundance

To measure abundances of pelagic bacteria and chytrid fungi, 10 mL of surface water from each reservoir was collected in pre-rinsed 20 mL scintillation vials. The samples were preserved with 1 mL 20% phosphate buffered saline (PBS) buffered formaldehyde fixing agent. Each sample was mixed thoroughly and stored at room temperature for no longer than two weeks before analyzing samples. Cells were counted by epifluorescence microscopy. Bacteria were stained with DAPI (4',6-diamidino-2-phenylindole) fluorescent stain and chytrid fungi were stained using calcofluor white M2R (Sigma-Aldrich®: Fluorescent Brightener 28). Brown track-etched poly carbonate membrane filters (Millipore® GTBP02500 Isopore™; 0.22 μm porosity, 25 mm

diameter) for bacteria and Cyclopore track etched PC membrane filters (Whatman®; 0.8 µm porosity, 25 mm diameter) for chytrids were rinsed with sterile DI water prior to use. Filters were placed on a Millipore® 1225 Sampling Manifold, and a maximum of 2 mL of lake water was added. If the remaining volume was too high, 0.5-1.5 mL of sample was added and the rest was filled with sterile deionized (DI) water that had been autoclaved at 121 °C and 17 psi for 15 minutes (Tuttnauer®). The well was shaken to disperse the sample evenly and 25 µL DAPI stain (1.25% of sample) was added for bacteria and 400µL calcofluor white M2R (20% of sample) for chytrids. The filter tower was covered to block any light and samples were stained for 20 minutes.

After 20 minutes, solution on top of the filter was removed and any unincorporated stain was rinsed off with 5 mL of sterile DI water. The filters were placed on top of one drop of non-fluorescent immersion oil on a clean microscope slide. One more drop of non-fluorescent immersion oil was placed on top of the filters and they were covered with a cover slip. The slides were kept in the dark until they were counted on an OMAX® EPI-fluorescent microscope (40X-1000X Top Quality Professional Infinite) within one hour. Using a 100X/1.25 objective lens for bacteria (0.22 mm in diameter) and a 40X/0.65 objective lens for chytrids (0.54 mm in diameter), at least 10 sections of each sample were counted. The average number of bacteria and chytrids per counting field were calculated and multiplied by the area of filter and focus to obtain the total number of bacteria and chytrids per liter.

Total Alkalinity

Alkalinity was measured by adding 2 mL of Orion™ total alkalinity solution to 20 mL of water sample. The pH of the sample was measured using a VWR® SympHony™ SB80PC Benchtop Meter and the resulting value was converted to alkalinity using an Orion™ Total Alkalinity Test Kit converter wheel.

Particulate Organic Matter (POM) and C/N ratios

Water for POM was filtered through either a 47 mm or 25 mm Whatman® glass microfiber filter (GF/F: 0.7 µm porosity), which had been pre-combusted in a drying oven at 500 °C for at least four hours. The filter was placed on a Büchner funnel on top of a flask and between 200 mL – 1 L of water sample was filtered depending on the level of productivity within the reservoirs. The filters were individually wrapped in aluminum foil and frozen at -20.5 °C until analysis. Samples were freeze-dried at -70 °C for 24 hours. Before analysis, filters were cut into quarters in a sterile environment, folded up in 9x10 mm aluminum tins (Costech Analytical Technologies Inc.) and desiccated until analysis. The samples were analyzed for carbon/nitrogen content using a ECS 4010 CHNSO Analyzer (Costech Analytical Technologies, Inc.) at Scripps Institution of Oceanography. The elemental analysis ran under Costech software: a semimicro amount of oxygen was used during a 5-minute total run time and water was removed. Five standards and a tin blank were run, spaced evenly throughout the samples. The standards were plotted versus weight and a linear fit was determined for calibration. Particulate organic carbon and nitrogen were determined and C/N ratios were calculated.

Dissolved Organic Carbon

Water for dissolved organic carbon (DOC) analysis was collected at 1m depth, filtered through a Whatman® 25mm GF/F (0.7µm porosity) which was pre-combusted in a drying oven at 500 °C for at least four hours, and into a pre-rinsed 40 mL vial (VWR®TraceClean®). The samples were preserved with 250 µL trace metal grade hydrochloric acid and analyzed with a Shimadzu® TOC-V CSN at Scripps Institution of Oceanography.

Zooplankton

Zooplankton were collected throughout the water column using a 63 µm mesh net (30 cm in diameter) lowered to 2 m above the bottom. One tow was sampled per lake per week resulting in 146 total samples. Zooplankton were preserved with 70% ethyl alcohol: zooplankton were counted by splitting samples using a Wildco® Folsom Plankton Splitter (0.5 L) and at least 179 animals total ($\bar{X} = 331$; *range* = 790) were counted for each aliquot using a Leica M125 stereo microscope. Copepods were counted by order and developmental stages while cladocerans were identified to species. To measure body size of zooplankton in order to estimate population weight, at least 25 animals of each species were photographed per sample using a Leica DFC295 camera and Leica V3.5.0 software. When fewer than 25 animals of a species were present in a sample, all individuals were measured. Animal lengths were measured using ImageJ (Rasband 1997-2014) from digitized analysis of calibrated images, and length-weight regressions (Appendix 1) were used to calculate average individual mass and population biomass.

Statistical Analyses

Multiple regression models including all candidate predictor variables sampled were run to determine main drivers of pCO₂ and pH across all lakes (R Development Core Team 2014). Log transformations were applied to independent variables to normalize variance as necessary, and second order terms were included when relationships were non-linear. The variables included in the base model to predict pCO₂ were as follows: log(conductivity), water temperature, log(POC), log(PON), log(TN), log(TP), log(TA), pH, log(chl-*a*), log(zooplankton community biomass), log(chytrids), log(bacteria), and log(DOC). These variables were used to identify the primary drivers of pCO₂. A stepwise elimination procedure based on AIC minimization (stepAIC in R) was used to identify the variables included in the most likely model. Since pCO₂ was calculated based on water temperature, pH, alkalinity, salinity, and total phosphorus, we also used these variables in a model to predict pCO₂ to determine which were responsible for most of the variation in pCO₂.

RESULTS

We found that pCO₂ concentrations increased during the winter and decreased during summer months in most of the reservoirs (Figure 3). pCO₂ in all reservoirs was primarily undersaturated compared to atmospheric CO₂ concentrations and was significantly different between reservoirs ($F_{(2,141)}$, $P \ll 0.001$). pCO₂ was most often highest in Lake Murray, the most productive of the reservoirs, lowest in Poway, and intermediate in Miramar. Lake Murray showed high pCO₂ during the summer of 2013 before declining around September, and then rising again in the winter months and declining in the following summer. The other two reservoirs showed more consistent patterns of low pCO₂ during the two summers and higher in the winter. The most likely model to predict pCO₂ included log(conductivity), log(zooplankton community biomass), water temperature, log(POC), log(TA), log(bacteria), log(DOC), and pH [Figure 4; Table 1]. However, log(conductivity), log(POC), log(bacteria), and log(DOC) were not significant predictors in the model ($P > 0.05$).

The model to predict pCO₂ based on the variables used to calculate it identified pH as the dominant factor determining pCO₂. pH explained 43.14% of the variation in pCO₂, while the other significant variables explained only between 7.60% and 12.64% of the variation. We therefore constructed a model to predict pH based on the other bio-physical variables that were not included in the calculation of pCO₂. The final model to predict pH included log(chytrids), log(chl-*a*), log(TN), log(POC), log(bacteria), and log(DOC).

Chlorophyll-*a* ($\mu\text{g L}^{-1}$) concentration was consistently highest in Lake Murray and lower in the other two reservoirs (Figure 5). Chl-*a* was higher in Lake Murray in the

winter than the summer, and higher in summer of 2013 than of 2014. The other two reservoirs showed consistent chlorophyll concentrations between 1-2 $\mu\text{g L}^{-1}$ with no pronounced seasonality. Chl-*a* was inversely correlated with zooplankton community biomass in Lake Murray ($r = -0.323$) but not in Lake Poway ($r = 0.001$) or Lake Miramar ($r = -0.047$). The seasonal patterns of pCO_2 were not mirrored in chl-*a* within or among lakes, and chl-*a* was not retained as a significant predictor of pCO_2 in the multiple regression model.

Total nitrogen (mg N L^{-1}) and total phosphorous (mg P L^{-1}) both had low concentrations consistent with oligotrophic conditions, and there were no seasonal trends for either nitrogen or phosphorus in the reservoirs (Figure 6, Figure 7). Lakes Miramar and Murray both showed peaks in total nitrogen concentration that coincided with precipitation events in Sept-Oct of 2013 and March of 2014. Similarly, Lake Poway showed two large peaks of total phosphorous, which coincided with precipitation events in Sept-Oct of 2013.

pH exhibited a seasonal trend of declining values during the winter months and increased during the summer, consistent with increased net ecosystem production in the warm seasons and greater respiration in the winter (Figure 8). Additionally, pH was inversely correlated to pCO_2 ($r = -0.810$). pH was generally highest in Lake Poway, lowest in Lake Miramar and intermediate in Lake Murray. The significant drivers for pH according to the multiple regression model were $\log(\text{chytrids})$, $\log(\text{chl-}a)$, $\log(\text{TN})$, $\log(\text{POC})$, and $\log(\text{DOC})$ [Figure 9; Table 2].

Zooplankton community biomass (mg L^{-1}) was highest in Lake Poway during the summer of 2013 and highest in Lake Murray's in summer of 2014 (Figure 10). Lake

Miramar typically had the lowest biomass and all reservoirs were significantly different in zooplankton biomass ($F_{(2,140)}, p=0.002$). Lake Murray was dominated by small cladocerans and copepods in 2013, while the other two reservoirs had a greater number of larger *Daphnia* and adult copepods. Zooplankton community average length (mm) was greatest in both Lakes Miramar and Poway in 2013 (Figure 11). In the summer of 2014, larger zooplankton became more abundant in Lake Murray and the mean size of the community reached that of the other two reservoirs during the second year.

Bacteria abundance ($\# L^{-1}$) increased during the winter and declined during the summer across all reservoirs (Figure 12). Bacterial abundance was inversely correlated to water temperature ($r = -0.661$). Pelagic chytrid fungi abundance ($\# L^{-1}$) showed the same seasonal trends as bacteria of peaks during the cold season (Figure 13).

Dissolved organic carbon concentrations ($mg C L^{-1}$) were consistently highest in Lake Murray, lowest in Poway and intermediate in Miramar, with relatively little seasonal variation in any of the reservoirs. Concentrations declined slightly during the summer and into the winter of 2013, but stayed relatively low during the summer of 2014 (Figure 14). Particulate organic carbon ($mg C L^{-1}$) [Figure 15] and particulate organic nitrogen ($mg N L^{-1}$) [Figure 16] concentrations both increased during the winter in Lake Murray and showed very high spikes in concentration during the spring in all three reservoirs. Lake Murray consistently had the highest concentrations of POC and PON while Lakes Poway and Miramar had similar, lower concentrations. C/N molar ratios for all reservoirs increased over time but exhibited no seasonal trends (Figure 17).

The water columns for Lakes Murray and Miramar were generally stratified throughout the year except between Oct 2013-Feb 2014 when the water column became mixed (Figure 18). Lake Poway's water column had a homogenous temperature from Sept 2013-Feb 2014 and then remained stratified thereafter. For all lakes, surface water temperatures were high during the summer and decreased during the winter by about 10 °C. Levels of dissolved oxygen (DO; mg L⁻¹) varied in each reservoir (Figure 19). Bottom DO in Lake Murray was very low throughout the year except from Nov 2013-Mar 2014 where concentrations were similar to that of surface DO. Lake Miramar exhibited a similar seasonal trend in DO except bottom DO remained at higher concentrations than Lake Murray. Lake Poway's DO was very different from the other reservoirs wherein bottom DO concentrations were very similar to surface DO concentrations except in Mar-June 2014 when surface and bottom DO differed by an average of 5 mg L⁻¹.

DISCUSSION

We found that three reservoirs in San Diego, CA were primarily undersaturated with CO₂ through an entire annual cycle, in contrast with those in more heavily vegetated temperate or tropical environments that function as sources of carbon to the atmosphere (Sobek et al. 2007; Roehm et al. 2009). This result suggests that biological uptake through photosynthesis and storage in sediments exceeded microbial respiration at most times of the year. In addition, pCO₂ increased in the winter and declined in the summer, indicating that seasonal variation in net ecosystem production is the primary driver of carbon flux. In the winter where daily light is limited, there would be less primary production and more heterotrophic respiration, resulting in higher pCO₂ concentrations. Finally, temporal variation in pCO₂ was related to nutrients that limit production (N and or P) but not chlorophyll-*a* concentration, the biomass of zooplankton, or the abundance of bacteria or pelagic fungi (chytrids). This pattern suggests that bottom-up control of primary production via limiting nutrients is the major control on the direction of CO₂ flux rather than top-down effects of grazing or interactions with microbes.

We measured *in situ* chl-*a* concentration as an indicator of the standing biomass of phytoplankton. However, chlorophyll-*a* may be poorly correlated with primary production, especially on a whole-lake scale. There were no clear seasonal trends in chl-*a*, indicating that nutrient concentrations maybe better indicators of primary production. In addition, net production is likely to be higher in the summer when temperatures are warmer and days are longer, although we saw no increase in the standing biomass of phytoplankton. Highly eutrophic lakes tend to function as carbon sinks due to high biological uptake, while dystrophic lakes emit CO₂ due to respiration of allochthonous

organic matter (Pacheco et al. 2013). However, seasonal and spatial variability in chlorophyll concentration did not correspond to variation in $p\text{CO}_2$ in our study, likely because variation in production within or among our reservoirs was small compared to the global range. We saw maximum chl-*a* concentrations around $10 \mu\text{g L}^{-1}$, indicating that the reservoirs were always within the oligotrophic-mesotrophic range. Our data indicate that variation in productivity within this range is not sufficient to alter patterns of $p\text{CO}_2$.

Reservoirs in San Diego are in a Mediterranean-type climate with precipitation only during the winter. Several precipitation events in the winter corresponded with spikes in TN for Lakes Murray and Miramar and spikes in TP for Lake Poway, but no detectable changes in DOC, POC or PON. N and P were likely leached from soil surrounding the reservoirs and deposited into the water column via runoff, but significant quantities of allochthonous organic matter were not introduced.

Studies of $p\text{CO}_2$ in reservoirs in semi-arid ecosystems or the western United States have been carried out on larger spatial scales, but with much less temporal resolution than our study (Therrien 2005). Soumis (2004) found that reservoirs in temperate regions, such as northern California, Oregon, Washington, and Idaho are primarily sinks for CO_2 , and Therrien (2005) demonstrated that reservoirs in the southwest were sources for CO_2 . These studies only sampled lakes for one or two days and focused on physico-chemical variables alone as drivers for $p\text{CO}_2$. They also did not include biological variables, discounting the possible effect that food web dynamics could be used to explain variations in abiotic trends and ultimately carbon sequestration.

The contrasts between these studies, in which reservoirs surrounded by terrestrial vegetation were CO₂ sinks and non-vegetated reservoirs were sources, indicate that a more thorough analysis is needed and for a longer time span. Our study demonstrated how seasonal trends in food web structure and climate variables are related to spatial and temporal variation in pCO₂. Since our data indicates that seasonal trends in nutrients, temperature and primary production are important drivers for pCO₂ in reservoirs of Southern California.

Most studies on pCO₂ have shown that reservoirs worldwide are primarily sources of C to the atmosphere (St. Louis et al. 2000; Sobek et al. 2005; Cole et al. 2007). These studies have mostly been conducted in highly vegetated systems, such as tropical and temperate forests (Marotta et al. 2009; Barros et al. 2011) where allochthonous inputs of terrestrial detritus are much higher and nutrients, such as N and P, are often leached from soils into reservoirs (Howarth et al. 1996; Peixoto et al. 2013). Allochthonous organic matter that is respired by heterotrophic microbes increases pCO₂ and C emissions to the atmosphere (Tranvik 1988; del Giorgio and Peters 1994; Cole et al. 2000; Jansson et al. 2000; Sobek et al. 2005). We observed very low and relatively constant DOC concentrations around 3-5 mg L⁻¹, which is low compared to the global mean of around 7 mg L⁻¹ (Sobek et al. 2007). Without high levels of decomposition of vegetation occurring within semi-arid reservoirs, primary production may exceed heterotrophic respiration and lead to a sequestration of atmospheric C. Thus, organic matter may be buried in their sediments for long periods of time throughout the year until either water from the bottom of the reservoir is released or when upwelling occurs.

Although variation in chlorophyll-*a* was not associated with pCO₂, we observed seasonal changes in chl-*a* concentrations across the reservoirs. In Lake Murray, concentrations were consistent until zooplankton community biomass and average length size for zooplankton increased in 2014, which was accompanied by a decline in chl-*a* concentrations. This suggests that an increase in abundance of large bodied zooplankton and elevated grazing pressure resulted in lower biomass of phytoplankton. In contrast, Lakes Miramar and Poway did not exhibit any seasonal or interannual changes in chl-*a* concentrations or zooplankton abundance or size structure. Although Lake Murray was more eutrophic than the other two for most of the study, it did not show consistently lower pCO₂ as we would expect if variation in primary production is the major factor controlling pCO₂.

Increases in pCO₂ during the winter may have been a result of heterotrophic respiration exceeding photosynthesis by phytoplankton during periods of greater light limitation and lower temperatures. Microbes that degrade organic matter, including both pelagic fungi and bacteria, also increased during colder months and may have contributed to higher respiration and greater pCO₂ (del Giorgio et al. 1997). During the winter, the water became less stratified, both in temperature and dissolved oxygen concentrations. With a more homogenous water column, sediment and buried organic matter from the bottom of the reservoirs could be brought up to the surface via upwelling/mixing and potentially be decomposed by pelagic bacteria.

Zooplankton community biomass did not show a consistent seasonal trend across all reservoirs, but there were large changes in community structure within each lake.

These changes over time were not strongly correlated with chl-*a*, indicating that zooplankton communities did not regulate phytoplankton biomass, except in Lake Murray where increases in zooplankton biomass and mean size in the summer of 2014 were associated with lower chlorophyll-*a* concentrations. This suggests that changes in the fish community or other factors caused shifts in the zooplankton community of Lake Murray. The average lengths for zooplankton were consistent over time in Lakes Miramar and Poway, but increased in Lake Murray during the spring. This increase in zooplankton size corresponds to the decrease in chl-*a* concentrations, indicating that zooplankton in Lake Murray had an effect on primary production.

The concentrations of DOC in the reservoirs we studied were uncorrelated with pCO₂, in contrast with most studies estimating CO₂ flux in reservoirs (Lennon 2004; Sobek et al. 2003; Sobek et al. 2007). We may have observed no association between DOC and pCO₂ because the concentrations were very low compared to the global range (Sobek et al. 2007). In addition, we saw little seasonality in DOC in contrast with temperate regions with deciduous vegetation that produces an annual leaf drop in the fall (Cottingham and Narayan 2013). Our bulk measure does not distinguish between DOC of autochthonous vs. allochthonous origin. The quality of terrestrial DOC as substrate for microbes is much lower than that produced by aquatic producers, and this difference may be important to determining pCO₂ (McKnight et al. 2001). However, our results show no evidence that spatial or seasonal variations in DOC concentration are a significant for determining pCO₂ in the studied reservoirs.

Ongoing changes in climate are likely to produce declines in the availability and quality of freshwater resources worldwide. This trend is likely to increase pressure to construct impoundments to capture more surface water for human uses. For instance, in spring 2014, San Vicente Reservoir in San Diego was expanded to hold double the volume of water than it originally held when it was built in 1947 (San Diego County Water Authority 2014c). Thus, it is essential to understand how water storage contributes to the global carbon cycle and whether feedbacks are likely to accelerate or dampen ongoing emissions of greenhouse gases to the atmosphere. In San Diego County, California, reservoirs are the main impoundments for human consumption and cover 0.46% of San Diego's surface area (California Department of Water Resources 2014; SDFish.com 2014; City of San Diego 2014). We found that three of the 24 major reservoirs in San Diego County are undersaturated in CO₂ throughout the year. Increased construction of reservoirs to store water is therefore unlikely to provide a significant new source of CO₂ to the atmosphere. Our data also indicate that seasonal changes in photosynthesis, driven by light availability and temperature, drive pCO₂ dynamics over time more than the abundances of consumers of phytoplankton (including zooplankton, bacteria, and fungi), or the concentration of DOC. Our results provide a framework for forecasting the impacts of reservoir construction in the arid southwest of North America on the regional carbon budget, and for understanding the ecological and environmental constraints on CO₂ uptake in these anthropogenic ecosystems.

FIGURES

*Sources of San Diego County's Water Supply
(2009-2013 five-year average)*



Figure 1. Sources of San Diego County's water supply over a five-year average [2009 – 2013] (San Diego County Water Authority 2014a).

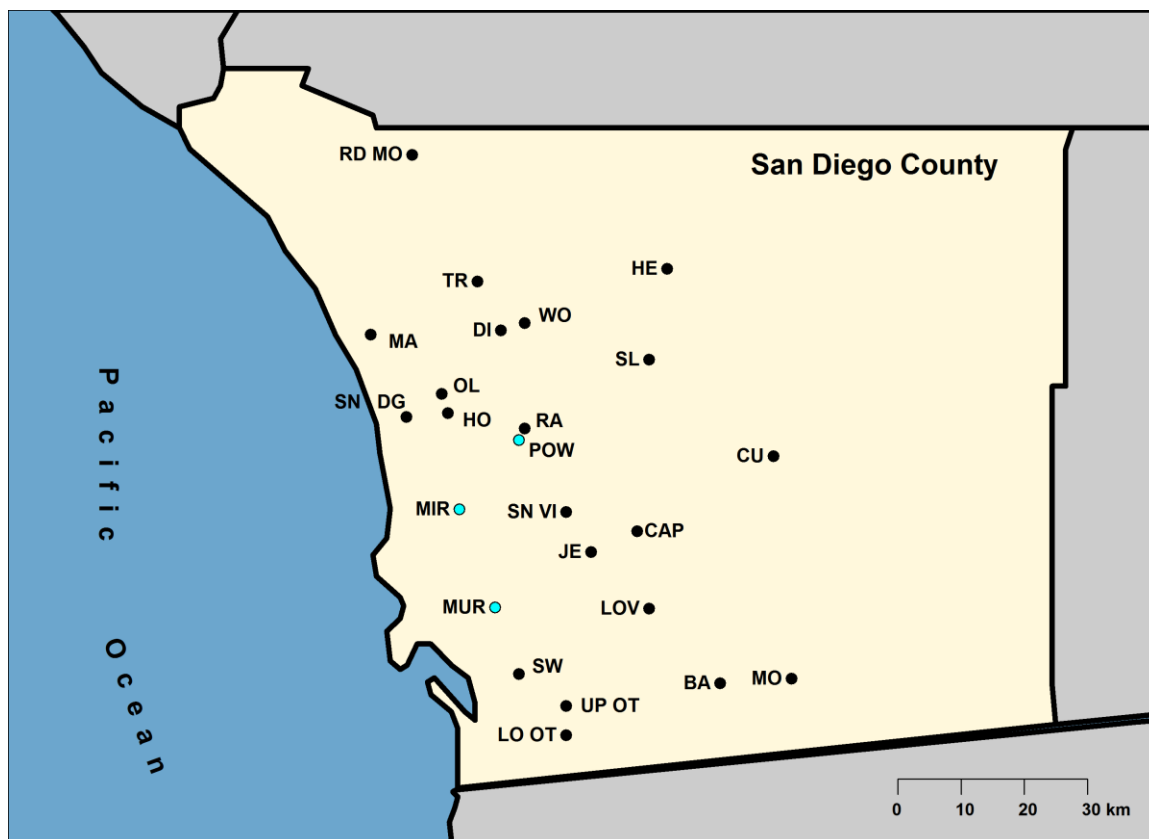


Figure 2. 24 major reservoirs in San Diego County (San Diego County Water Authority 2014b). Barret (BA) 32°68' N, 116°67' W; Cuyamaca (CU) 32°99' N, 116°58' W; Dixon (DI) 33°16' N, 117°04' W; El Capitan (CAP) 32°89' N, 116°81' W; Henshaw (HE) 33°24' N, 116°76' W; Hodges (HO) 33°05' N, 117°13' W; Jennings (JE) 32°86' N, 116°89' W; Loveland (LOV) 32°78' N, 116°79' W; Lower Otay (LO) 32°61' N, 116°93' W; Maerkle (MA) 33°15' N, 117°11' W; **Miramar (MIR) 32°91' N, 117°11' W**; Morena (MO) 32°69' N, 116°55' W; **Murray (MUR) 32°78' N, 117°05' W**; Olivenhain (OL) 33°07' N, 117°14' W; **Poway (POW) 33°01' N, 117°01' W**; Ramona (RA) 33°02' N, 117°00' W; Red Mountain (RD MO) 33°40' N, 117°19' W; San Dieguito (SN DG) 33°04' N, 117°20' W; San Vicente (SN VI) 32°91' N, 116°93' W; Sutherland (SL) 33°12' N, 116°79' W; Sweetwater (SW) 32°69' N, 117°01' W; Turner (TR) 33°22' N, 117°08' W; Upper Otay (UP OT) 32°65' N, 116°93' W; Wohlford (WF) 33°17' N, 117°00' W. **Bolded reservoirs marked by blue points are the three we studied.**

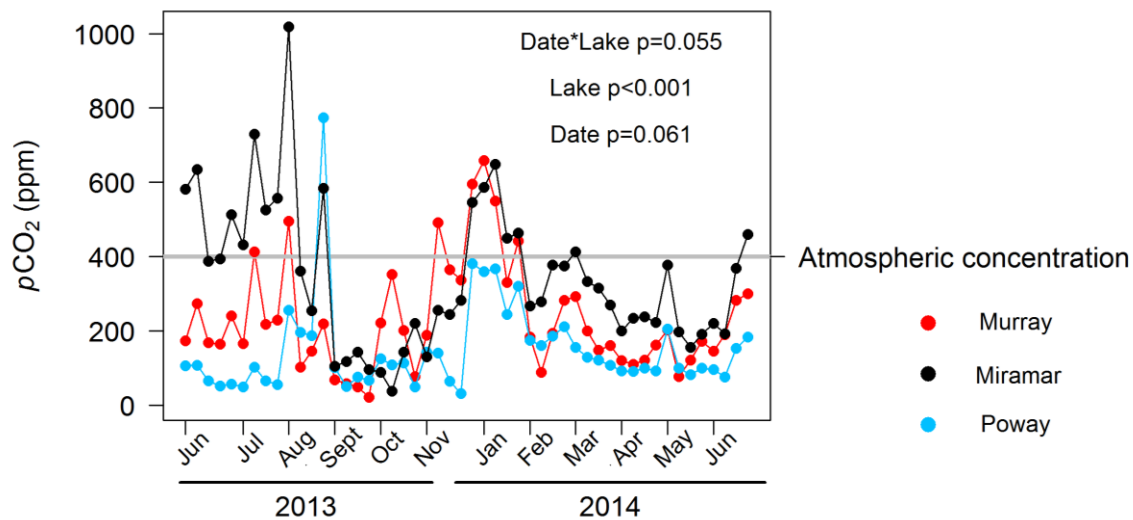


Figure 3. Partial pressure of carbon dioxide ($p\text{CO}_2$) in ppm for 50 sampling weeks. $p\text{CO}_2$ for all reservoirs is generally undersaturated compared to atmospheric concentrations of $p\text{CO}_2$ (~400ppm). Average $p\text{CO}_2$ concentrations for all reservoirs are as follows: Murray \bar{X} = 231.87 ppm, Miramar \bar{X} = 344.72 ppm, and Poway \bar{X} = 149.25 ppm. The average $p\text{CO}_2$ for all lakes was 241.95 ppm. $p\text{CO}_2$ concentrations increased during the winter and decreased during the summer.

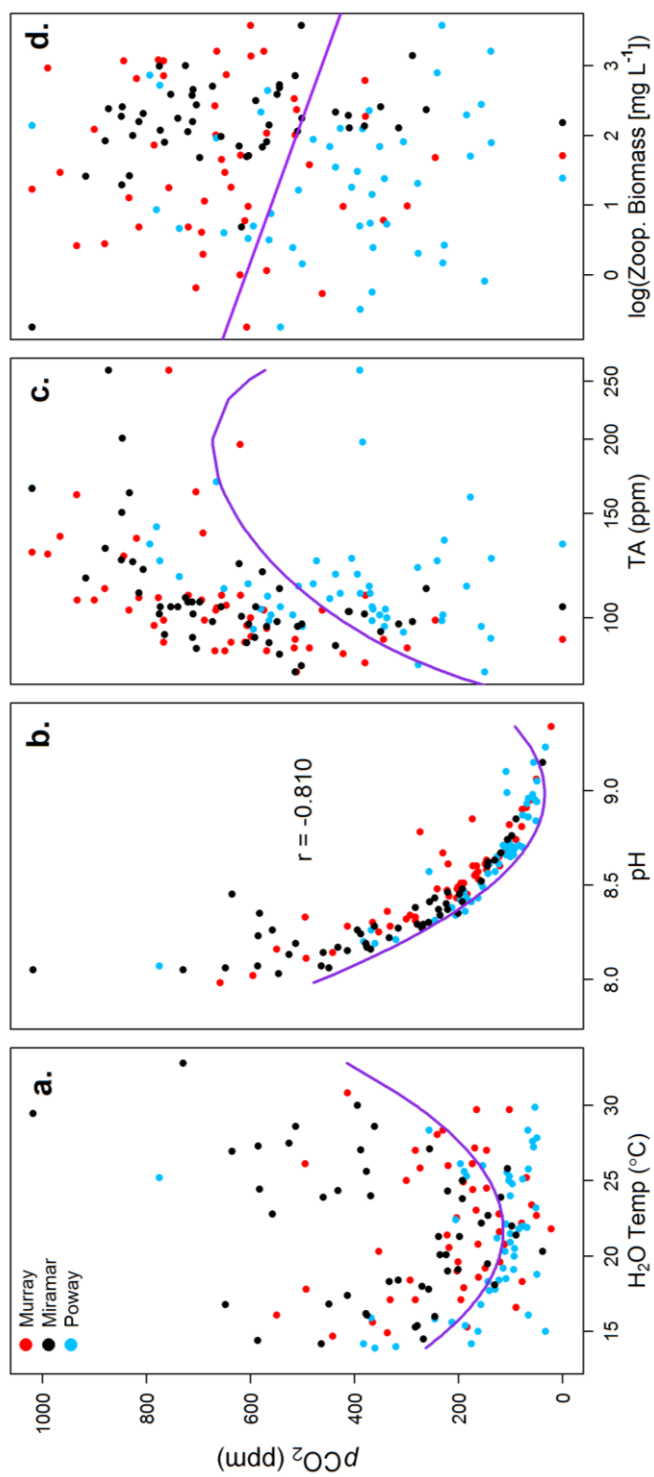


Figure 4. Significant drivers of $p\text{CO}_2$ across all reservoirs **a.** water temperature ($^\circ\text{C}$) **b.** pH **c.** total alkalinity (ppm) **d.** zooplankton community biomass (mg L^{-1}). pH was inversely correlated to $p\text{CO}_2$ ($r = -0.810$).

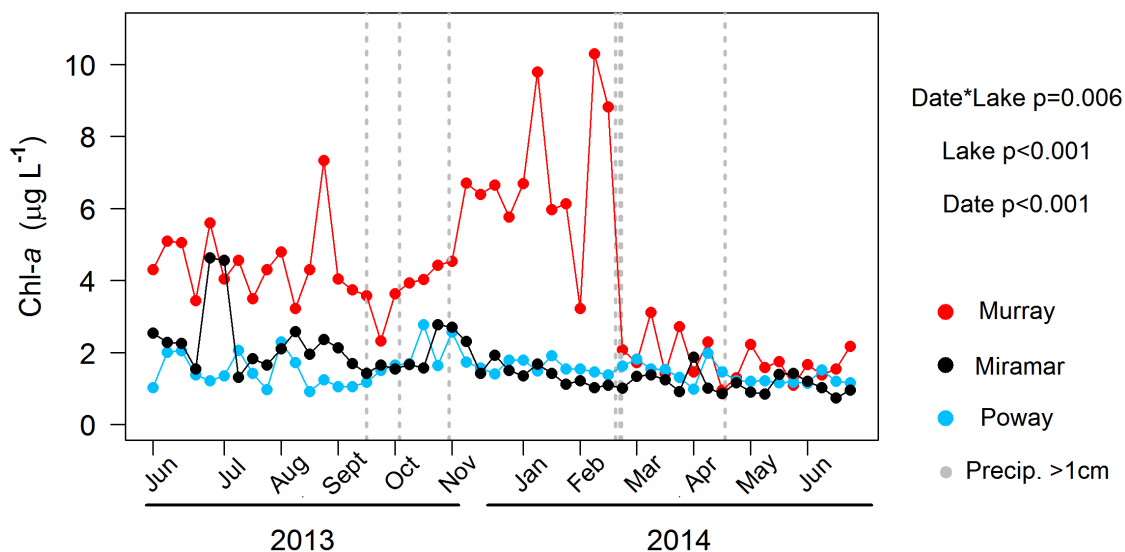


Figure 5. Chlorophyll-*a* ($\mu\text{g L}^{-1}$) for 50 sampling weeks. Chl-*a* concentrations were consistent across all three reservoirs with Lake Murray containing the highest concentration ($\bar{X}=4.017 \mu\text{g L}^{-1}$) which decreased in the spring. Lakes Miramar and Poway alternated with the lowest concentrations of chl-*a* (Miramar $\bar{X}=1.684 \mu\text{g L}^{-1}$, Poway $\bar{X}=1.516 \mu\text{g L}^{-1}$) and precipitation events did not have an effect on phytoplankton biomass.

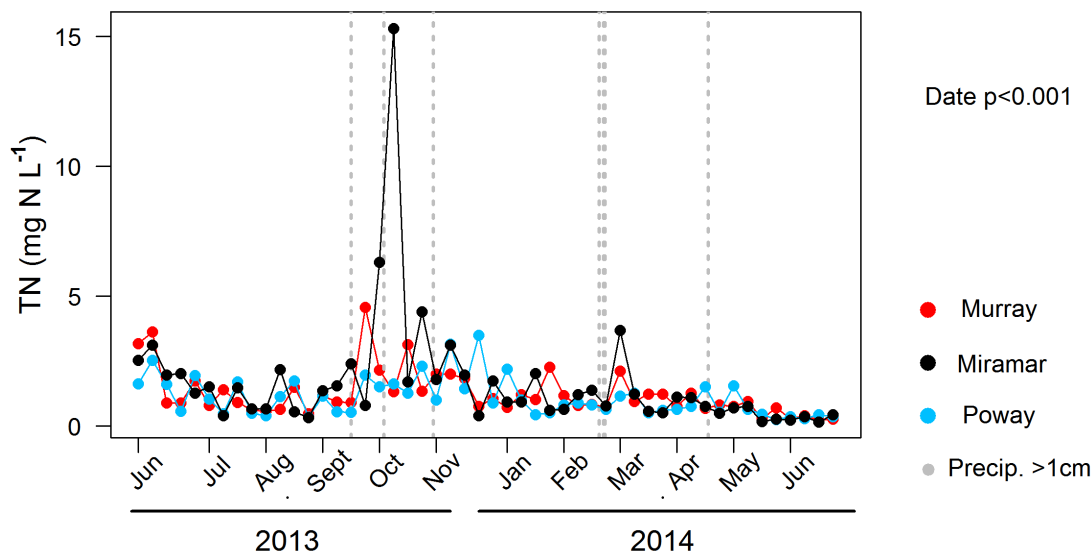


Figure 6. Total nitrogen (TN) concentrations (mg N L^{-1}) for each reservoir for 50 sampling weeks. Average TN concentrations for each lake are as follows: Murray $\bar{X}=1.244 \text{ mg N L}^{-1}$, Miramar $\bar{X}=1.652 \text{ mg N L}^{-1}$, and Poway $\bar{X}=1.104 \text{ mg N L}^{-1}$ and average TN across all lakes was 1.33 mg N L^{-1} . Lakes Miramar and Murray had peaks in TN concentrations ($4.5 - 15.3 \text{ mg N L}^{-1}$) after precipitation events.

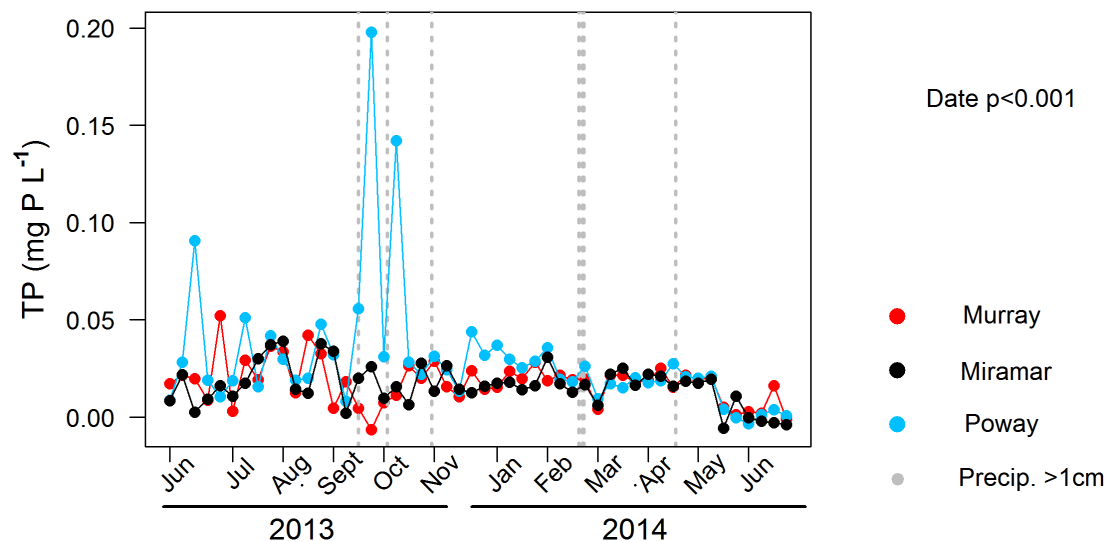


Figure 7. Total phosphorus (TP) concentrations (mg P L^{-1}) for each reservoir for 50 sampling weeks. Average TP concentrations for each lake are as follows: Murray $\bar{X}=0.018 \text{ mg P L}^{-1}$, Miramar $\bar{X}=0.016 \text{ mg P L}^{-1}$, and Poway $\bar{X}=0.030 \text{ mg P L}^{-1}$. Average TP across all lakes was 0.02 mg P L^{-1} . Lake Poway had large peaks in TP concentrations ($0.14 - 0.20 \text{ mg P L}^{-1}$) after two precipitation events.

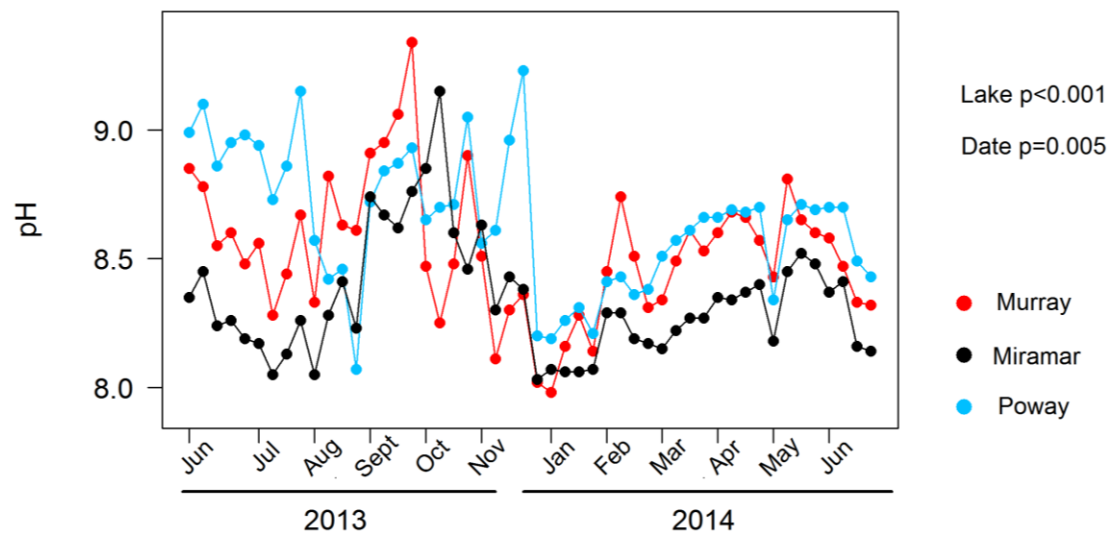


Figure 8. pH for each reservoir for 50 sampling weeks. pH was generally highest in Lake Poway and lowest in Lake Miramar. pH decreased during the winter and increased during the summer. Average pH for each reservoir are as follows: Lake Murray ($\bar{X}=8.530$), Lake Miramar ($\bar{X}=8.339$), and Lake Poway ($\bar{X}=8.649$). The average pH across all lakes was 8.51.

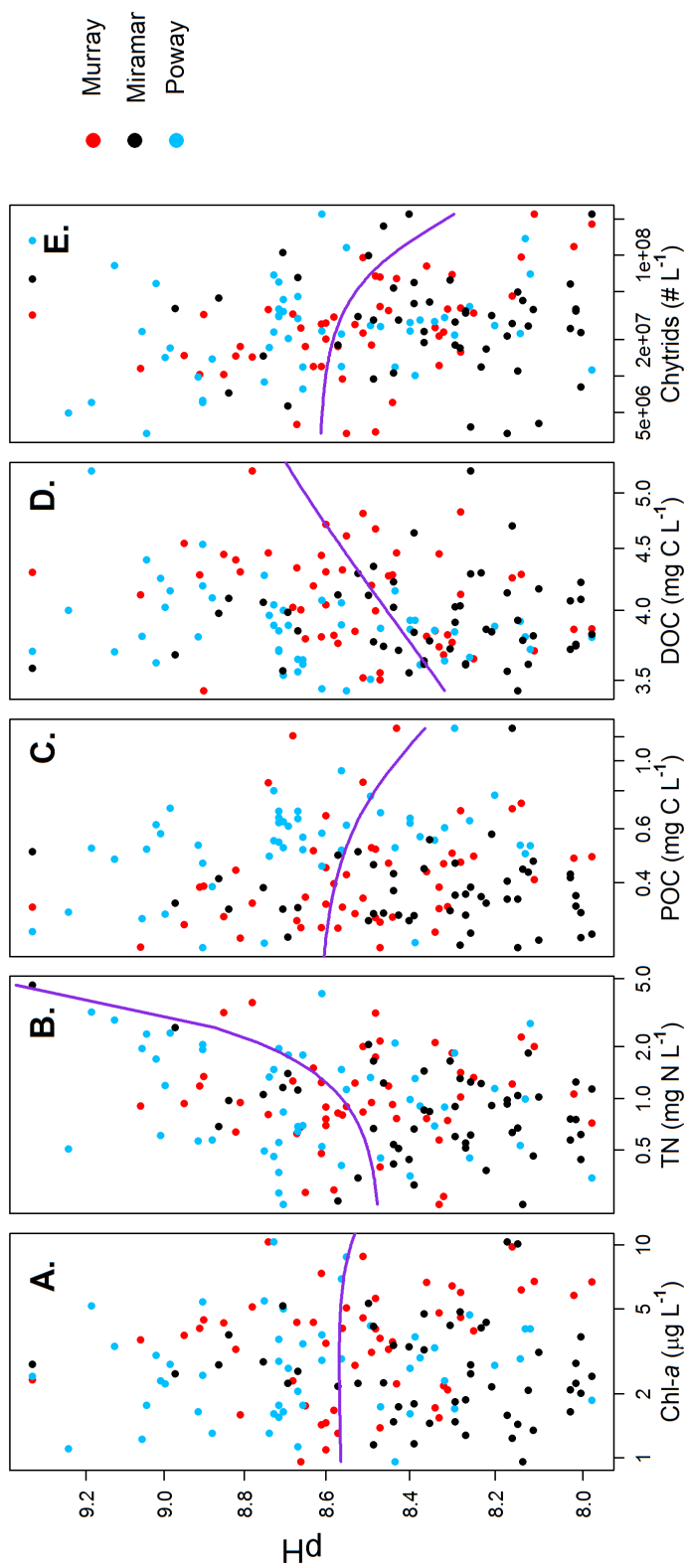


Figure 9. Significant drivers of pH across all reservoirs **A.** chlorophyll-*a* ($\mu\text{g L}^{-1}$) **B.** total nitrogen (mg N L^{-1}) **C.** particulate organic carbon (mg C L^{-1}) **D.** dissolved organic carbon (mg C L^{-1}) **E.** chytrid fungi ($\# \text{ L}^{-1}$)

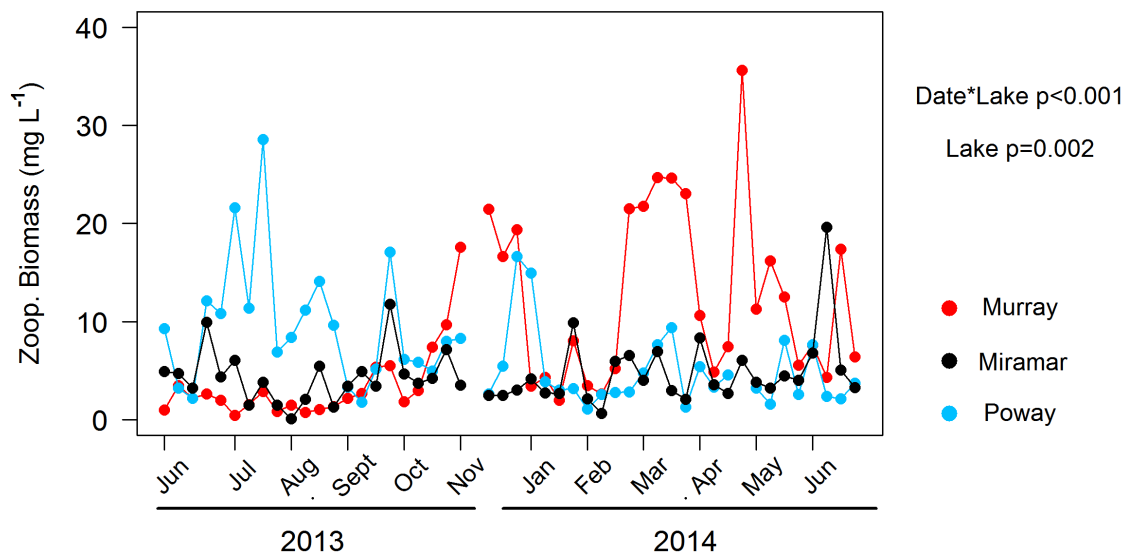


Figure 10. Zooplankton community biomass (mg L^{-1}) for all reservoirs for 49 sampling weeks. Zooplankton biomass in Lake Poway ($\bar{X}=7.028 \text{ mg L}^{-1}$) was high during the summer and low during the winter while Lake Murray's biomass ($\bar{X}=8.558 \text{ mg L}^{-1}$) was low during the winter and rose during the summer. Lake Miramar had the lowest average biomass ($\bar{X}=4.618 \text{ mg L}^{-1}$).

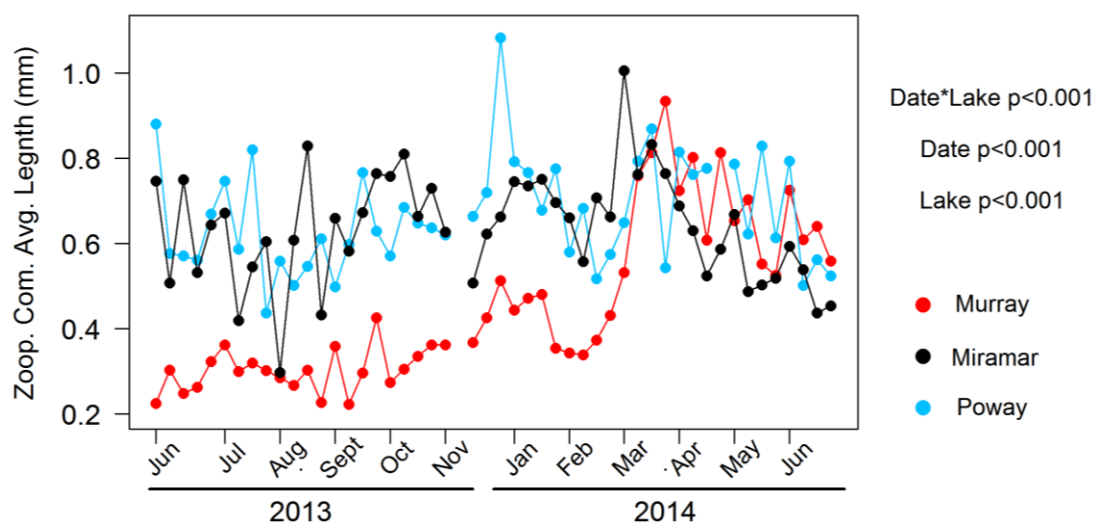


Figure 11. Zooplankton community average length (mm) for all reservoirs over 50 sampling weeks. Lakes Miramar and Poway had the greater average zooplankton lengths than Murray (Murray $\bar{X}=0.453 \text{ mm}$, Miramar $\bar{X}=0.636 \text{ mm}$, Poway $\bar{X}=0.668 \text{ mm}$). There were no seasonal trends for average zooplankton lengths for Lakes Miramar and Poway but Lake Murray's average zooplankton length increased during spring months.

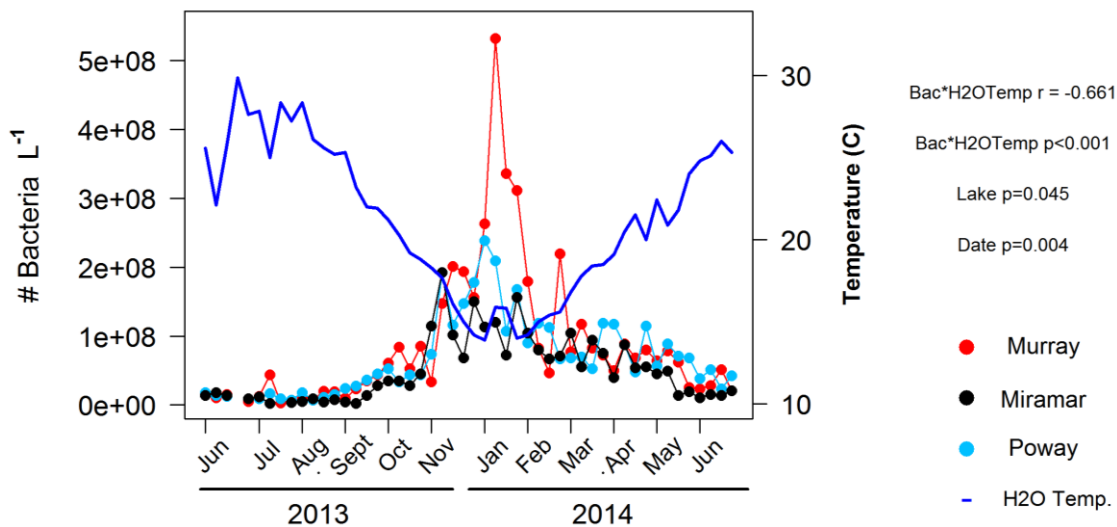


Figure 12. Bacteria abundance ($\# \text{L}^{-1}$) for all reservoirs for 50 sampling weeks. Bacteria abundance increased during colder months and decreased during warmer months. Abundance was inversely correlated to water temperature ($r = -0.661$).

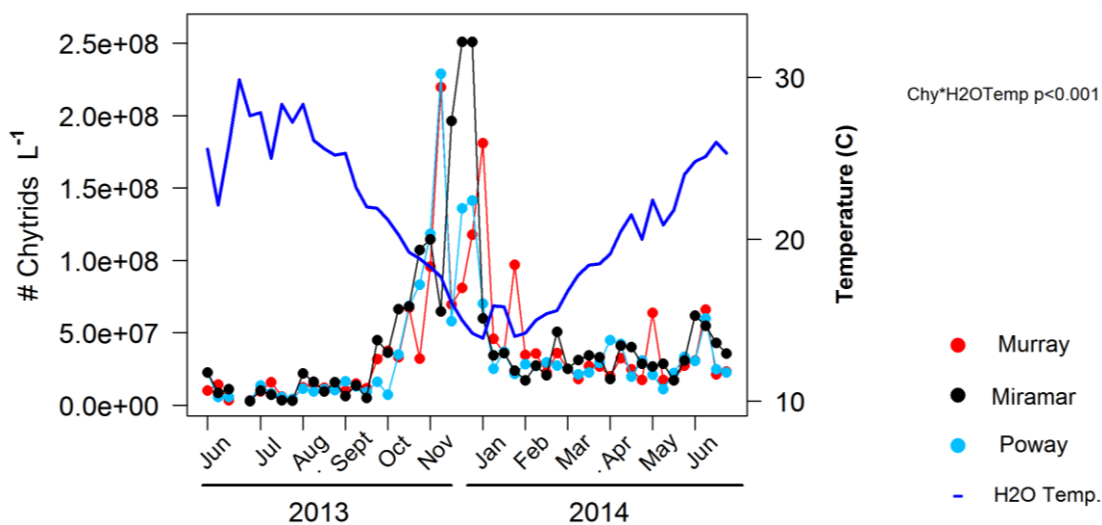


Figure 13. Chytrid abundance ($\# \text{L}^{-1}$) for all reservoirs for 50 sampling weeks. Chytrid abundance increased during colder months and decreased during warmer months.

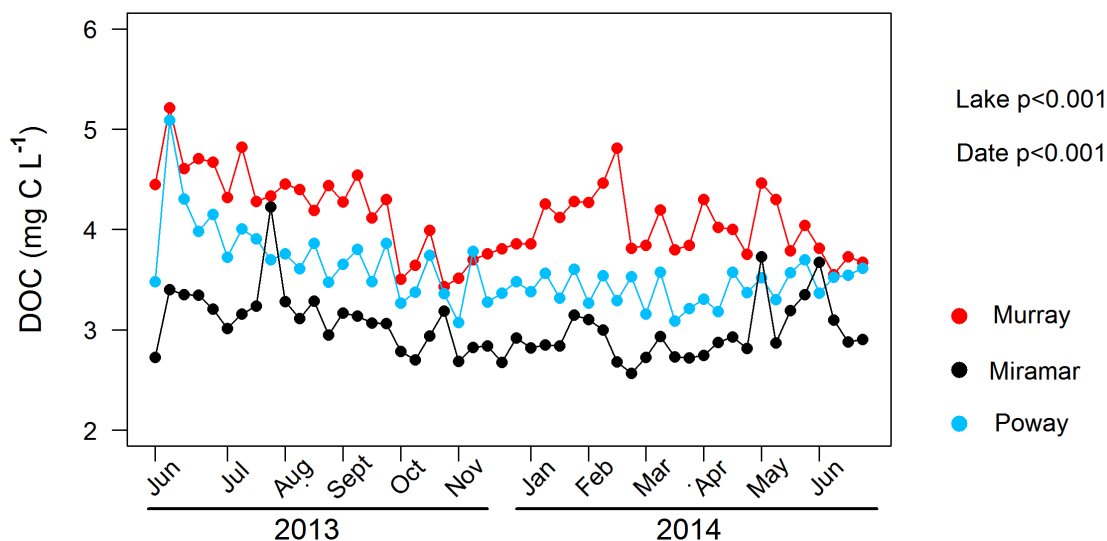


Figure 14. Dissolved organic carbon (DOC) concentrations (mg C L^{-1}) for all reservoirs for 50 sampling weeks. DOC concentrations were consistent across lakes with Lake Murray containing the highest concentration ($\bar{X}=4.127 \text{ mg C L}^{-1}$) and Lake Miramar containing the lowest concentration ($\bar{X}=3.030 \text{ mg C L}^{-1}$). Lake Poway had an average DOC concentration of $3.574 \text{ mg C L}^{-1}$. The concentrations of all reservoirs decreased during colder months and increased during warmer months.

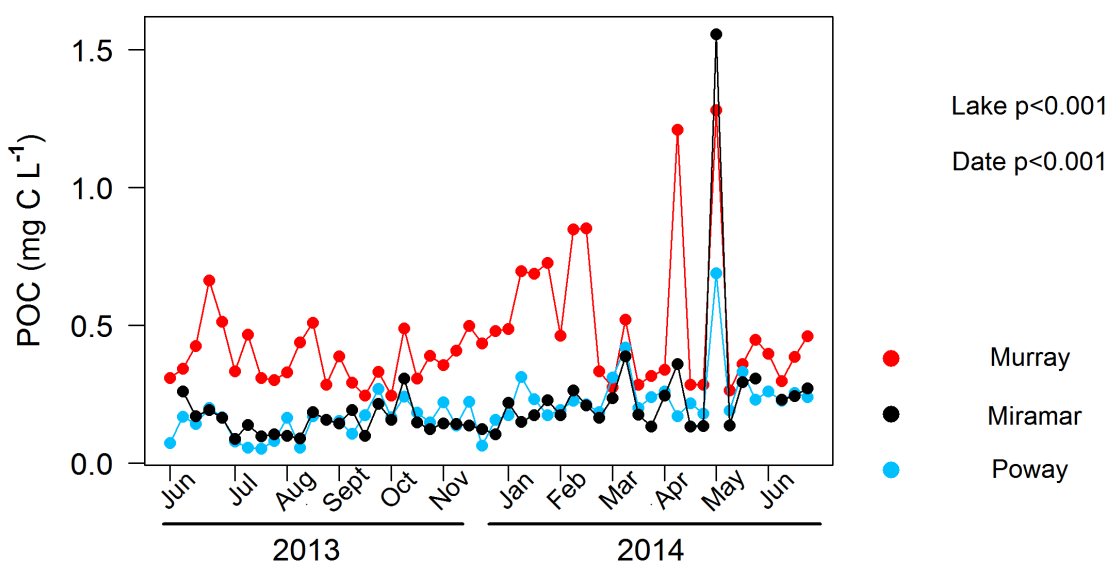


Figure 15. Particulate organic carbon (POC) concentrations (mg C L^{-1}) for each reservoir for 50 sampling weeks. Lake Murray had the highest POC concentration ($\bar{X}=0.452 \text{ mg C L}^{-1}$) and Lakes Miramar and Poway fluctuated in containing the lowest POC concentrations (Miramar $\bar{X}=0.213 \text{ mg C L}^{-1}$, Poway $\bar{X}=0.200 \text{ mg C L}^{-1}$). In spring, all lakes had spikes in POC concentrations.

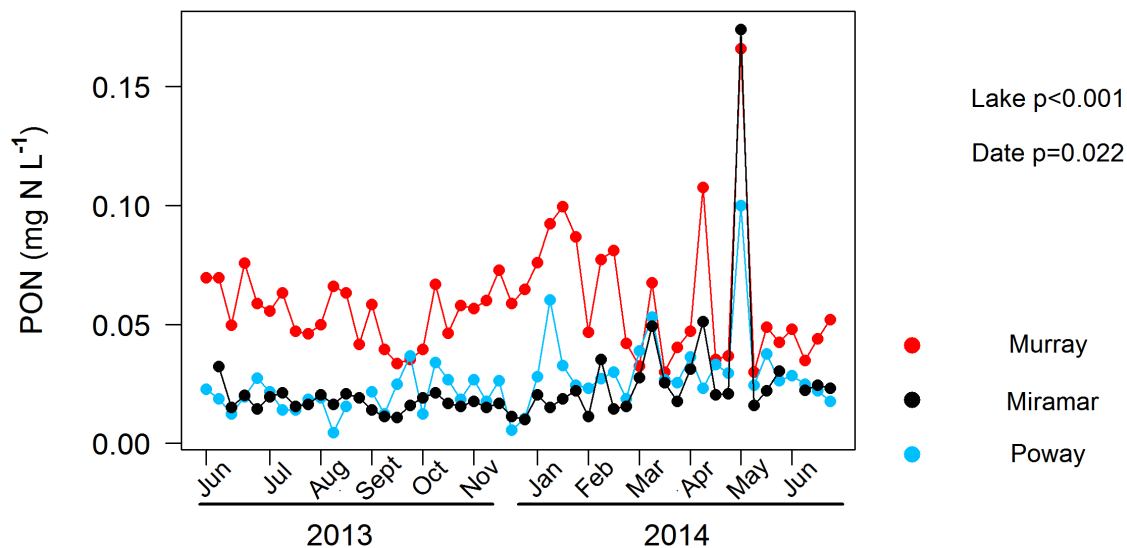


Figure 16. Particulate organic nitrogen (PON) concentrations (mg N L⁻¹) for each reservoir for 50 sampling weeks. Lake Murray had the highest PON concentration (\bar{X} = 0.058 mg N L⁻¹) and Lakes Miramar and Poway fluctuated in containing the lowest PON concentrations (Miramar \bar{X} = 0.024 mg N L⁻¹, Poway \bar{X} = 0.026 mg N L⁻¹). In spring, all lakes had spikes in PON concentrations.

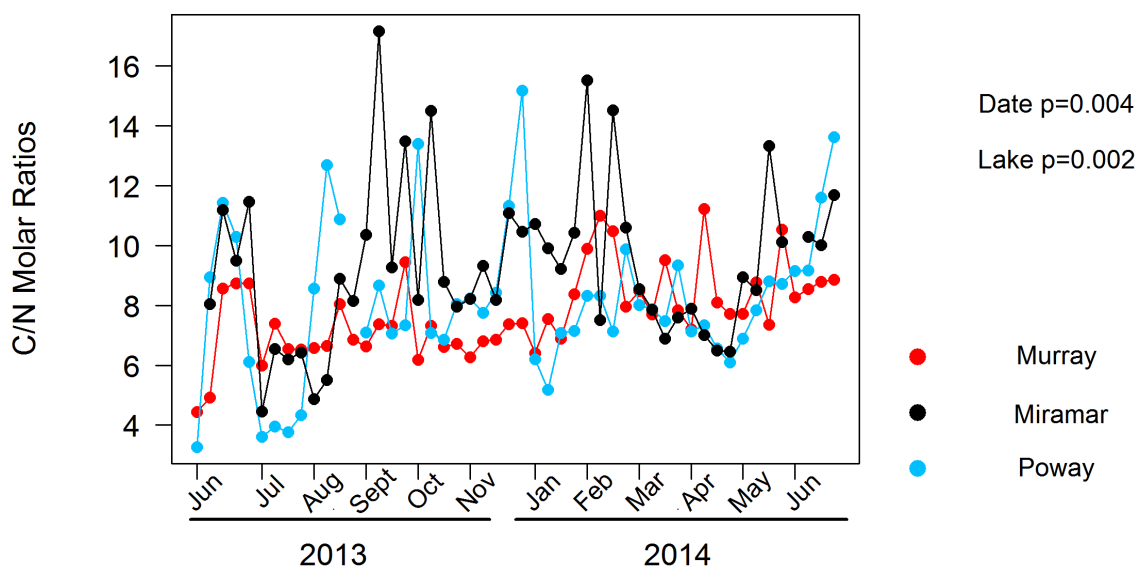


Figure 17. Carbon/nitrogen (C/N) molar ratios for all reservoirs over 50 sampling weeks. The C/N ratios for all reservoirs increased over time, but there was no seasonality.

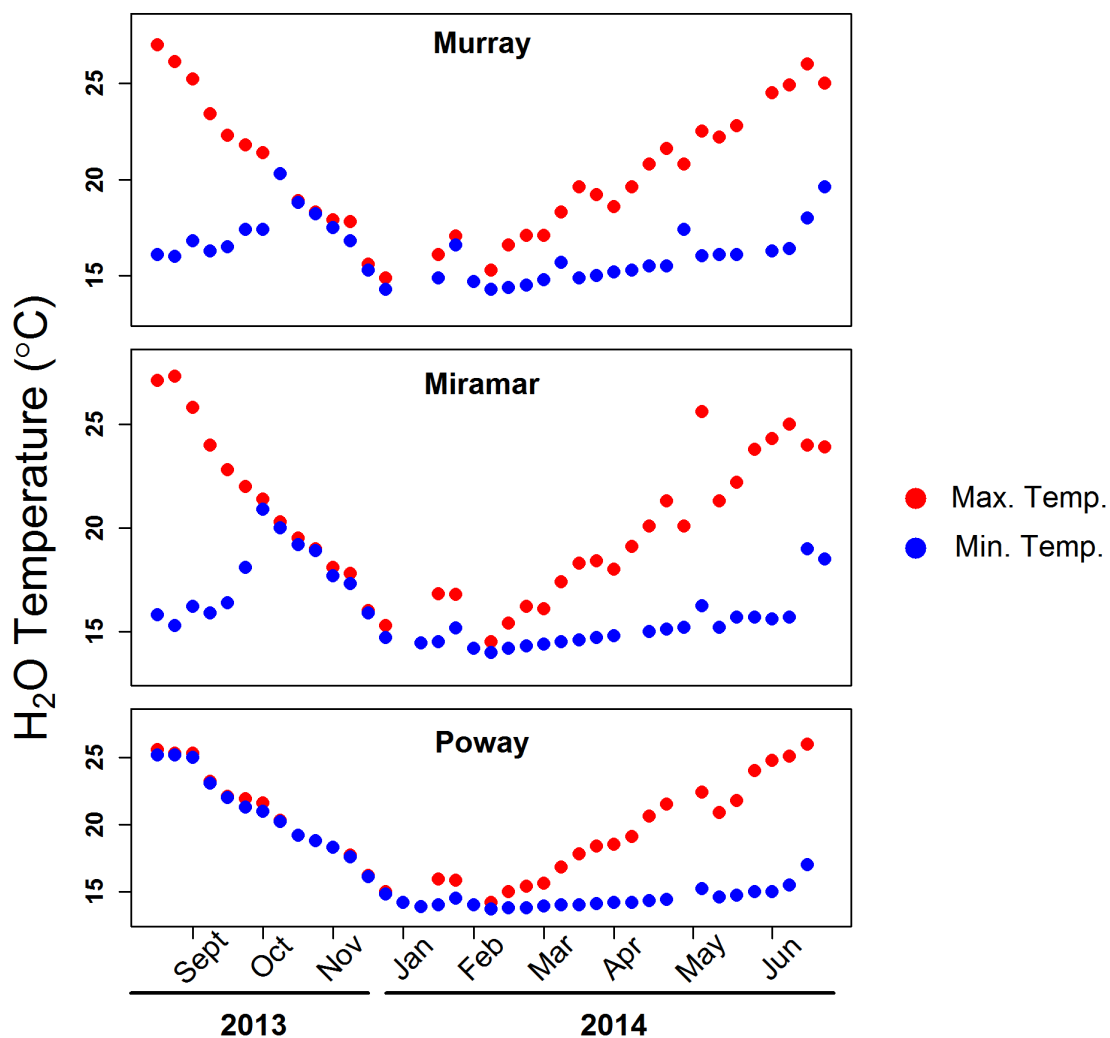


Figure 18. Minimum and maximum water temperatures (°C) for each reservoir over 37-38 sampling weeks from Sept 2013-June 2014. The water columns for Lakes Murray and Miramar were generally stratified throughout the year except for Oct 2013-Feb 2014 where both surface water and bottom temperatures were nearly equal. Lake Poway's water column was homogenous in temperature from Sept 2013-Feb 2014 and then it became stratified. For all lakes, surface water temperatures were high during the summer and decreased during the winter by about 10 °C.

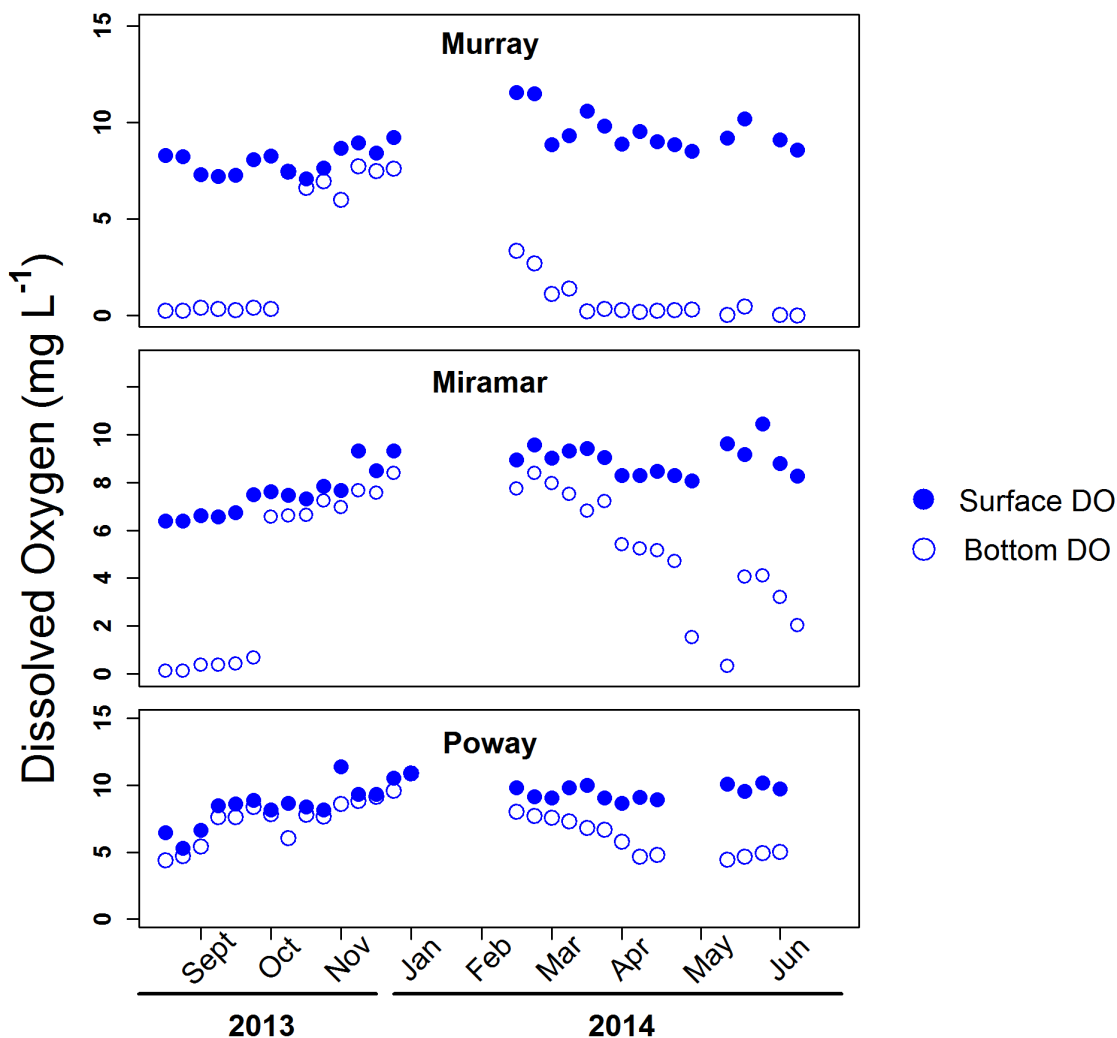


Figure 19. Surface and bottom dissolved oxygen (DO) concentrations (mg L^{-1}) for all reservoirs over 28-30 sampling weeks. Lakes Murray and Miramar typically had different surface and bottom DO concentrations throughout the year except for Oct 2013-Feb 2014 where both surface water and bottom DO concentrations (mg L^{-1}) were nearly equal. Lake Poway's water column was homogenous in DO from Sept 2013 – Feb 2014 and then DO between surface and bottom separated. The average surface DO concentration for each lake are as follows: Murray $\bar{X}= 5.66 \text{ mg L}^{-1}$, Miramar $\bar{X}= 6.67 \text{ mg L}^{-1}$, Poway $\bar{X}= 7.88 \text{ mg L}^{-1}$. The average surface DO concentration for all lakes was 6.72 mg L^{-1} .

TABLES

Table 1. Multiple regression model for partial pressure of carbon dioxide (pCO₂) as a function of variables sampled.

Model term	Estimate	Std. Error	t-value	p-value	
log(conductivity)	-67.118	47.454	-1.414	0.160	
log(zoop. com. biomass)	-16.118	6.183	-2.729	0.007	**
water temperature	0.176	0.048	3.669	<0.001	***
log(POC)	-17.181	11.363	-1.512	0.133	
log(TA)	272.820	25.100	10.870	<0.001	***
log(bacteria)	15.257	8.780	1.738	0.085	.
log(DOC)	-65.794	46.035	-1.429	0.155	
pH	-26.135	1.300	-20.120	<0.001	***

. $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p \leq 0.001$.

Residual standard error: 61.03 on 125 degrees of freedom

Multiple R-squared: 0.867, Adjusted R-squared: 0.858

F-statistic: 101.6 on 8 and 125 DF, p-value: $< 2.2 \times 10^{-16}$

Table 2. Multiple regression model for pH as a function of variables sampled.

Model term	Estimate	Std. Error	t-value	p-value	
log(chytrids)	0.067	0.033	2.001	0.048	*
log(chl- <i>a</i>)	-0.143	0.045	-3.151	0.002	**
log(TN)	0.107	0.029	3.679	<0.001	***
log(POC)	-0.110	0.0422	-2.611	0.010	*
log(bacteria)	-0.044	0.025	-1.743	0.084	.
log(DOC)	1.113	0.181	6.165	<0.001	***

. $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p \leq 0.001$.

Residual standard error: 0.2332 on 127 degrees of freedom

Multiple R-squared: 0.3105, Adjusted R-squared: 0.2779

F-statistic: 9.53 on 6 and 127 DF, p-value: 1.22×10^{-8}

APPENDIX

Appendix 1. Formulae and references used to estimate invertebrate biomass. W = (dry weight (μg)); L = length (mm).

Taxon	Formula Used	Reference
<i>Bosmina</i>	$\ln W = 4.9344 + 4.849 * \ln L$	Rosen (1981)
Calanoid copepodids	$\ln W = 0.9227 + 2.4235 * \ln L$	Malley et al. (1989)
<i>Ceriodaphnia</i>	$\ln W = 1.915 + 2.02 * \ln L$	Dumont et al. (1975)
Cyclopoid copepodids	$\ln W = 1.3135 + 2.9005 * \ln L$	Malley et al. (1989)
<i>Daphnia ambigua</i>	$\ln W = 1.54 + 2.29 * \ln L$	McCauley (1984)
<i>Daphnia longiremis</i>	$\ln W = 1.0727 + 2.8915 * \ln L$	Bottrell et al. (1976)
<i>Daphnia lumholtzi</i>	$\ln W = 1.468 + 2.829 * \ln L$	Watkins et al. (2011)
<i>Daphnia pulex</i>	$\ln W = 1.4663 + 3.1932 * \ln L$	Bottrell et al. (1976)
Nauplii	$\ln W = 0.6977 + 0.569 * \ln L$	Rosen (1981)

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