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Effects of climate and water use on the ecology of mountain lakes and rivers in the Western United States

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ABSTRACT

Climate change and over-use of natural resources impacts ecosystems worldwide. Understanding physical impacts from climate and natural resource use on biological processes at multiple scales of spatial and ecological organization is needed to make useful predictions under global change scenarios. Mountain aquatic ecosystems are of particular concern because they are sensitive to climate change, represent hot spots of biodiversity, and they integrate atmospheric, terrestrial and aquatic processes into biological responses. The objective of this dissertation is to quantify physical impacts and biological responses of climate and water use on mountain aquatic ecosystems in the Western United States. In Chapter 1, I developed a data set of ice break-up dates using remote sensing techniques for mountain lakes across the Sierra and Cascade Mountain Ranges coupled with downscaled climate data to quantify drivers of lake ice phenology. I developed a predictive linear mixed effects model and used and ensemble of 15 global climate models to project changes in lake ice break-up dates through the 21st century. The results suggest that low snowpack and increased energy fluxes associated with elevated air temperatures drive earlier ice break-up dates. Projections of ice break-up show that ice break-up will be 61 ± 5 days if greenhouse gas emissions are not reduced. In Chapter 2, I analyzed specific ecological responses to earlier ice break-up dates in Castle Lake, California (a natural, sub-alpine lake). I predicted that consumer (Brook Trout; *Salvelinus fontinalis*) energetics and habitat use would be regulated by either climate driven water temperature or variation in food availability. The data suggest that earlier ice break-up results in a longer duration of surface water temperatures > 15 °C, coupled with decreased and increased food production in the pelagic and littoral zones, respectively. Isotopic and telemetry data showed that consumer resources and habitat use were driven by water temperature and were independent of food availability. In early ice break-up years, consumers grew less because they were thermally excluded from productive littoral zones when water temperatures were warmer for longer periods of time relative to late ice break-up years. In Chapter 3, I demonstrate that decreased streamflow in mountain rivers can reduce abundance and size structure of food supply to drift foraging Rainbow Trout (*Onchorhynchus mykiss*). In response to changes in streamflow and food availability, trout abandoned their energetically profitable drift foraging strategy and actively searched for prey. The shift in foraging behavior resulted in negative bioenergetic efficiencies in flow impaired sites. Taken collectively this research demonstrates that both predictable and unpredictable consequences of physical change drive biological responses across spatial gradients, ecosystem types, and levels of ecological organization.

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GENERAL INTRODUCTION

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GENERAL INTRODUCTION

A fundamental process in science and the goal of numerous research efforts is to understand the effects of change on natural systems. Earth is currently undergoing unprecedented, rapid change through anthropogenic climate change and exploitation of natural resources (Corlett 2015). Increased warming coupled with changes to the frequency and duration of drought (Dai 2013) and large storms (Dettinger 2011) have influenced all levels of ecological organization from individual behavior (Root et al. 2003) to ecosystem process (Walther et al. 2002, Grimm et al. 2013). For example, in terrestrial landscapes changing temperatures are anticipated to change habitat ranges for mobile organisms, while some species may expand their range, others may perish due to shrinking habitat (Bentz et al. 2010). Non-mobile species, such those observed in coral reefs, are unable to evade human pressures and their abundance is reduced globally due to increased water temperatures and acidity in oceans (Hoegh-Guldberg et al. 2007). As climate and exploitation pressures are intensifying, there is a need to understand how these perturbations will cause multivariate responses across physical, thermal, chemical and biological gradients at numerous spatial scales.

Freshwater ecosystem response to anthropogenic influence are of significant concern because they provide valuable ecosystem services (Wilson et al. 1999). They sources for drinking and irrigation waters, biodiversity hotspots (Dudgeon et al. 2006), and scarce, representing only about 0.01% of all water on earth (Shiklomanov 1993), with increasing anthropogenic demands (Vörösmarty et al. 2000). The use of freshwater ecosystems as "sentinels" of change over long term and inter-annual basis has become widely recognized because of their integration of multiple ecological processes across landscapes (Williamson et al. 2008, 2009, Adrian et al. 2009). For example, long term decreases to the duration of ice cover on lakes and rivers has been documented (Magnuson 2000, Benson et al. 2012), which has been shown to alter nutrient levels and biological activity (Park et al. 2004, Preston et al. 2016). In rivers, drought and dam construction have homogenized flow regimes and caused reductions to biodiversity (Poff and Zimmerman 2010). Future conservation efforts of freshwaters in a time of global change requires a thorough understanding of the biological changes caused by climate and water use drivers.

Aquatic systems in mountains are specifically not well understood due to their general inaccessibility. However, higher elevations are projected to have enhanced warming (Pepin et al. 2015) and mountain lakes are highly sensitive to change (Thompson et al. 2005). Currently, our understanding of climate and water use change on freshwaters is focused on lowland systems, yet mountain systems may act as the best integrators of environmental change (Catalan et al. 2006, Williamson et al. 2008).

The goal of this research is to quantify biological response to physical and thermal drivers induced by climate and water use. Specifically, I ask the question “how mountain lakes and rivers respond biologically across multiple trophic and ecological levels of organization?”. In lakes, I use variation in ice phenology as an indicator of climate change and quantify what drives ice break-up in mountain lakes and how earlier ice-break up dates impact ecological responses (Figure 1). In rivers, I use decreased flow regimes to understand how increased water use and drought may influence food availability and bioenergetics for fish consumers (Figure 1). The specific research questions in each chapter are:

Chapter 1: What are drivers of mountain lake ice break-up and how will ice break up dates change under future climate?

Chapter 2: Does ice-break up in mountain lakes influence secondary production, consumer energetics and behavior?

Chapter 3: How does low streamflow impact food availability and fish energetics in a mountain stream?

In Chapter 1, I examined the role of winter climate on the ice phenology of mountain lakes, across the Sierra Nevada and Cascade mountain ranges. While a number of models exist to predict ice processes on lakes, the majority of them are focused on lowland systems (Shuter et al. 2013). I extracted ice formation and ice break-up dates from 41 mountain lakes across the region using remotely sensed data and coupled that with downscaled climate data to quantify drivers of ice break-up and build a predictive model that was applied to projected climate scenarios from global climate models. The results suggest that less snow and warmer water temperatures drive earlier ice break-up dates and influence smaller lakes stronger than larger lakes. Predictions under future climate projections from the model show that under future greenhouse gas emissions pathways ice break-up dates will be approximately 60 days earlier by the year 2099 under "business as usual" emissions scenarios.

In Chapter 2, I developed a conceptual model to predict how earlier ice break-up driven by climate would affect ecological process in a mountain lake and tested it using empirically collected data. Earlier ice break-up dates are related to primary productivity (Park et al. 2004), but little attention has been given to how climate processes cascade across ecological levels of organization (Woodward et al. 2010, Grimm et al. 2013). I estimated habitat specific invertebrate production rates to test the prediction that earlier ice break-up would drive productivity. I then quantified consumer (Brook Trout; *Salvelinus fontinalis*) food resources and habitat use through stable isotopes and acoustic telemetry, respectively, to examine what resources and habitats were utilized. Results demonstrate that littoral zone secondary production increased under early ice break-up while pelagic zone secondary production decreased. Consumer resource and habitat usage was driven not by prey availability but by water temperature. Specifically, Brook Trout were excluded from food rich littoral zones during early ice break-up years by warmer water temperatures and foraged in food depleted pelagic zones. In early ice break-up years Brook Trout grew to smaller sizes when compared to late ice break-up years, indicating that climate change has complex and negative impacts on fish in mountain lakes.

Streamflow is considered the “master” variable in lotic systems effecting thermal, chemical and biological process (Power et al. 1995). In Chapter 3, I examined the influence of decreased streamflow on the food availability, foraging behavior and energetics of Rainbow Trout (*Onchorhynchus mykiss*) in a mountain river. I collected invertebrate drift and monitored fish behavior in flow impaired and flow un-impaired sites. The data suggest that the size structure and abundance of invertebrate drift decreased with streamflow and resulted in increased foraging behavior as fish were required to shift to “search” based foraging. Using the empirical data, I adapted a fish net rate of energetic intake model (Hughes and Dill 1990) and updated it using measured fish movement data. The model showed that in impaired flows, energetic efficiencies are negative during late summer, low food availability conditions.

Collectively, the results of this dissertation show that anthropogenic activity influences physical (earlier ice break-up and decreased streamflow; Chapters 1 and 3), thermal (longer duration of warm water temperatures; Chapter 2), and ecological processes (altered productivity, habitat selection, foraging behavior, and growth; Chapters 2 and 3) in mountain aquatic ecosystems. I demonstrate that changes to physical characteristics of ecosystems can cascade through to complex and unforeseen biological responses that can have impacts at multiple levels of ecological organization (ecosystem, habitat, community, population and individual).

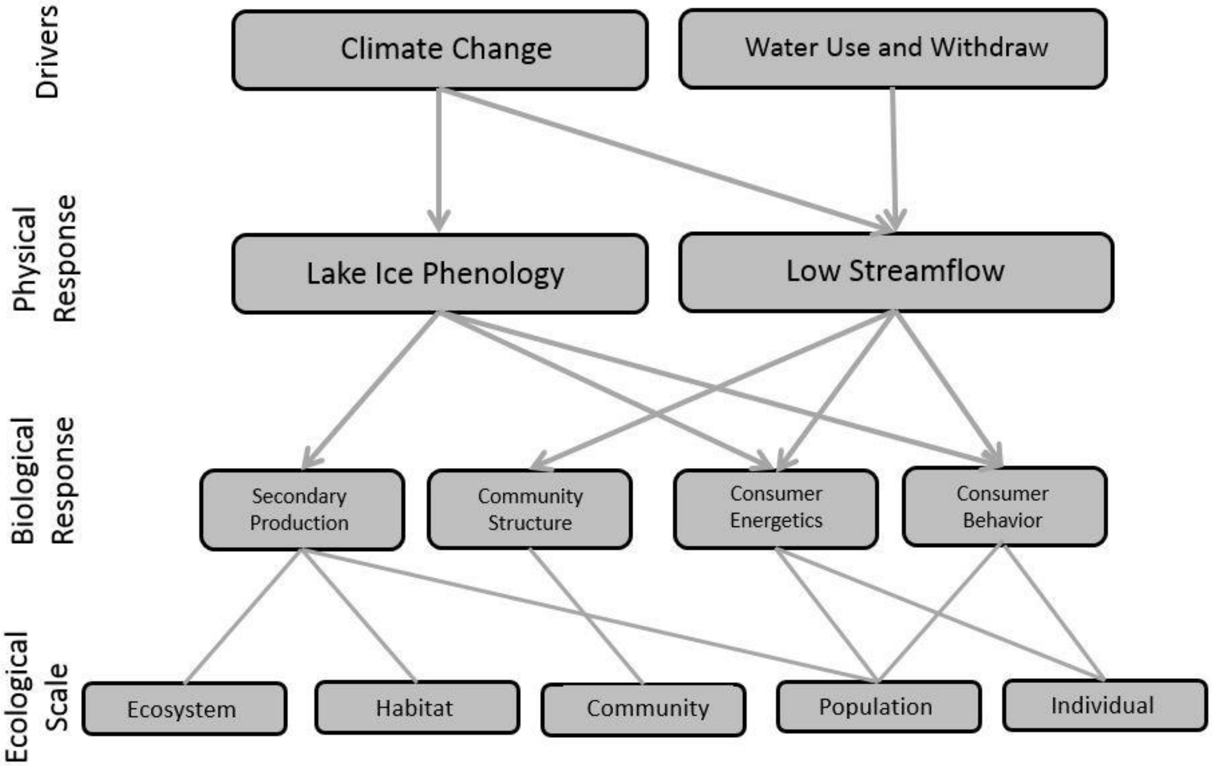

Figure 1. Conceptual model describing anthropogenic driver on physical and biological responses and at what ecological scale the response is at. The model describes the general links and processes tested in this dissertation.

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CHAPTER 1. Drivers and predictions of ice phenology in mountain lakes in the Western United States derived from remote sensing.

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ABSTRACT

In mountain watersheds, the rate of change for air temperatures caused by climate change is greater than at lower elevations, while precipitation in form, frequency and magnitude is highly variable. Mountain lake physical, chemical and biological processes serve as sentinels because they integrate large scale environmental change from atmospheric and terrestrial habitats into freshwaters. Ice break-up dates in mountain lakes can regulate thermal, chemical and biological processes within lakes, resulting in unforeseen ecological consequences while also altering carbon flux to the atmosphere. Forecasting changes to mountain lake ecology as a function of ice phenology requires an understanding of climate-based processes that cause ice break-up that can be used for prediction. We synthesized and analyzed a data set of mountain lake ice break-up dates from remote sensing tools, downscaled climate data, and global climate model projections to determine drivers, construct a predictive model, and project future ice break-up dates. Our analysis used a random forest analysis to suggest that snowpack and factors associated with air temperature (sensible energy flux and radiation) are the important climatic drivers of ice break up, while larger lakes typically iced out earlier than smaller lakes. Interactions between climate variables and lake surface area suggest that smaller lakes (< 2 km^2)

will be more affected than larger (> 2 km^2) lakes by shifts in air temperature and precipitation. Random forest results were used to inform the development of a linear mixed effects model (RMSE of 18 days). Using an ensemble of 15 global climate models we predict that end-of-century ice break-up in mountain lakes will be earlier by a mean (± standard error among models) of 25 ± 4 and 61 ± 5 days, depending on which representative concentrating pathway (RCP 4.5 or 8.5, respectively) society's greenhouse-gas emissions follow. We project that shifts in ice-break up dates will be earlier than projections for lowland systems and suggest that ecological function will be altered.

INTRODUCTION

Mountain ecosystems are at an increased risk of climate change due to the enhanced warming projected at high elevations (Pepin et al. 2015). Increasing air temperatures (IPCC 2014) and drought frequency (Dai 2013, Mann and Gleick 2015) coupled with higher magnitude, more common and warmer extreme precipitation events (Dettinger 2011, Dettinger et al. 2015) have resulted from climate change and will continue in Western United States mountain watersheds. Snow droughts (Harpold et al. 2017) and earlier snowmelt-caused runoff is forecast to increase in mountain ecosystems (Hidalgo et al. 2009, Clow 2009, Harpold et al. 2012, Sadro et al. 2018b, Harpold and Brooks 2018). Mountain lakes are highly sensitive to climate change (Thompson et al. 2005) and integrate change from atmospheric, terrestrial and aquatic environments serving as indicators of climate change at the ecosystem level (Williamson et al. 2008, Adrian et al. 2009).

Timing of ice break-up in mountain lakes impacts fundamental ecological process during the ice-free season (Goldman et al. 1989, Park et al. 2004, Parker et al. 2008, Preston et al. 2016, Sadro et al. 2018b) . Lake heat budgets, nutrient concentrations, primary production, zooplankton biomass (Park et al. 2004, Parker et al. 2008, Preston et al. 2016, Sadro et al. 2018b, 2018a), and reduction to consumer reproduction and energetic efficiencies (Farmer et al. 2015, Caldwell et al. *in review*) are related to ice break-up date. Understanding drivers and making predictions of ice break-up dates for mountain lakes serves as an ecological indicator of climate change (Sánchez-López et al. 2015, Preston et al. 2016).

Snow and ice melt is the fundamental process that drives lake ice break-up. Air temperature is a state variable which serves as a proxy for energy fluxes such as longwave radiation and sensible energy that cause lake ice melt (Ohmura 2001). Mountain lake ice is covered by snow and the snowpack insulates lake ice from energy fluxes that drive melt and increases albedo which reflects incoming radiation, slowing melt processes (Ohmura 2001, Duguay et al. 2003). Thus, the energy flux required for ice break-up must melt the combined snow and ice. Water in liquid phase also represents a mechanism of heat and energy loss from lake ice. Models by Vavrus et al. (1996) include a basal heat flux from lake water to the ice bottom, while runoff and tributary inflows also have been correlated to ice break-up (Brown and Duguay 2010, Arp et al. 2013).

Previous models built for lowland and artic lakes have used air temperature coupled with lake geographical variables (e.g. latitude, elevation, and size) to predict ice break-up and formation (Gao and Stefan 1999, Shuter et al. 2013), while runoff (Brown and Duguay 2010, Arp et al. 2013), snowpack and extreme climate events were secondary (Vavrus et al. 1996, Duguay et al. 2003, Benson et al. 2012). Shuter et al. (2013) used empirical regression models to forecast ice phenology across Canada and found that their models, which relied on air temperature and lake mean depth, had low accuracy in mountain regions compared to lowland lakes. Studies which specifically describe mountain lake ice phenology are limited to single lakes or small groups of lakes within a small geographic region, but suggest a higher reliance on snowpack than studies in lowland systems (Park et al. 2004, Parker et al. 2008, Sánchez-López et al. 2015, Preston et al. 2016). Previous research is useful for understanding drivers within specific regions, but a predictive model that can be used across latitude and elevation gradients of lakes and watersheds of varying sizes is required for predicting broad scale ecological change in mountain lakes

The enhanced warming (Pepin et al. 2015) and reduced snowpack (Harpold et al. 2017) from climate change will result in higher energy fluxes acting on less frozen material that will theoretically cause earlier ice break-up dates in mountain lakes. Given that lower latitudes in the Western United States have higher variation in inter-annual precipitation (Cayan et al. 1998, 2016) the impacts of climate change on lake ice break-up date may vary with latitude. Specifically, we predict that; 1) warm air temperatures and low snowpack will drive earlier ice break-up dates; 2) larger watersheds with higher amounts of runoff will have earlier ice break up dates; and 3) climate change will drive earlier ice break up dates, that varies latitudinally. To test these predictions, we used a remote sensing based approach (Wynne et al. 1996, Reed et al. 2009, Arp et al. 2013) to determine ice break-up dates of mountain lakes (> 1 km^2) in Western United States. We acquired downscaled climate data to determine meteorological drivers, build a predictive model, and project ice break-up dates in response to climate projections through the 21st century from multiple global climate models and emissions scenarios.

METHODS

Study area and lakes:

The study included mountainous areas of California, Oregon, Washington and Idaho in the Western United States (1300 km). The area includes the Sierra, Cascade, and Northern

Rocky Mountain ranges and was selected because of its gradient of inter-annual variation in precipitation increases from north to south (Cayan et al. 1998) and location in the Western United States. The Sierra Nevada Mountains extend 640 km from southern to northern California, with peak elevations of 4,421 m. The southern end of the Cascades begins at the northern end of the Sierras, extend north and include several stratovolcanoes with a maximum elevation of 4,392 m. Th portion of the Northern Rockies located in Northern Idaho was included in our analysis, it has similar characteristics as the Cascades.

Forty-one lakes across the study area were identified as usable based on size requirements of the satellite image pixel resolution, classification as a mountain lake, and whether they freeze annually (Figure 1, Table B1). The National Hydrography Dataset (NHD) Hydrological Unit-8 (sub-basin scale) was filtered to determine usable lakes for our analysis using ArcGIS (ESRI 2011). First, all lakes less than 1 km^{-2} (size limited by remote sensing resolution, see below) were removed from the data set and overlaid onto US Geological Survey 30 m digital elevation models (DEM) because they were below the detection limit of the satellite imagery. Elevation, lake surface area, latitude, and watershed size were extracted from each lake. Mountain lakes were classified by elevations greater than 1500 m and 500 m, in Sierra Nevada and Cascade Mountains, respectively. The elevation-based filter was determined from the general elevations in each range, and that Sierra Mountains lakes have higher elevations required to freeze compared to those in the Cascade Mountains due to their latitude. Lake elevations, latitude, surface area, and watershed size ranged, respectively, between 580 m to 2583 m, 37.24 °N to 48.78 °N, 1.02 km^2 to 7.97 km^2, and 6.74 km^2 to 449.04 km^2 (Table B1).

Ice break-up date:

Ice break-up dates were quantified using MOD10A1 (Hall and Riggs 2016), a daily snow cover product from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite. The product returns a daily value (0-100) of Normalized Difference Snow Index (NDSI) snow cover, cloud cover masks, and a quality assurance value from each pixel on a daily time step. We assumed that a NDSI snow cover value of > 50 indicated that the lake was completely ice covered, and that < 50 indicated it was breaking up or partially ice-covered, and 0 indicated ice-free. Because snow is a highly reflective surface, we felt that using > 50 NDSI was a conservative approach to determine full ice-cover. MOD10A1 has a 0.25 km^2 pixel size, thus we only used lakes which had a 1 km^{-2} surface area to ensure that multiple pixels fell within the lake (Reed et al. 2009, Arp et al. 2013). In addition, we visually inspected each lake site by overlaying the MOD10A1 image pixel grid with each lakes surface area and data extraction point (geometric center of lake) and removed any lakes where the pixel associated with the extraction point had any portion on land (Figure B1). We downloaded daily image values from the geometric center pixel in each lake from winter 2002 (mission start of MODIS satellite) to winter 2017 using Google Early Engine (GEE; Gorelick et al. 2017). In addition to dates collected by remote sensing, ice break-up date was visually determined for Castle Lake, CA through a record of daily images captured each day by a pre-programed digital camera (Figure 1). Castle Lake was 0.20 km^2 (below minimum surface area for MODIS) and was not able to be used in validation of remotely sensed lake ice break-up. Ice break-up date was determined as the day which the lake was completely ice free. Ice break-up dates which were obscured by cloud cover by more than 10 days were removed from the data set. The middle date between the last observed ice on and most recent observed ice off was taken observations that were obscured by less than 10 days of cloud cover. The average number of cloudy days that obscured ice off was 6 ± 1 (mean and standard error).

Historical downscaled climate data:

Downscaled climate data from each lake and all years was acquired using GEE from the GRIDMET climate data set (Abatzoglou 2013). GRIDMET is a gridded surface meteorological dataset which covers the continental United States on a 4 km X 4 km grid size. The data set includes minimum and maximum temperatures, precipitation accumulation, downward surface shortwave radiation, wind velocity, and relative and specific humidity on a daily time step. GRIDMET has been utilized previously on the effects of snowpack for Western US mountains and is suitable for this application (Harpold et al. 2017b).

Projected downscaled climate data:

Projections of climate conditions from global climate models were used to project ice break-up dates through year 2099. We acquired historical (1950-2006) and projected (2007-2099) climate data from 15 of 31 Global Climate Models (GCM) presented in the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC 2014). The subset of models we used were identified to be the best for Western United States by California’s Climate Change Technical Advisory Committee (Lynn et al. 2015). We elected to use the ensemble approach because of the variability among projections for the individual GCMs; given these model-to-model differences, the ensemble approach gives general and robust results. The projections used here are daily maximum and minimum air temperatures and precipitation, downscaled onto 4 km X 4 km grid cells. Future projections were acquired for representative concentrating pathways (RCP) 4.5 and RCP 8.5 simulations. RCPs are atmospheric greenhouse-gas (GHG) emissions scenarios reflecting –in this case—two different assumptions about future land uses, economic activities, lifestyles, energy uses, population growth rates, technology advancements, and climate policies (IPCC 2014, Lynn et al. 2015). RCP 4.5 is an optimistic emissions scenario with GHG concentrations in the atmosphere leveling off by midcentury, whereas RCP 8.5 represents a pessimistic scenario with high GHG emissions and rising GHG concentrations throughout the century (IPCC 2014). Historical values are simulations of climate under historical emissions and concentrations. The set of models used here are historical and RCP 4.5 and RCP 8.5 simulations from the ACCESS-01, BCC-CSM1-1, CanESM2, CCSM4, CESM1-BGC, CESM1-CAM5, CMCC-CM, CMCC-CMS, CNRM-CM5, GFDL-CM3, GFDL-ESM2M, HadGEM2-CC, HadGEM-ES, MIROC5 and MPI-ESM-LR GCMs (IPCC 2014, Lynn et al. 2015).

Drivers of ice break-up:

Mean temperature, snow and rain fraction, downward surface radiation, and windspeed were converted to an index value by summing them over winter (October 1– May 31) and spring only (March 1 to May 31) periods . The cumulative sum of variables was used instead of other metrics because it sums the total variation over the course of winter and spring (Preston et al. 2016). Variables were not standardized to variation from the mean because energy required to melt ice and snow will be dependent on absolute values and will not change relative to site specific means. Mean daily temperature was determined as the mean between minimum and maximum temperatures. Snow fraction (portion of precipitation that falls as snow) was calculated from a simple temperature based regression model based on equations from Dingman (2002), where precipitation falls as snow when temperature is < 0 °C and rain > 6 °C, between 0

°C and 6 °C is estimated as a function of the melt factor (0.167) multiplied by mean daily temperature. All other variables were utilized in their raw form.

Random forest (RF) regression algorithm (Breiman 2001, Liaw and Wiener 2002) was used to identify climatic and physical characteristics of lakes which are drivers of ice break-up. Random forest is a tree-based regression tool where each split is based on a subset of predictors chosen at random, this procedure is done 1000's of times and results are averaged. The method is non-parametric, has no required assumptions on data distribution, robust to outliners, handles many continuous predictors, and is efficient at identifying effects of bi-variate interactions on the response variable. Variable importance was ranked based on the % increase in mean square error (MSE) if the variable was removed from the model and visually assessed using partial dependency plots. Partial dependency plots perform model iterations on a single variable, when all others are held at their median value (Milborrow 2018). The dependent variable was Julian day of ice break-up, and independent variables were cumulative sums of rain fraction, snow fraction, mean daily temperature, downward surface radiation and static lake variables of surface area, elevation, latitude, delivery ration (surface area to watershed size) and watershed area. The model was run for winter and spring periods and compared using the % variance explained. Final models were run with 10,000 trees, models were constructed with the R statistical software (R Core Team 2015) with package randomForest (Liaw and Wiener 2002), partial dependence analysis was done with the package plotmo (Milborrow 2018) .

Model development and forecasting:

We used linear mixed effects models (LMEM) to build a predictive model of ice break-up Julian date. The data was first subset into a training and test set. The test data set included Castle Lake (because it had visual estimates of lake ice break-up dates, and testing it was independent of remotely sensed data) and 8 randomly selected lakes from the data set that used remote sensing to determine ice break-up date. The remainder of the data was used for modeling training. We started our model building processing with the top three predictors identified in the random forest algorithm and added individual lower ranked variables stepwise to determine if they improved model performance. Fixed effects included climate and lake characteristic variables, while the random intercept term was used for lake identity. Model fit was evaluated by comparing AIC values, log likelihoods and R^2. Model performance was evaluated by calculating the root mean square error (RMSE) and absolute mean error (AME) between predicted and observed data with the test data.

The LMEM for ice break-up prediction was used with future and historical climate projections to project ice-break-up dates over all lakes from 1950-2099 using historical conditions, RCP 4.5, and RCP 8.5. Projected temperature and precipitation climate data were summarized in the same way as GRIDMET climate data and used for predictions. The predict function in R (R Core Team 2015) was used to project ice-break-up dates. The number of days different between projected ice break-up date and observed current (2001-2017) and modeled historical (1950 – 1980) mean ice break-up dates were determined for each lake and GCM for each year under RCP 4.5 and RCP 8.5 scenarios. Current mean ice break-up date for each lake was estimated using remotely sensed observed data from 2001-2017. The difference between each year and each lake from each GCM projected ice break-up date and mean observed current ice break-up date was calculated and meaned across lakes, and then across models. Historical mean ice break-up date was estimated using the mean break-up date for each lake under each historical GCM output from 1950-1980. The difference between projected and historical ice break-up date was calculated for each GCM and lake, meaned across lakes and then GCM's.

Mean difference among lakes for each GCM was plotted individually and as the mean of all models. For each lake, a regression of predicted ice break-up day and year was done; the slope of that line was used to estimate the trend of ice break-up for each lake and related to elevation, latitude, and surface area to explore geographic variation in mountain lake sensitivity to climate change.

RESULTS

Drivers of ice break-up:

Random forest models that used the winter period was a better fit model than (77.2% of variance explained) spring period (69.4% of variance explained). For the remainder of the paper we use results from the winter period. Random forest identified snow fraction, air temperature and lake surface area as the top three drivers of ice break-up (Figure**Error! Reference source not found.** 2). Random forest partial dependence plots identified that increasing snow fraction resulted in later ice break-up dates, while increasing air temperature and surface area resulted in earlier break-up dates (Figure 2) other variables had much smaller effects and were ranked as less important (Figure B2). Important interactions identified by the random forest analysis were between snow fraction, air temperature, and surface area (Figure 3). Interactions suggest that smaller lakes are more affected by increasing snow fraction and cooler air temperatures. While air temperature is used to derive snow fraction, it was not correlated and did not differentially impact the model.

Model development and forecasting:

The LMEM (linear mixed effects models) using the top 3 predictors identified in the random forest included snow fraction, air temperature and lake surface area. These variables had significant effects for univariate predictors (snow fraction: $\beta = 0.03$, SE = 0.01, $p < 0.01$;

temperature β = -0.07, SE = 0.01, $p < 0.01$; surface area: β = -8.73, SE = 2.71, $p < 0.01$), and bi-variate and the tri-variate interactions (all values $p < 0.001$). We explored additional co-variates by introducing them stepwise to the base model; several of these models had lower AIC values than the base model (Table 1). Further explorations show that those variables which improved model fit were confounding in our study (e.g. latitude is correlated to elevation); thus, we elected to use the base model for projections. RMSE from model predictions (Figure 4) using the test data set was 18 days, absolute mean error (AME) was 14 ± 2 days (mean ± standard error) and median absolute error was 10 days. The model accuracy increased if Castle Lake, which is smaller (0.20 km^2) than lakes (> 1 km^2) used for model training, is omitted form the test data set to 15 days (RMSE) and 13 ± 1 days for AME.

The mean (± standard error) of all GCM projections under the RCP 4.5 and RCP 8.5 scenarios predicted ice break-up to be 25 ± 4 and 61 ± 5 days earlier for all lakes than historically modeled (1950-1980) ice break-up dates in 2099, respectively (Figure 5). The mean (± standard error) difference between projected (2099) and current (2002-2017) ice break-up dates were mean (± standard error) 18 ± 3 and 54 ± 2 days for RCP 4.5 and RCP 8.5, respectively.

Trends of ice break-up were not significantly related to elevation or latitude for RCP 4.5 (elevation: $\beta < 0.01$, SE < 0.01, $p = 0.08$; latitude: $\beta < 0.01$, SE < 0.01, $p = 0.80$) or RCP 8.5 (elevation: $\beta < 0.01$, SE < 0.01, $p = 0.95$; latitude: $\beta < 0.01$, SE < 0.01, $p = 0.26$; Figure 6). Surface area was related to the slope of ice break-up for RCP 4.5 (β = 0.02, SE = 0.01, $p = 0.05$) and RCP 8.5 ($\beta < 0.06$, SE < 0.01, $p < 0.01$); larger lakes had a weaker trend in ice break-up date than smaller lakes (Figure 6).

DISCUSSION

The compilation and analysis of the data suggest that larger snowpack and lower energy fluxes associated with colder air temperatures drive later ice break-up dates. The mechanisms which drive lake ice break-up affect smaller lakes stronger than larger lakes. The analysis also identified that inclusion of downwelling solar radiation, elevation and latitude improve model performance but are secondary controls. These results are consistent with other reports for mountain lakes where break-up date was influenced by snow fraction and temperature (Sánchez-López et al. 2015, Preston et al. 2016). Projections from our models suggest that lake ice break-up dates will be earlier under both RCP 4.5 and RCP 8.5 climate scenarios and are independent of lake latitude or elevation, but smaller lakes will be more affected than larger lakes.

In our analysis, meteorological variables (i.e. snow fraction and air temperature) were the strongest predictors of ice break-up in mountain lakes, while lake characteristics (e.g. surface area) add improvement to model performance. Snow fraction is an estimate of the amount of snowfall and larger snowfall generally equates to larger snowpack. Thicker ice and larger snowpack require more energy to melt and therefore, are consistent with later lake ice break-up and less sensitive to climate change. Air temperature is a state variable that is the outcome of the energy budget (e.g. more incoming than outgoing energy results in warming temperature). Warmer air temperatures are associated with sensible energy fluxes to snow and ice, but temperature is generally thought to be an effective predictor of melt due to its correlation with longwave radiation (Ohmura 2001).

We predicted that larger watersheds with higher delivery ratios (watershed to surface area) would experience earlier ice break-up, but a strong relationship was not detected in our analysis. Brown and Duguay (2011) determined that runoff from the surrounding watershed decays lake ice and Shuter et al. (2013) found the highest error of ice break-up predictions in mountain systems and attributed it to inflows from the watershed. Their results suggest that runoff and inflows act as a loss of energy from lake ice. In mountain systems, we suggest that either snowpack over-rides watershed influences or discharge from the watershed was inadequate to cause ice break-up in the size of watersheds that were included in our data set.

Our results suggest that direct use of air temperature and snow fraction was more accurate than geographic descriptors. Elevation and latitude were used as predictors of lake ice break-up in the Pyrenees, Tetras, and Rocky Mountains (Šporka et al. 2006, Sánchez-López et al. 2015, Preston et al. 2016). While our study included elevation and latitude in the random forest and LMEM analyses, they carried less weight than climate variables. We attribute this disagreement in their studies and ours to variation in air temperature and precipitation observed over small scales in mountain systems (Elder et al. 1991, Anderton et al. 2004), coupled with elevation independent factors like humidity and cloudiness that can influence snow and ice melt (Harpold and Brooks 2018, Sumargo and Cayan 2018). In our study area, lower latitude lakes which freeze were at relatively high elevations and higher latitude lakes were lower in elevation due to the lower general elevation of the Cascade Range. The correlation of latitude and elevation that was a function of our study area made these terms less useful and were not included in our final model.

Interactions of smaller lake surface area with colder air temperature and higher snow fraction resulted in later ice break-up dates as identified in the random forest. Previous evidence has suggested that lake depth rather than surface area drives earlier ice break-up (Brown and Duguay 2010, Arp et al. 2013, Magee and Wu 2017). Lakes with large volume have large thermal inertia (Wetzel 2001), and typically freeze later and require greater energy loss to form ice, yielding thinner ice over the winter that thaws more rapidly than in lakes with smaller volumes (Vavrus et al. 1996). We were unable to obtain lake depth for our study lakes but suggest that lake volume, a function of lake depth and surface area, is the lake characteristic influencing ice break-up. We did not have lake bathymetry nor lake depth for our study sites and were unable to calculate lake volume, but if we assume that mountain lakes with larger surface area generally have a larger volume, then this mechanism is likely causing earlier ice-break updates for larger lakes in our study. As a result, smaller lakes were more affected under climate change scenarios than larger lakes in our model projections.

Climate variables from the winter period provided clearer identification of drivers and better predictions of ice break-up in our geographic region than the spring period used by others (Lei et al. 2012, Arp et al. 2013, Preston et al. 2016). Utilizing only spring weather implies that spring supersedes the overall winter conditions as a driver of lake ice break-up, the presumed mechanism identified is that a warm and dry spring will override any previous snow accumulation to drive rapid melt. We disagree, and suggest that the winter period snowpack results in later ice break-up dates through two mechanisms that depend on timing of snowfall. First, early season snow at the snow-ice interface can convert to “gray ice” and effectively thickens ice; second, late season snow creates a thicker and more reflective surface that requires more energy to melt (Vavrus et al. 1996). In addition, lakes in our study had variation in latitude and elevation that resulted in mean ice break-up dates from Julian date 60 to 160. Thus, the timing of the spring period which would influence ice break-up would vary with mean break up date. For instance, a larger, low latitude lake with an early mean ice break-up date (e.g. Julian date 74, March 15), would have a spring time weather importance window of February to early March, where a higher alpine lake would be May to June. We simplified our model and used standardized time windows for climate variable summation. Had we created a shifting time window for each lake its plausible that model performance would increase, but our goal was to create a parsimonious and simple model that could be applied to lakes with little previous information to project changes in ice break-up dates. Inclusion of a shifting time window would require prior knowledge about the mean time of lake ice break-up dates and would change over time as a function of climate, making predictions difficult.

Predictions from our LMEM model were within 14 days (absolute mean error) of observed dates of ice off. In years when ice break-up was significantly earlier than the lake specific mean break-up date, the model typically predicted later than what was observed. The training data had fewer observations in this area of parameter space which resulted in less certainty about predictions with extremely low snowfall. Others have experienced similar uncertainty for lowland lakes, where less climate variation and simpler hydrological processes are observed (Brown and Duguay 2011, Shuter et al. 2013).

We observed no clear relationships between projected rates of shift to earlier ice break-up dates with latitude or elevation. The Sierra Nevada Mountains in California have the highest variation in interannual precipitation in the continuous United States (Cayan et al. 2016), are highly influenced by extreme precipitation events (Ralph and Dettinger 2011), and are likely to receive more rain than snow under future climate scenarios (Hayhoe et al. 2004, Dettinger et al. 2015). Given the importance of snow fraction in our model, we expected lakes with lower latitudes located in the Sierra Nevada range, which are exposed to higher variation in snowfall, to respond to future climate with a faster rate of change to ice out dates than lakes higher in latitude, but that was not projected. Our model had the same coefficients for lakes of all latitudes and results are dependent on GCM projections and scenarios. Warming projections by GCM’s are typically enhanced at higher latitudes (Ficklin et al. 2015) which may counter any relatively stable projections of precipitation and drive more rain than snow in that area, resulting in similar rates of change across latitudes. Alternatively, other results show that sensitivity of ice phenology to air temperature is increased at latitudes below 61°N where effects of solar radiation were decreased (Weyhenmeyer et al. 2011). Our highest latitude is at 48 °N and all lakes in our study were equally sensitive to temperature changes and offers another explanation for the ambiguity in trends of earlier ice break-up times across latitude.

Our data suggested stronger shifts to ice break-up date for mountain lakes in the Western United States than what has been observed in other regions. Historical observations show ice cover in aquatic systems has decreased globally (Magnuson 2000, Sharma et al. 2016), while ice-break up in lowland lakes is projected to occur a maximum 20 days earlier than the historical (1961-1990) mean by the year 2070 under A2 emissions scenarios, which is comparable to our RCP 8.5 scenario (Shuter et al. 2013). When controlling for the same time frame (2070) projected mountain lake ice break-up dates under RCP 8.5 were double (40 ± 2 days) lowland lake predictions. Several explanations for discrepancies include; 1) GCMs project stronger shifts in temperature and more variable precipitation in mountain systems relative to lower elevations and especially in the Western United States (Dettinger et al. 2015, Pepin et al. 2015); 2) after variable importance analysis, final models from Shuter et al. (2013) did not include a precipitation term, the strongest predictor of ice break-up for mountain lakes; or 3) their models only utilized one GCM while ours utilized 15 models. We argue that the sensitivity to snow of mountain lake ice combined with the lower projected snowfall in higher elevations is driving the higher rate of shifts predicted to ice break-up timing relative to lower elevation lakes.

Ice covered lakes in Scandinavia and in the northern hemisphere are increasing their frequency and probability of having ice-free winters (Weyhenmeyer et al. 2008, 2011). We were unable to accurately model ice formation using climate drivers (Appendix A). Ice formation is dependent on lake intrinsic factors such as volume that regulate its thermal energy and wind which can break up newly formed ice (Duguay et al. 2003). Thus, we were unable to determine if any of our lakes would be ice-free under climate change. However, it remains a strong probability as Castle Lake had visual observations of ice durations that were approximately 15% (or 120 days less) of average during extreme drought years.

The earlier ice break-up dates projected in our model suggest that mountain lakes are at risk of altered ecological processes. Early ice break-up dates will increase water temperatures and primary productivity rates, which may have unpredictable consequences for lake water chemistry, zooplankton, benthic macroinvertebrate and fish consumers (Park et al. 2004, Parker et al. 2008, Preston et al. 2016, Sadro et al. 2018b). For example, increased water temperatures may exclude consumers from utilizing energetically efficient habitats, resulting in decreased growth (Guzzo et al. 2017). While longer ice-free periods will increase the duration which lakes omit carbon into the atmosphere (Catalan and Pla 2009). We suggest that future research efforts focus on expanding the geographic range of ice break-up modeling to provide further insight into changes to ecological function in mountain lakes.

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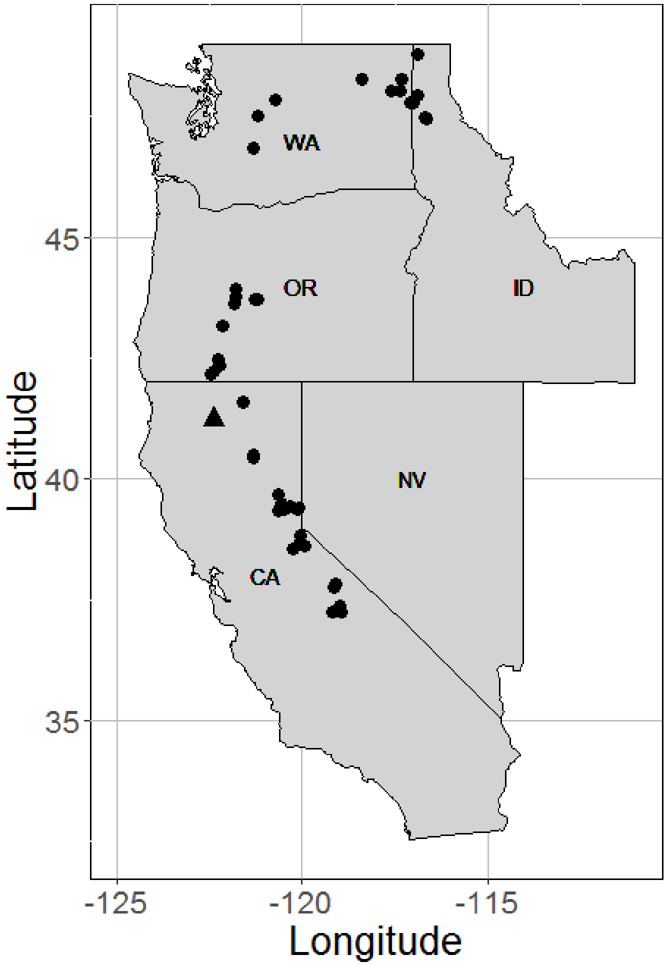
TABLES

Table 1. Performance of linear mixed modeling results, models are organized by AIC score. Fixed effects are listed in the Model column, all models included a random intercept term for lake identity. 480 observations were used for each model (only those data used in training data set). The bolded model was selected for projection. See text for rationale on model selection.

Model	*Parameters (k)*	AIC	Log Likelihood	R^2 (corrected)
Snow Fraction*Temperature*Surface Area*Radiation	4	3890	-1927	0.88
Snow Fraction*Temperature*Surface Area*Elevation	4	3937	-1950	0.81
Snow Fraction*Temperature*Surface Area*Latitude	4	3939	-1951	0.8
Snow Fraction*Temperature*Surface Area	**3**	**3939**	**-1959**	**0.79**



FIGURES

Figure 1: Map of lake locations used in analysis after filtering for size (> 1 km^{-2}), elevation (> 1500 m for Sierra Nevada Mountains and > 500 m for Cascades), if they freeze annually, and determination of accuracy for MODIS use. Black circles are lakes where ice break-up was determined from MOD10A1, the larger black triangle (Castle Lake, CA) was determined visually.

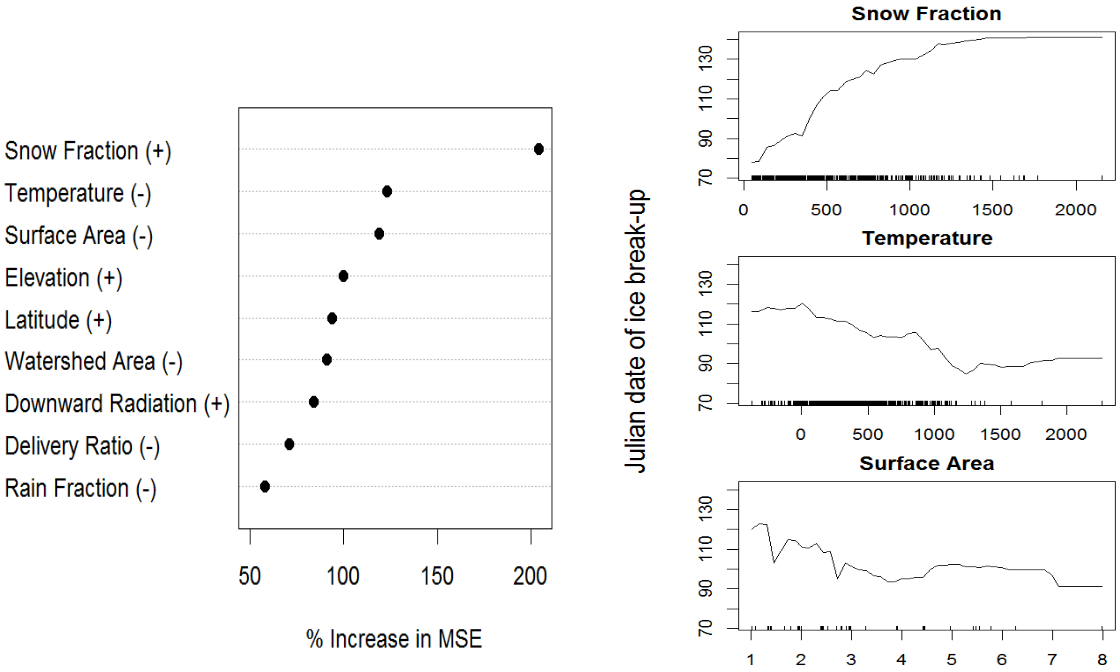


Figure 2. Left panel: variable importance plot from random forest analysis describing the drivers of ice break-up in mountain lakes of the Western United States. Variables are listed in descending order of importance from top to bottom. The x-axis describes the decrease in model performance when omitting a given variable, larger values indicate higher importance. Positive signs indicate that an increase in the variable results in later ice break-up date, while negatives indicate that an increase in the variable results in early ice break-up date. Right panel: partial dependence plots showing the relationships of the top 3 predictor variables (ordered in descending order of importance top to bottom) to the ice break-up Julian date. Partial dependence plots are the results of the model if all other variables are held at their median value. Partial dependence plots for all other variables is in Supplementary Material (Figure B2).

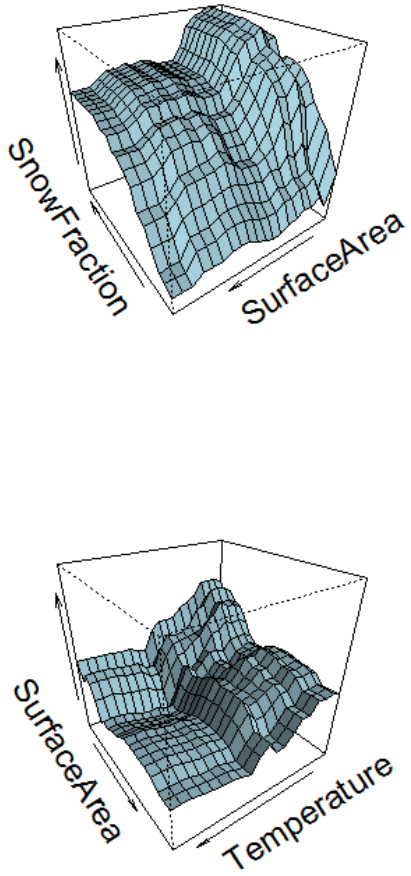


Figure 3. Random forest partial dependence plots for bi-variate interactions of surface area with snow fraction (top) and temperature (bottom). The Z-axis represents relative change in the ice break-up day in response to the interactions when all other variables are held at their median. The interactions were significant (p <0.01) within the LME model. The plot shows that smaller lakes are more effected by higher snow fraction and cooler temperatures.

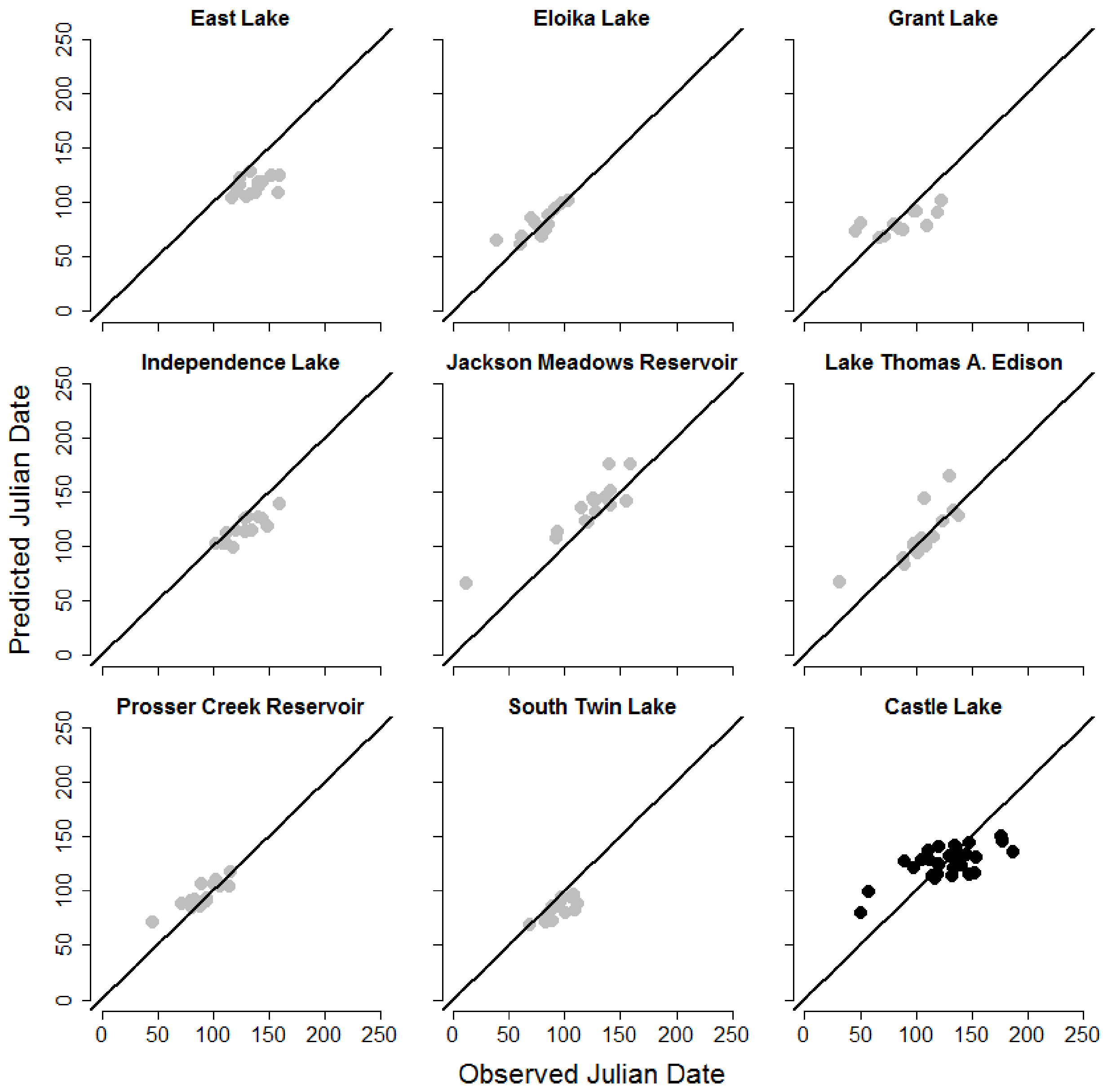


Figure 4. Regression of predicted to observed Julian date of ice break-up from the test lakes predicted by the base linear mixed model (terms = snow fraction*temperature*surface area). Plots with grey dots are lakes with ice break-up determined by the MOD10A1 remote sensing snow product, plots with black dots were visually observed. The black regression is the 1:1 line. RMSE was 18 days, mean (± standard error) and median residuals were 14 ± 2 days and 10 days, respectively.

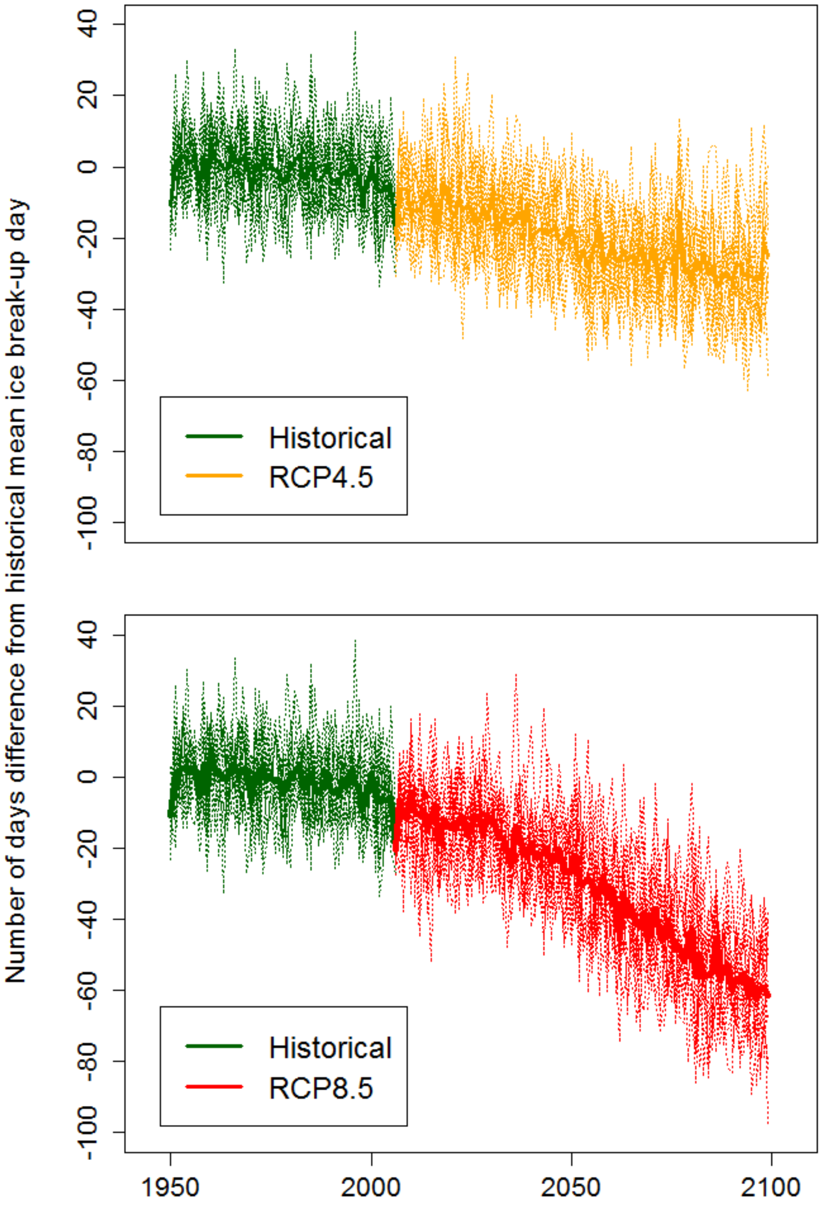


Figure 5. The difference in days between projected future and modeled historical (1950-1980) ice break up in days from historical mean across lakes for each GCM. Model predictions under historical (1950-2006) greenhouse gas emissions (green) and under future climate scenarios from 2007 to 2099 under representative concentrating pathways (RCP) 4.5 (top, orange) and 8.5 (bottom, red). Dashed lines are the 15 individual climate projections under each scenario, the solid line is the average of all models.

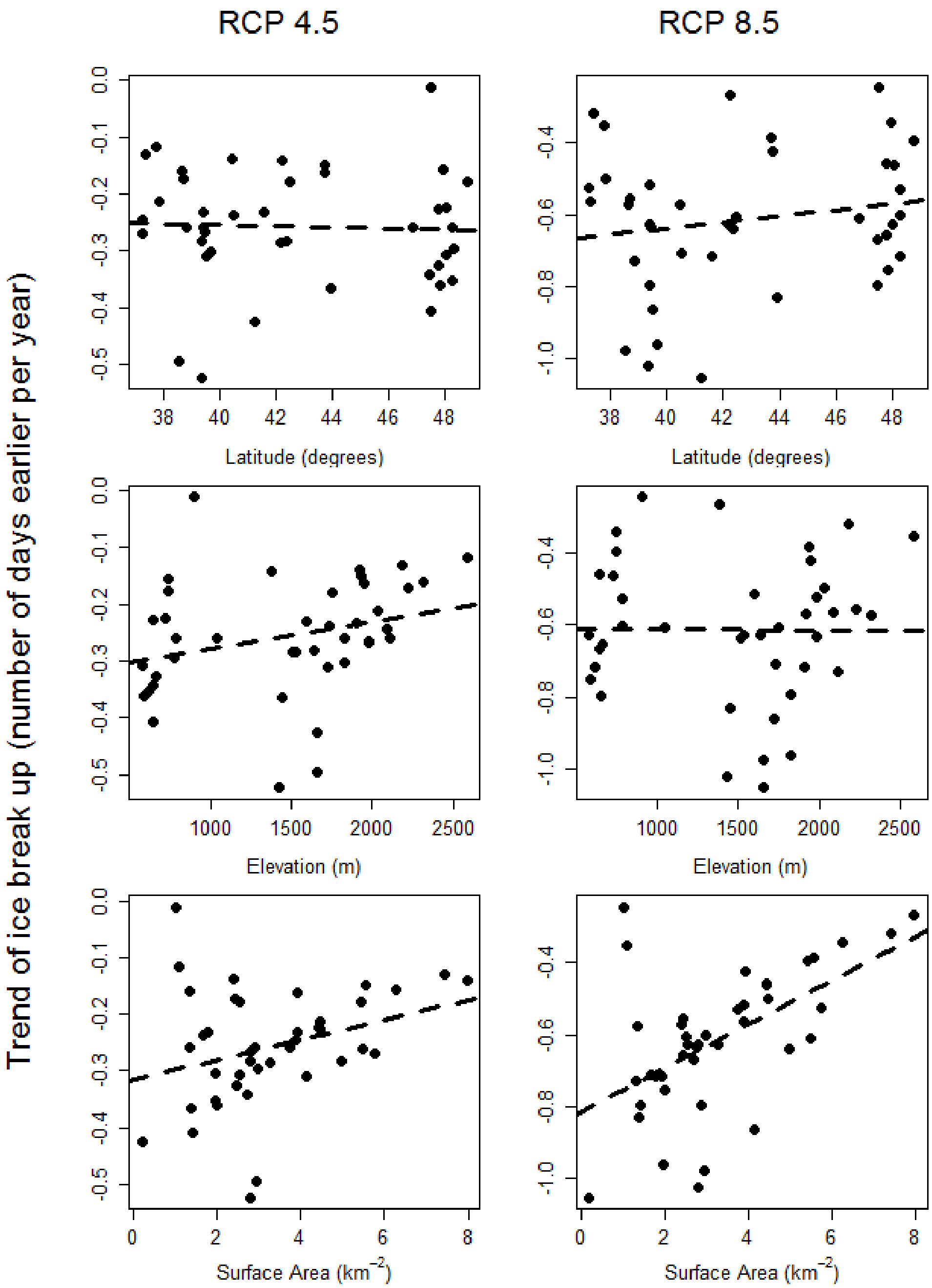


Figure 6. Lake specific ice break-up trend predicted by the base LMEM model for RCP 4.5 (left) and RCP 8.5 (right) related to latitude, elevation, and surface area. The relationship of surface area to trend of ice break-up was significant ($p < 0.05$ for both RCP 4.5 and RCP 8.5) but was not for latitude or elevation.

CHAPTER 2. Consumer response to earlier ice break-up date: The role of habitat specific production and water temperature in fish resources and habitat use.

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ABSTRACT

Production of food resources for consumers is expected to shift with climate change. However, the ability of consumers to utilize these resources is complex because climate change also shifts suitable habitat. Earlier ice break-up dates caused by climate change in mountain lakes can increase production rates, but it is unclear how productivity will transfer to consumers because warming water temperatures may limit obligate cool water consumer habitat use. To determine how productivity and habitat changes, we measured water temperature, production of pelagic zooplankton and littoral zoobenthos across naturally variable ice break-up dates in a subalpine lake. Next, we measured the food resources and habitat use with stable isotope analysis and acoustic telemetry of an obligate cool water fish to determine if consumer energetics, growth and fitness was dictated by thermal habitat suitability or food avialability. Our data suggest that, under earlier ice break-up conditions, littoral zoobenthos production increased while pelagic zooplankton production decreased. This coincided with an increase in littoral water temperatures, which excluded consumers from resource rich littoral habitats. In response, 87% of fish consumer resources were sourced in the pelagic habitat during early ice break-up. Decreased reliance on littoral resources was significantly related to a 29 to 50% reduction in average size of consumers. We conclude that obligate cool-water consumers will be excluded from productive

habitats under warmer climate, which will decrease their fitness and may threaten their sustainability in some ecosystems.

INTRODUCTION

Understanding the impact of global climate change on ecological function has focused on single trophic level production, individuals and populations (Walther et al. 2002). For example, declines in numbers of terrestrial (Spooner et al. 2018) and aquatic (Ricciardi and Rasmussen 1999, Heino et al. 2009, Farmer et al. 2015) species have been documented, and decreases to algal production rates have been observed (Park et al. 2004, Parker et al. 2008). A complete study that incorporates climate driven changes to productivity, individuals and populations to understand and forecast ecosystem level responses is required (but see Stoner et al., 2018).

Climate change has increased and decreased production rates in terrestrial (Nemani et al. 2003), marine (Gregg et al. 2003, Hoegh-Guldberg and Bruno 2010), and freshwater ecosystems (Carpenter et al. 1992, Park et al. 2004, Preston et al. 2016). However, understanding how changes in ecosystem and habitat production will cascade across levels of ecological organization is unclear (Walther et al. 2002, Woodward et al. 2010, Grimm et al. 2013). One hypothesis is that consumer fitness will increase through bottom up stimulation (Power 1992, Pace et al. 1999, Bluhm and Gradinger 2008). Similarly, Stoner et al. (2018) noted linear decreases in herbivore and carnivore abundance with climate driven reductions to terrestrial primary productivity. Change to physical or thermal habitat characteristics also caused by climate change reduces accessibility to productive habitats (Sekercioglu et al. 2008, Wenger et al. 2011, Guzzo et al. 2017) and culminates in reduced fitness (Farmer et al. 2015). Increased climate variation (Min et al. 2011, Dai 2013) is likely to drive complex effects on ecosystem and habitat production, with unclear results for consumers and their habitat use.

In annually ice-covered aquatic ecosystems, climate change results in decreased durations of ice cover and earlier ice break-up dates (Goldman et al. 1989, Magnuson 2000, Weyhenmeyer et al. 2008, Benson et al. 2012, Beyene and Jain 2015). Earlier ice break-up in mountain lakes causes increased water temperature and primary production (Jassby et al. 1990, Park et al. 2004, Preston et al. 2016), which may increase habitat specific resources (e.g. zooplankton; Adrian et al., 1999) but decreases usable habitat for certain consumers through higher water temperatures. Thus, earlier ice break-up may cascade from ecosystem level (habitat productivity) to individual (consumer) habitat and resource use. Here we present and test a conceptual model (Figure 1) for the role of ice break-up date on ecosystem to consumer level processes in mountain lakes.

First, we consider littoral zoobenthic and pelagic zooplankton production, which are primary food sources of consumers (Vander Zanden et al. 2011). We predict that early ice break-up will increase pelagic secondary production through increased pelagic water temperatures and light (Figure 1). Adrian et al. (1999) have shown that magnitude of peak daphnia abundance in shallow lakes was postively influenced by springtime water temperatures. Similarly, Jassby et al. (1990) and Park et al. (2004) found relationships between ice break-up date, water temperature, primary productivity, and *Daphnia rosea* biomass in Castle Lake, California. In the littoral zone, we predicted that zoobenthic production rates would be stable due to longer life cycles of zoobenthic organisms (Thorp and Covich 2010), but their relative contributions to the lake budget would decrease as pelagic secondary production increases. However, positive relationships between zoobenthic production and warm, well-oxygenated waters (Craig et al. 2015) with little light limitation (Karlsson et al. 2009) have been observed elsewhere, suggesting increases to littoral zoobenthic production may be observed under earlier ice break-up.

The majority of fish energy resources are derived from the littoral zone (Vander Zanden et al. 2011), but it is unclear how this may change with earlier ice break-up. We predicted that early ice break-up would increase fish consumer reliance on zooplankton production in the pelagic zone through two mechanisms (Figure 1); first, through a hypothesized increase to pelagic secondary production (Jassby et al. 1990; Park et al. 2004; Figure 1, top); second, through increases to littoral water temperature caused by early ice break-up that will limit efficient littoral foraging (Vander Zanden et al. 2006) by obligate cool water fish (Guzzo et al. 2017).

Lastly, we developed a prediction on the importance of allochthonous carbon to fish consumers (not shown in Figure 1). Fish consume terrestrial carbon primarily through consumption of terrestrial invertebrates falling into nearshore habitats (Baxter et al. 2005). Other allochthonous sources (e.g. leaf litter) are poorly utilized by aquatic producers and consumers (Brett et al. 2017; Thorp and Bowes 2017). Climate change predictions suggest decreased terrestrial invertebrate flux to aquatic systems through less connection to riparian zones and phenological mismatches between terrestrial invertebrates and fish consumers (Durant et al. 2007, Larsen et al. 2016). We expected either a decrease or no change in the contribution of allochthonous carbon sources to consumers under early ice break-up conditions due to the low reliance of fish on terrestrial resources in mountain lakes (Vander Zanden et al. 2006), inaccessibility of aquatic organisms to process allochthonous carbon (Brett et al. 2017, Thorp and Bowes 2017) and potentially decreased flux of terrestrial insects to freshwaters (Larsen et al. 2016) during the time when aquatic food webs are depleted (Nakano and Murakami 2001).

To test our conceptual model (Figure 1, top) we quantified ice break-up dates, water temperatures, pelagic zooplankton production, and littoral zoobenthic production under early, average and late ice break-up conditions in Castle Lake, a sub-alpine meso-oligotrophic system in California, USA. We then quantified the influence of these variables on Brook Trout (*Salvelinus fontinalis*) food resources (pelagic vs littoral, terrestrial vs aquatic), habitat use and fitness, using stable isotopes and acoustic telemetry.

METHODS

Study Site:

Castle Lake is a natural sub-alpine, meso- to oligotrophic lake in the Siskiyou Mountains of Northern California, USA (N41°13'; W122°22', elevation = 1657 m; Figure 2). The maximum depth is 32 m with a mean depth of 11.4 m, and the surface area is 20.1 ha (Vander Zanden et al. 2006). Summer stratification reaches a depth of 6-10 m, with the Secchi depth between 7-13 m. Littoral habitat (< 6 m deep) comprises 9.2 ha (45% of lake area) and pelagic habitat comprises 10.9 (55% of the lakes area (Axler and Reuter 1996). The lake was naturally fish-less but currently hosts non-native Brook Trout (*Salvelinus fontinalis*), Golden Shiner (*Notemigonus crysoleucas*) and Rainbow Trout (*Onchorhynchus mykiss*). The zooplankton community consists of *Daphnia rosea, Bosmina longirostris, Diaptomus novamexicanus and Diacyclops thomasi.* Zoobenthos consists of Chironomidae, Trichoptera (Limnephilida, Leptoceridae, Lepidostomatidae), Ephemeroptera (Baetidae, Ephemerellidae), Megaloptera (Sialidae) and Odonata (Corduliidae, Libelludiae; Brownstein 2010).

Evidence of climatic forcing (e.g. El-Nino events, Pacific Decadal Oscillation) on timing of ice break-up (Goldman et al. 1989), and its subsequent effect on the temperature, stratification and primary production patterns during ice-free seasons has been observed (Strub et al. 1985, Jassby et al. 1990, Park et al. 2004). Castle lake is typically ice covered from approximately November or December to April or May (Vander Zanden et al. 2006).

Ice break-up date and water temperature:

From 2012 to 2016, four pictures were taken daily of Castle Lake with a programmed digital camera, earlier years were determined from visual observations. The photo record and visual observations were used to determine the complete ice break-up date (Julian day) each year. Water temperature was measured with weekly profile measurements from 2008 to 2014 from the surface to 32 m. In 2014 a series of temperature loggers (Thermochron iButtons) were deployed year-round, which logged depths from the surface to 25 m incrementally. The average temperature < 5 m was used to determine littoral water temperature. Temperature at 10 m was used to represent pelagic water temperature. During years prior to the installation of the temperature loggers, temperatures were linearly interpolated between sampling dates. To quantify habitat specific temperature, we counted the number of days that littoral and pelagic zone temperatures were greater than 15 °C and 10°C, respectively. We used 15 °C for littoral because it was observed to be a limiting temperature for Brook Trout from our temperature sensing acoustic tags (see consumer habitat use section) and was used to examine habitat limitation of other *Salvelinus* species (Biro 1998, Guzzo et al. 2017). We used 10 °C for pelagic temperature because there were only 8 days > 15 °C during our study period at 10 m, and thus were unable to relate ice break-up date and water temperature.

Habitat specific secondary production:

Zooplankton were collected weekly at night from three depths in the epilimnion (0, 3 and 5 m), pooled and preserved in Lugol’s from June to September (2008-2016) using a 15 L Schindler trap (80 µm mesh). Individuals were enumerated from each sample and converted to density and biomass per m^3 for each species. All cladocerans were measured from the top of the head to the base of the apical spine, and eggs of gravid females were counted.

Production (mg C m^{-3} day^{-1}) of the dominant zooplankton species (*Daphnia rosea*), was calculated using the egg-ratio method (Edmondson and Winberg 1971, Edmondson 1972, Paloheimo 1974), following methods used previously in the lake (Vander Zanden et al. 2006). This method calculates a numeric growth rate (*b)* which is multiplied by the mean biomass of individuals (Paterson et al. 1997). The *Daphnia rosea* production estimate was scaled to whole lake pelagic secondary production (mg C m^{-2} day^{-1}) by multiplying by 1.24 (average ratio of other zooplankton to cladoceran production), the pelagic area of the lake (10.9 ha), and the depth (5 m) represented by our sampling (Vander Zanden et al. 2006). Biomass was converted to carbon using an assumed 40% carbon content (Vander Zanden et al. 2006). Production was calculated for each week sampled and then averaged across all dates.

Zoobenthic samples were collected from 2009 to 2016 in June, July and September at 4 sites in the littoral zone and 2 sites in the profundal zone (Figure 2). Littoral zone samples with coarse substrate were collected using a modified stove-pipe method, and at soft sediment sites an Eckman grab sampler (0.023 m^2) was used. The modified stove-pipe method started by driving a sample cylinder (0.045 m^2 diameter) 3 cm into the sediment, the area was disturbed (e.g. rocks were scrubbed, sticks washed) and then water and sediment were sieved for invertebrates. Profundal samples were collected at 20 m and 25 m using an Eckman grab sampler. Each zoobenthic sample was preserved, and individuals were identified to family (Thorp and Covich 2010) and measured to the nearest 0.1 mm.

Zoobenthic secondary production (mg C m^{-2} day^{-1}) was estimated as the product of species average dry mass, population density, and production to biomass (*P/B)* ratios (Strayer and Likens 1986, Vander Zanden et al. 2006, Craig et al. 2015). Dry mass was estimated from published length to dry mass ratios (Benke et al. 1999, Sabo et al. 2002, Baumgärtner and Rothhaupt 2003, Edwards et al. 2009) for all species except for oligochaetes, which were estimated volumetrically (Woodward and Hildrew 2002, Craig et al. 2015). To convert to carbon we assumed that 45% of dry mass was carbon (Strayer and Likens 1986). Taxon specific *P/B* ratios were developed from the allometric equation (Banse and Mosher 1980). Production by each taxon was summed for each sampling site and sampling period and then averaged across sites in each habitat per month per year. Annual estimates of zoobenthic production were divided by the number of ice free days each year (Vander Zanden et al. 2006) to estimate daily production (mg C m^{-2} day^{-1}). Littoral and profundal zoobenthic production was scaled to the whole lake by multiplying the daily production estimate by the area of each zone.

Consumer sampling:

Gill nets (20 m long) were used to collect fish each month from June until October from 2010-2016. One standard (2.5 cm mesh) and one experimental (3.2, 2.5 and 1.9 cm mesh) were set at deep (7 m) and shallow depths (3 m) at 2 sites for 2 consecutive nights per month. One net (deep or shallow depth) was set at each site per night, then switched between sites.

Consumer energetic resources:

Ecosystem level (autochthonous and allochthonous) energetic resources were determined for Brook Trout using amino acid compound-specific stable isotope analysis (AA-CSIA; Chikaraishi et al. 2009; Thorp and Bowes 2017). The proportion of habitat specific (littoral vs pelagic) energetic resources was determined using bulk $\delta^{13}C$ (Peterson and Fry 1987, Vander Zanden et al. 2006). AA-CSIA isotopes were analyzed for fish collected in early (June or July) and late (September) summer of 2011 to 2016 and 2010 to 2016 for bulk tissue stable isotopes, and averaged per year. In addition to fish, bulk isotopes for *Daphnia rosea* and littoral zoobenthos (Trichopterans, Chironomids and Oligochaetes) were also used to determine baseline signatures of $\delta^{13}C$ for pelagic and littoral habitats.

AA-CSIA is a relatively new ecological technique which offers greater analytical precision and provides move tracers to distinguish among food resources. It is especially accurate at distinguishing between autochthonous and allochthonous carbon sources (Thorp and Bowes 2017). To process AA-CSIA, a sample of fish tissue was dried at 60 °C for 48 hrs and shipped to the UC-Davis Stable Isotope Facility. The specific techniques for analyzing AA-CSIA are detailed in Walsh et al. (2014) and summarized in Thorp and Bowes (2017). We obtained $\delta^{13}C$ and $\delta^{15}N$, expressed as per mil (‰), for essential (phenylalanine, valine, leucine and isoleucine) and non-essential (glycine, proline, alanine, and glutamate) amino acids.

Bulk tissue $\delta^{13}C$ stable isotopes were collected from the same fish that were processed for AA-CSIA. Muscle tissue from each fish was taken from the dorsal muscle, dried at 60 °C for 48 hrs, ground into a fine powder and packed into 8 x 5 mm tin capsules. Samples were shipped to the University of New Mexico Center for Stable Isotopes for analysis. $\delta^{13}C$ concentrations were expressed per mil (‰). Specific details of the isotopic analysis are found in Peterson and Fry (1987) and Vander Zanden et al. (2006).

Consumer percent reliance on resources was estimated using the FRUITS (Food Reconstruction Using Isotopic Transferred Signals; Fernandes et al. 2014) isotopic mixing model. For AA-CSIA, mean and associated uncertainty (1 ± SD) of consumers $\delta^{13}C$ for each amino acid was incorporated into the model as the target. We used published values of cyanobacteria, green algae, fungi, C_3 (aquatic macrophyte and terrestrial combined) and C_4

terrestrial plants as sources for AA-CSIA (Thorp and Bowes 2017). Amino acid signatures are highly conserved among broad taxonomic groups and are not significantly influenced by space and time, thus published values can be used for baseline signatures (Larsen et al., 2013). For bulk stable isotopes, pelagic baseline (*Daphnia rosea*) and littoral baselines (Trichoptera, Chironomid and Oligochaeta) of $\delta^{13}C$ for each year were used as sources because their signature can vary over space, time and taxonomic groups. Profundal zone invertebrates were not included in dietary estimates based on a qualitative assessment of fish diets and their absence in fish diets historically in Castle Lake (Elser et al. 1995, Vander Zanden et al. 2006). The FRUITS model is a Bayesian based isotopic mixing model, that accounts for dietary routing (contribution of sources towards the target signal). For both AA-CSIA and bulk tissue isotopes, we used an unweighted model with un-informative priors and assumed that all sources had an equal chance to make up 100% of the diet. The model draws on the BUGS (Bayesian Inference Using Gibbs Sampling) algorithm, to generate posterior distributions of percent contributions of each potential food source to the consumer. We used the mean of the posterior distributions to describe results. Percent reliance on autochthonous resources was calculated by summing the mean of the posterior distributions for reliance on aquatic algae and cyanobacteria.

Consumer habitat use:

To quantify consumer habitat use, Brook Trout were marked and tracked with an acoustic telemetry array. Eighteen total large (>150 g) Brook Trout were tagged with Vemco V9T (VEMCO Ltd.) temperature-sensing acoustic transmitters on November 13, 2015 and on June 15, 2016 (9 on each date). Each tag transmitted a paired time stamped signal (individual to each fish) and temperature every 60 – 180 seconds. Locations and depths of transmitter-implanted fish were monitored from November 2015 until February 2017 based on battery life. The acoustic array had 8 acoustic hydrophones (Vemco VR2W; VEMCO Ltd.) with overlapping detection ranges and was instrumented throughout the study period (Figure 2). Detections ranges were determined using a pilot study in which a test tag was lowered to 10 m and slowly rowed in the opposite direction of the hydrophone. We had approximately 80% detection at 500 m away from the hydrophone, and complete coverage of the lake.

The Vemco positions system (VPS) was used to obtain time-stamped GPS positions with coupled temperatures for each fish (Espinoza et al. 2011, Smith 2013, Roy et al. 2014). VPS uses a hyperbolic positioning algorithm, which is based on the difference in time (micro-seconds) a transmission arrives at different hydrophones. Time is then converted to distance and a position is triangulated (Smith 2013). Because this method required exact time synchronization of hydrophones, we deployed 4 time synchronizing transmitters (Vemco V13; VEMCO Ltd.).

Tag position data was imported into a geographic information system (GIS) and each data assigned a pelagic or littoral classification based on its location. We calculated the average daily time spent in the littoral zone, average number of forays into the littoral zone, and the average duration of each foray for each day and individual for the duration of the study (Guzzo et al. 2017). We considered a foray to be when a fish crossed from the pelagic to the littoral zone, and the duration was the sum of time between consecutive detections within the littoral zone.

Consumer fitness:

We used the average late summer (September and October) body size and egg mass of large (> 100 g) Brook Trout as fitness and reproduction success estimates, respectively. The size class was selected because it corresponded to the size of fish used to estimate littoral reliance and habitat use, and the late summer period incorporated the growth response from the entire growing season. Egg mass was weighed for each female that was captured. All fish were captured using gill nets as outlined previously.

Data Analysis:

General linear models or Kolmogorov – Smirnov (KS) tests were used for statistical analysis (Faraway 2010). Relationships analyzed included: 1) Julian date of ice break-up to littoral and pelagic water temperatures; 2) pelagic zooplankton production and littoral zoobenthic production to ice year type; 3) mean percent reliance of Brook Trout consumers on littoral and autochthonous material to Julian date of ice break-up and water temperature; and 4) average size of Brook Trout to percent reliance on littoral zone resources. Univariate normality was assessed using a Shapiro-Wilk normality test and visually assessed using quantile to quantile regression plots. Heterogeneity of variances among ice year types was analyzed using Bartlett's test (Faraway 2010). If needed, data were either $\log_{10}$ or square root transformed to better meet assumptions (Faraway 2010) as noted in the results.

The data for time spent in littoral zone habitats between warm water periods (> 15 °C) and cold water periods (< 15°C) were unable to meet standard statistical assumptions after multiple attempts at normalization through log, square root, and cube root transformations. Two sample non-parametric KS tests were used to compare daily time spent in, number of forays into, and average duration of each foray into the littoral zone when littoral zone water temperature was > 15 °C and < 15 °C. To determine if the temperature fish experienced was more reflective of the littoral zone or the pelagic zone we computed the differences in daily average fish temperature to daily littoral and pelagic water temperatures and compared them using a KS test. All statistics and computations were done using the R open source statistical software (R Core Team 2015).

RESULTS

Ice break-up date and water temperature:

Ice break-up date ranged from Julian day 178 (June 27th) in 2011 to Julian day 51 (February 20th) in 2015 (Table 1). Ice break-up date was grouped into average, early and late ice break-up year classifications. Average ice break-up years were within 1 SD of the 55-year historical mean of ice break-up date (Julian day 133 ± 25 days), while late and early ice break-up years were outside of that range. Earlier ice break-up dates were had significant positive relationships to days littoral water temperature was greater than 15 °C ($R^2 = 0.63$, $p < 0.05$) and days pelagic water temperature was greater than 10 °C ($R^2 = 0.48$, $p = 0.02$).

Habitat specific secondary production:

Daphnia and *Diaptomus* were the most common species. Mean (± standard error) biomass was lower during early ice years (*Daphnia* = 28.7 ± 7.1, *Diaptomus* = 2.6 ± 1.1 mg drymass m^{-3}) than later and average ice break-up years (Figure C1), but the difference was only statistically significant for *Diaptomus* ($p < 0.05$). There was no statistical relationship for the less common species (*Bosmina* and *Diacyclops*) between standing stock and ice year type (Figure C1), but on average they consisted of only 29% of all zooplankton standing stock. Littoral zoobenthic biomass (mg dry mass m^{-2} was dominated by Trichoptera, Diptera, and Hirudenia (Figure C2). Nearly all species had a higher mean biomass during early ice years compared to average and late ice years but only Diptera and Ephemeroptera were significantly ($p < 0.05$) different (Figure C2).

Daily pelagic zooplankton production was estimated at 0.97 ± 0.13 (mean ± SE) mg C m^{-2} day^{-1} during early ice years, and was significantly (square root transformed, $p < 0.05$) lower than pelagic zooplankton production during average (2.17 ± 0.27 mg C m^{-2} day^{-1}) and late (1.72

± 0.83 mg C m^{-2} day^{-1}) ice years (Figure 3a and b). Daily littoral zoobenthic production was estimated to be 2.44 ± 0.35 mg C m^{-2} day^{-1} during early ice years and was significantly ($p < 0.05$) greater than zoobenthic production during average (1.49 ± 0.28 mg C m^{-2} day^{-1}) and late (1.61 ± 0.33 mg C^{-1} m^{-2} day^{-1}) ice years (Figure 3a and b). Daily profundal zone zoobenthic production was not significantly different across years but averaged 1.02 ± 0.31 mg C^{-1} m^{-2} day^{-1}. The percent contribution of pelagic zooplankton was highest in late and average ice years 81% and 82%, while the highest contribution (75%) of littoral zoobenthic production was in early ice years (Figure 3c), profundal zone was not included because it did not vary across years.

Consumer energetic resources:

The dominant basal resources among aquatic and terrestrial sources for consumers was algae (range = 57-46%) followed by C_3 plants (range = 29-21%) across varying ice break-up dates (Figure C3a, b and c). To be conservative we did not include C_3 plants in our estimate of percent reliance on autochthonous carbon and only used cyanobacteria and green algae derived carbon. There was no significant relationship between autochthonous or allochthonous carbon reliance by consumers and ice year type, water temperature, or Julian date of ice break-up (Figure 4a and b).

$\delta^{13}C$ from bulk tissue used to estimate percent reliance on littoral and pelagic habitat carbon sources varied across different ice year types (Table 2). Values were more negative for consumers but more positive for zooplankton and littoral invertebrates during early ice break-up years (Table 2). The percent reliance of consumers on pelagic and littoral zone resources also varied across different ice year types (Figure C3d, e and f). In early ice years, littoral reliance was 13%, in average ice years was 46% and in late ice years was 91% (Figure C3d, e and f). The mean of the posterior distribution of estimated percent reliance on littoral zone resources was significantly related to both Julian date of ice break-up and number of days littoral water temperature exceeded 15 °C (Figure 4c and d). Percent reliance on pelagic and littoral resources as not significantly related to habitat specific secondary production (littoral, $R^2 = 0.06$, $p = 0.30$; pelagic, $R^2 = 0.30$, $p = 0.12$).

Consumer habitat use:

Habitat use data showed that consumers visited the littoral zone more frequently, for longer during each visit, and spent more total time in the littoral zone when water temperatures were < 15 °C (Figure 5). The daily average time spent in, number of forays into, and average duration of foray into the littoral zone were all significantly greater (KS test, $p < 0.01$) when littoral water temperature was < 15 °C. The variation among individuals in daily time spent in the littoral zone was also higher when littoral water temperature was < 15 °C (SD = 125 minutes) when compared to times when littoral water temperature was > 15 °C (SD = 73 minutes). The water temperature fish experienced was more closely related to pelagic water temperatures when littoral zone temperatures were > 15 °C (KS test, $p < 0.01$). The average difference between fish temperature and littoral and pelagic zone water temperature was 12.2 ± 3.6 °C (mean ± 1 SD) and 2.1 ± 1.3 °C, respectively.

Consumer fitness:

The average size of Brook Trout consumers was significantly smaller during early ice break-up conditions compared to late ice break-up condition, and was significantly ($R^2 = 0.60$, $p = 0.02$) related to the percent reliance on littoral zone prey items (Figure 6a). The egg mass of female Brook Trout was not significantly ($R^2 = 0.08$, $p = 0.48$) related to ice break-up or littoral zone reliance (Figure 6b).

DISCUSSION

Climate change is expected to have unprecedented and complex impacts on ecosystems (Walther et al. 2002, Grimm et al. 2013). For example, pelagic feeding mammals in arctic systems are expected to increase their fitness in response to increased pelagic productivity, while obligate coastal species are expected to perish as increased runoff reduces production and visibility (Bluhm and Gradinger 2008). However, changes to productivity are coupled with physical and thermal habitat alterations, which could exclude species with narrow temperature tolerances (Sekercioglu et al. 2008, Wenger et al. 2011, Guzzo et al. 2017).

Our data suggest that earlier ice break-up date drives complex ecological interactions by increasing habitat production but limiting consumer utilization though thermal exclusion. Specifically, under early ice break-up, we describe decreased summer pelagic zooplankton production and increased littoral zoobenthic production. Reliance on littoral zone resources by Brook Trout increased with later ice break-up dates and was independent of habitat specific secondary production. Rather, Brook Trout were excluded from littoral zone habitats by warmer water temperatures, which increased their reliance on pelagic resources. In addition, our data show that consumers will consistently rely on autochthonous carbon independent of ice break-up date.

Previous studies (Straile and Adrian 2000, Park et al. 2004) suggest that biomass of zooplankton was positively related to the water temperature and ice break-up date. We found that zooplankton production was significantly less in early ice years with more days of warmer water temperatures than average and late ice years. The earliest ice break-up dates used by Park et al. (2004) were Julian date 90 (1988) and Julian date 98 (1990), while the earliest ice break-up dates in our data set were Julian date 51 (2015) and 57 (2014). We suggest the disparity between Park et al. (2004) and our study is rooted in the differences between the timing of ice break-up dates used in each study. Our estimate was for summer (June, July, August, September) production, but shifts in phenology of phytoplankton blooms to early spring under warming, create a mismatch between zooplankton and food resources (Winder and Schindler 2004, Durant et al. 2007). Thus, our data may have captured a threshold of ice break-up date in which zooplankton are resource limited in the summer, but not by the average ice break-up years used in Park et al. (2004) data. For example, de Senerpont Domis et al. (2007) found only in extreme warming scenarios were zooplankton decoupled from algal food resources. Alternatively, phytoplankton community succession may be accelerated under warming scenarios providing a lower quality food resource for zooplankton and limiting their production in extremely warm years (Sommer et al. 2012). Though it is possible our scaling calculation from species specific (*Daphnia*) to zooplankton community production is flawed, the dominant taxa declined similarly with ice year type. Thus, we feel our estimates reflect community wide changes.

We predicted that littoral zoobenthic production would be stable across ice break-up years, but we observed increases in early ice break-up years. One possible mechanism is that increases to littoral benthic primary production drove littoral zoobenthic production. This seems unlikely as Northington et al. (2010) found little evidence for this in artic lakes. Craig et al. (2015) suggest that zoobenthic production is related to warm and well oxygenated waters, which occurred in Castle Lake during early ice break-up years and likely explains our observations.

The reliance of fisheries on benthic and littoral resources is well established (Vander Zanden et al. 2011) but how that will change under climate mediated effects (e.g. ice break-up) on mountain lakes is unclear. We provide evidence that the percent of littoral zone reliance for Brook Trout consumers decreases with earlier ice break-up dates. The relationship was independent of habitat production, but directly related to littoral zone water temperature. Similar findings by Guzzo et al. (2017) showed that water temperatures, not prey density drove Lake Trout (*Salvelinus namaycush*) habitat and resource use. Biro (1998) also found that young-of-year brook trout reduced littoral habitat use when water temperatures became unsuitable. As water temperatures warm (O'Reilly et al. 2015) and ice break-up dates become earlier (Magnuson 2000, Beyene and Jain 2015, Sharma et al. 2016), cool water fishes are likely to increase their reliance on less efficient (Vander Zanden et al. 2006) pelagic resources.

The thermally induced habitat exclusion identified in our study and by others resulted in less littoral zone reliance and reduced fitness at temperatures > 15 °C (Biro 1998, Guzzo et al. 2017). Experimental studies on Brook Trout suggest that their growth rate is reduced above 16 °C (Chadwick and McCormick 2017). Reductions in body size and fecundity have been associated with climate change across both terrestrial and aquatic systems (Sheridan and Bickford 2011), for plants, animals and fish (Walther et al. 2002, Farmer et al. 2015). We did not observe a reduction in egg mass, but others have suggested that the spawning rate of Brook Trout may decrease under warmer water temperatures (Robinson et al. 2011). To fully understand the impacts of consumer resources and habitat use on Brook Trout reproduction we suggest a detailed assessment of spawning rate and egg incubation success, or an analysis of the number or average size of eggs may be reduced. Rising air temperatures (IPCC 2014) will lead to increased water temperatures (O'Reilly et al. 2015) and decreased reliance on littoral habitats (Guzzo et al. 2017, this study). The associated decrease in growth rates and body size with limitation to littoral food resources may culminate in reduced fecundity and lower recruitment, limiting or extirpating populations.

The role that climate change and ice off date will have on consumer reliance on autochthonous carbon is not well studied. The main source of terrestrial carbon for fishes is through flux of terrestrial insects (Baxter et al. 2005, Wipfli and Baxter 2010), because other forms (e.g. leaf litter) do not incorporate into lake food webs (Brett et al. 2017). Climate change induced shifts to phenology of terrestrial insect subsidies to lakes is expected (Larsen et al., 2016) and due to phenological mismatch, these subsidies may not be used by fish (Durant et al. 2007). For example, Nakano et al. (2001) highlighted the importance of terrestrial subsidies when autochthonous resources are depleted. Under climate change, shifts in terrestrial primary production may result in an earlier life history of terrestrial insects that are not available to aquatic consumers during periods with low autochthonous production. Additionally, warmer water temperatures excluded Brook Trout consumers from the littoral zone in our study and elsewhere (Guzzo et al. 2017), further limiting their ability to utilize terrestrial insects that land in the near shore. We show that ice break-up was unrelated to fish reliance on autochthonous carbon and posit that autochthonous production will drive fisheries regardless of climate scenario.

We conclude that under early ice break-up conditions, the foraging duration in productive, energetically efficient littoral habitats (Vander Zanden et al. 2006) will be reduced for obligate cool water consumers. Instead these consumers will forage in a resource poor pelagic zone, causing lower fitness (Figure 2, bottom). While numerous studies have examined the effect of ice break-up on single variables (Parker et al. 2008, Helland et al. 2011, Preston et al. 2016), our data-set demonstrates that ice break-up date can cascade from thermal properties to ecosystem secondary production budgets, ultimately causing impacts to consumer habitat use, resources, and fitness level.

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TABLES

Table 1. Observed Julian date of ice break-up, ice year classifications and number of days water temperature exceeded 15°C and 10 °C in the littoral and pelagic zone, respectively. The 55-year average ice break-up date was Julian date 133 (May 13th).

Year	Julian Date of Ice break-up	Ice Year Type Classification	Days littoral zone temperature > 15 °C	Days pelagic zone temperature > 10 °C*
2008	140	Average	106	42
2009	141	Average	96	27
2010	176	Late	72	2
2011	178	Late	91	10
2012	121	Average	120	71
2013	135	Average	127	94
2014	57	Early	135	101
2015	51	Early	126	104
2016	112	Average	113	0

*We calculated both days above 15 and 10 °C. Because there were 8 days in all years which had water temperatures at 10 m greater than 15 °C we presented 10 °C instead.

Table 2 Mean ± 1 SD of AA-CSIA δ^{13}C stable isotope values for Brook Trout in and bulk tissue δ^{13}C stable isotope values for zooplankton *(Daphnia rosea;* pelagic), littoral benthic invertebrates (Trichopterans, Chironomids and Oligochaetes; littoral), and Brook Trout across early, average and late ice years.

<table>
<tr><th></th><th colspan="4">Consumer Essential AA-CSIA δ^{13}Carbon Isotopes</th><th colspan="4">Consumer Non-Essential AA-CSIA δ^{13}Carbon Isotopes</th></tr>
<tr><th>Ice Year Type</th><th>Isoleucine</th><th>Leucine</th><th>Pehnylalanine</th><th>Valine</th><th>Glycine</th><th>Proline</th><th>Alanine</th><th>Glutamate</th></tr>
<tr><td>Early</td><td>-29.04+/-2.91</td><td>-34.58+/-2.9</td><td>-33.86+/-2.55</td><td>-30.85+/-3.05</td><td>-13.33+/-2.93</td><td>-21.58+/-3.05</td><td>-23.36+/-2.95</td><td>-22.57+/-2.84</td></tr>
<tr><td>Average</td><td>-29.60+/-2.71</td><td>-35.17+/-2.71</td><td>-34.29+/-2.24</td><td>-31.86+/-2.90</td><td>-15.18+/-3.08</td><td>-21.64+/-2.78</td><td>-24.46+/-3.06</td><td>-23.20+/-2.60</td></tr>
<tr><td>Late</td><td>-28.75+/-1.43</td><td>-34.31+/-1.60</td><td>-33.41+/-1.71</td><td>-30.51+/-1.58</td><td>-14.02+/-2.13</td><td>-20.98+/-2.00</td><td>-23.83+/-2.04</td><td>-21.95+/-1.70</td></tr>
<tr><th rowspan="2"></th><th colspan="8">Bulk δ^{13}Carbon Isotopes</th></tr>
<tr><th colspan="3">Consumer</th><th colspan="3">Littoral</th><th colspan="2">Pelagic</th></tr>
<tr><td>Early</td><td colspan="3">-26.99+/-0.58</td><td colspan="3">-21.83+/-0.88</td><td colspan="2">-25.09+/-1.53</td></tr>
<tr><td>Average</td><td colspan="3">-26.02+/-0.49</td><td colspan="3">-24.58+/-0.60</td><td colspan="2">-28.99+/-0.50</td></tr>
<tr><td>Late</td><td colspan="3">-24.53+/-0.51</td><td colspan="3">-25.21+/-0.47</td><td colspan="2">-29.02+/-1.08</td></tr>
</table>

FIGURES

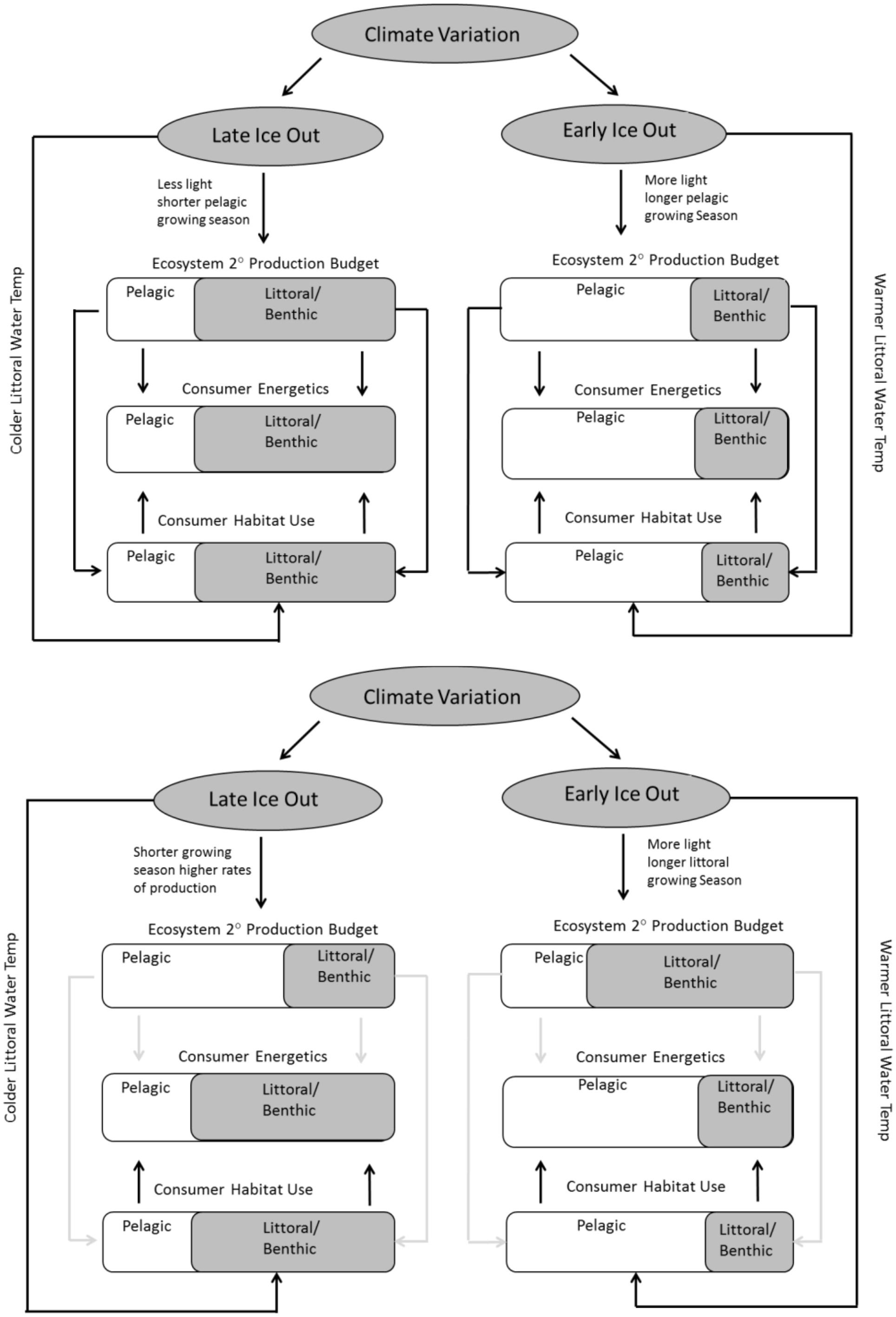

Figure 1. Conceptual model describing predicted (top) and data supported (bottom) effects of ice break-up date on ecosystems processes. Grey arrows in the bottom figure represent tested hypotheses that data did not support. We predicted that decreased light and cooler littoral water temperature as a result of late ice break-up would result in decreased pelagic secondary production coupled with shorter periods of thermally induced littoral zone exclusion. Thus, a higher proportion of consumer resources would be sourced from littoral zone prey. Under early

ice break-up, we predicted that increased light and warmer littoral temperatures, would result in increased pelagic secondary production and longer periods of thermally induced littoral zone exclusion, ultimately causing increased reliance on pelagic prey items by consumers. Contrary to our predictions, our data suggested that there was decreased littoral zone production in late ice break-up years and increased pelagic zone secondary production. However, in agreement with our predictions, our data suggested that littoral zone water temperatures would drive consumer habitat use and consequently consumer resources.

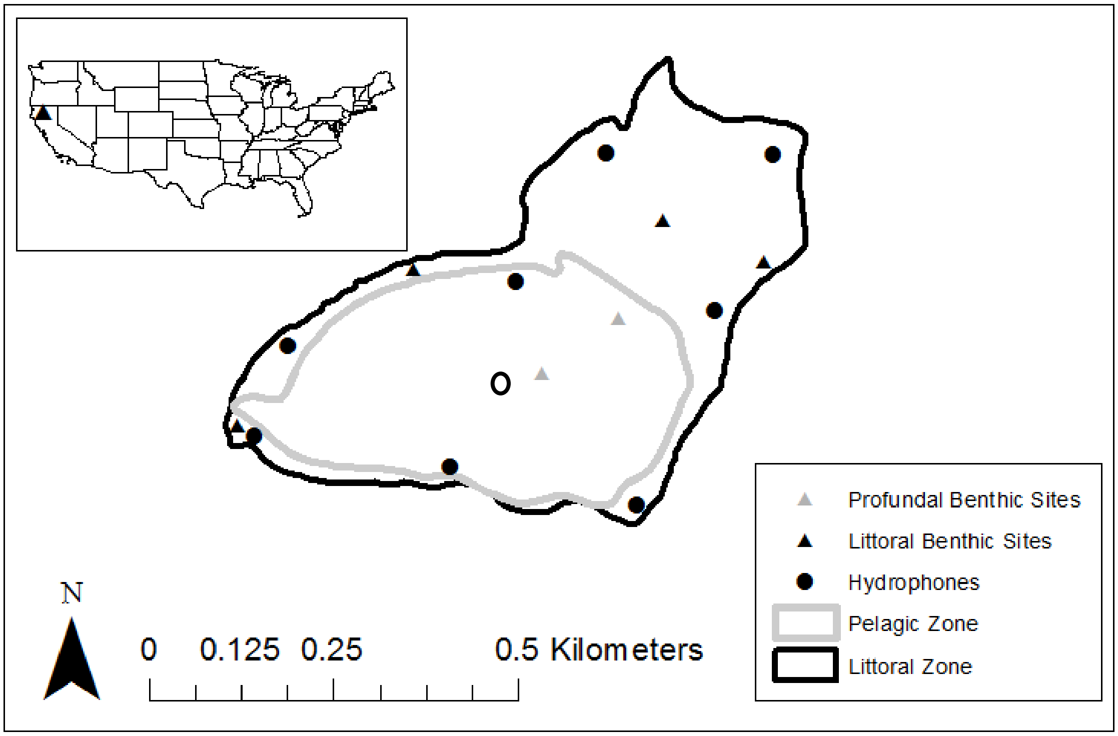

Figure 2. Map of zoobenthic sampling sites and hydrophone locations for acoustic array used for fish telemetry at Castle Lake, California. Open circle is the zooplankton sampling location at the center of the lake.

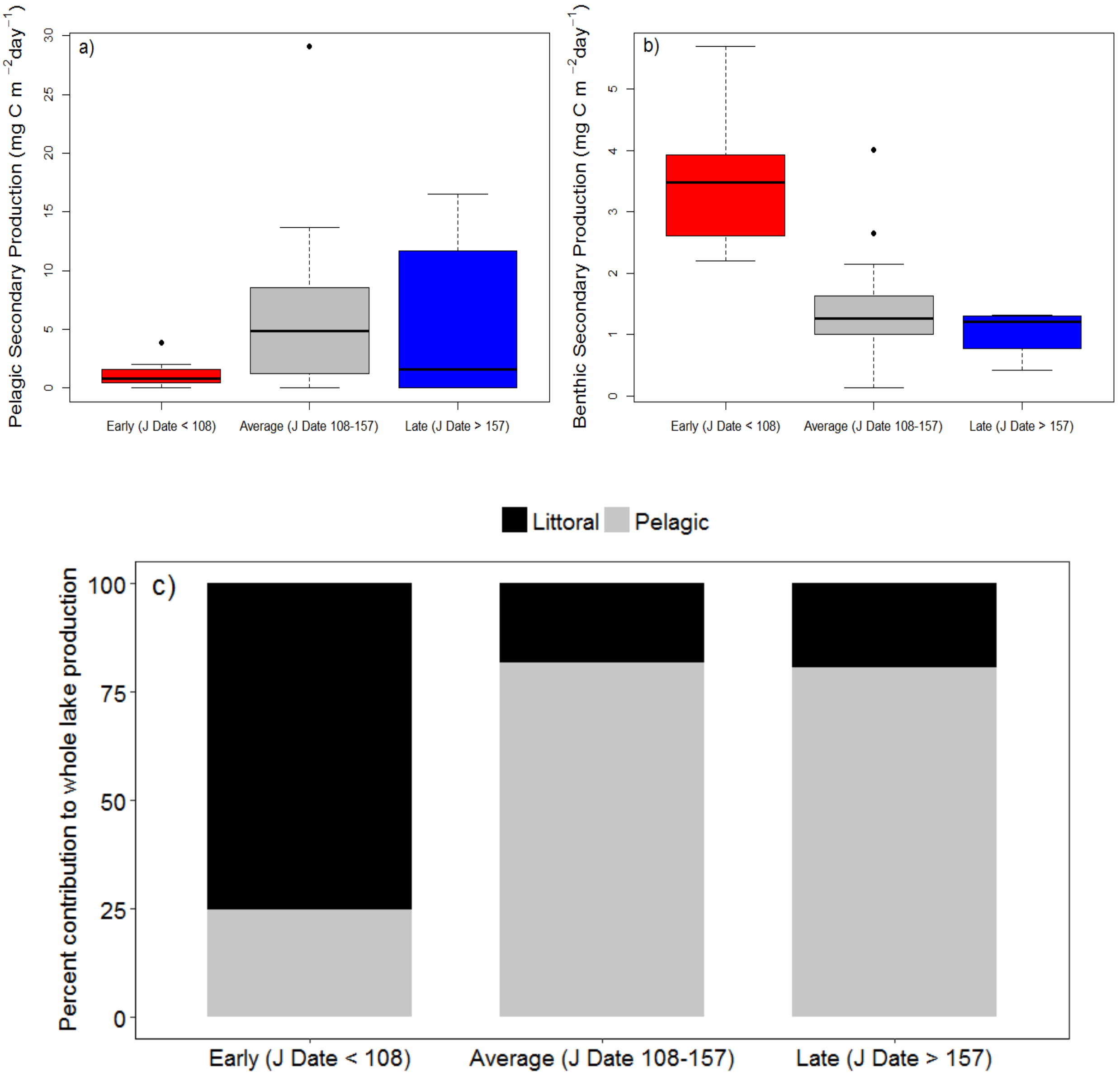

Figure 3. Daily average secondary production estimates of (a) pelagic zooplankton during each sampling week (b) and littoral zoobenthos during each month (June, July, September) in Castle Lake, California during different ice year types. Average and late ice break-up years were statistically ($p < 0.05$) greater than early years for pelagic zooplankton production, while the opposite was observed for littoral zoobenthos production. (c) Percent contributions of pelagic zooplankton and littoral zoobenthos to lake secondary production budgets in ice year types. Julian date (J date) of ice break-up year types is denoted on the x-axis of each plot.

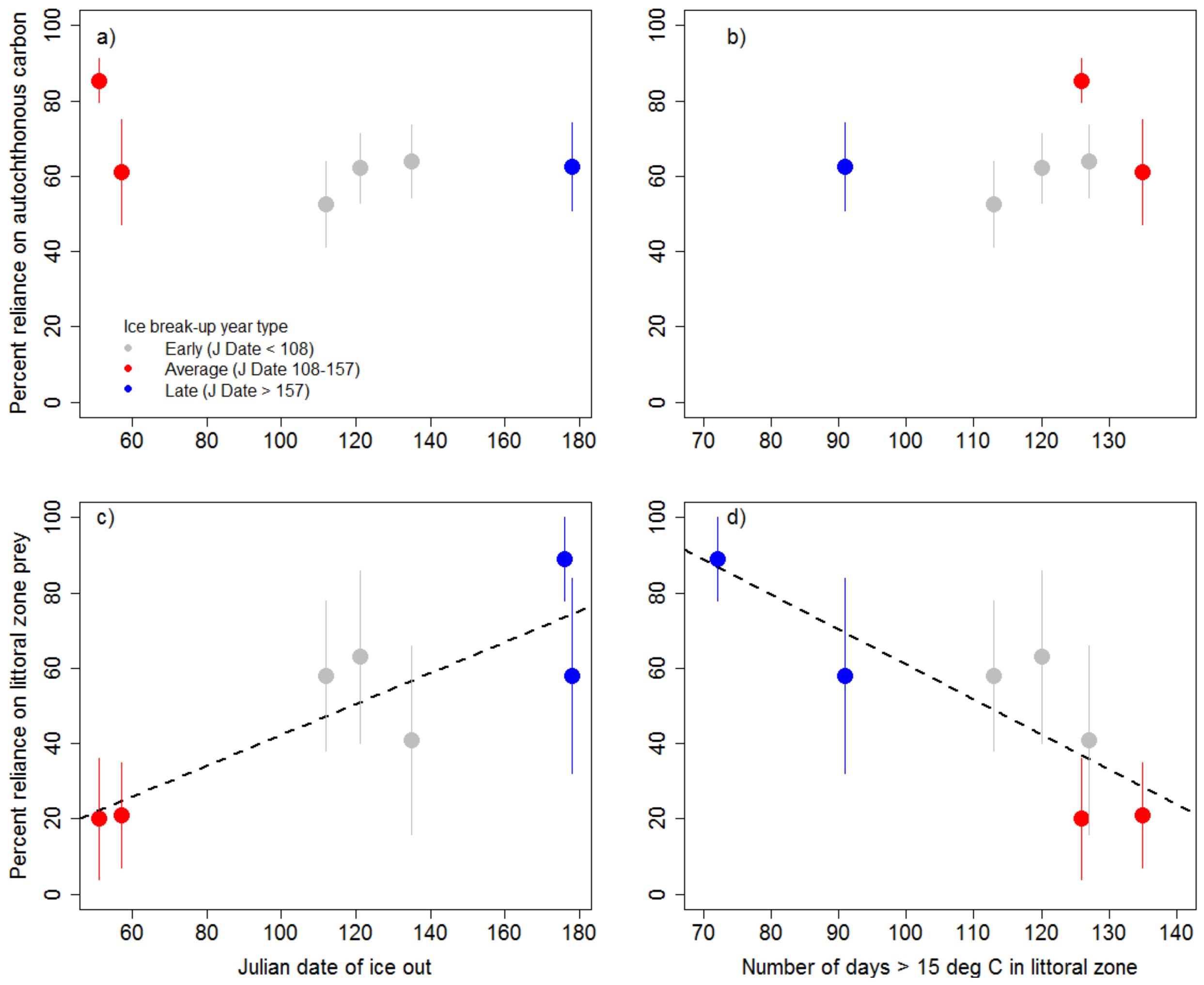

Figure 4. Relationships of mean ± 1 SD percent reliance on autochthonous (cyanobacterial and algal) production and littoral zone production by Brook Trout consumers in each ice year type to (a,c) Julian date of ice break-up; and (b,d) number of days littoral zone temperatures exceeded 15 °C. Relationships for autochthonous carbon were calculated for 2011 to 2016 using AA-CSIA and were not significant. Relationships for littoral zone prey and were calculated from 2010 to 2016 using FRUITS mixing model with bulk tissue and were significant for ice break-up date ($R^2 = 0.66$, $p < 0.05$) and water temperature (d, $R^2 = 0.67$, $p < 0.05$).

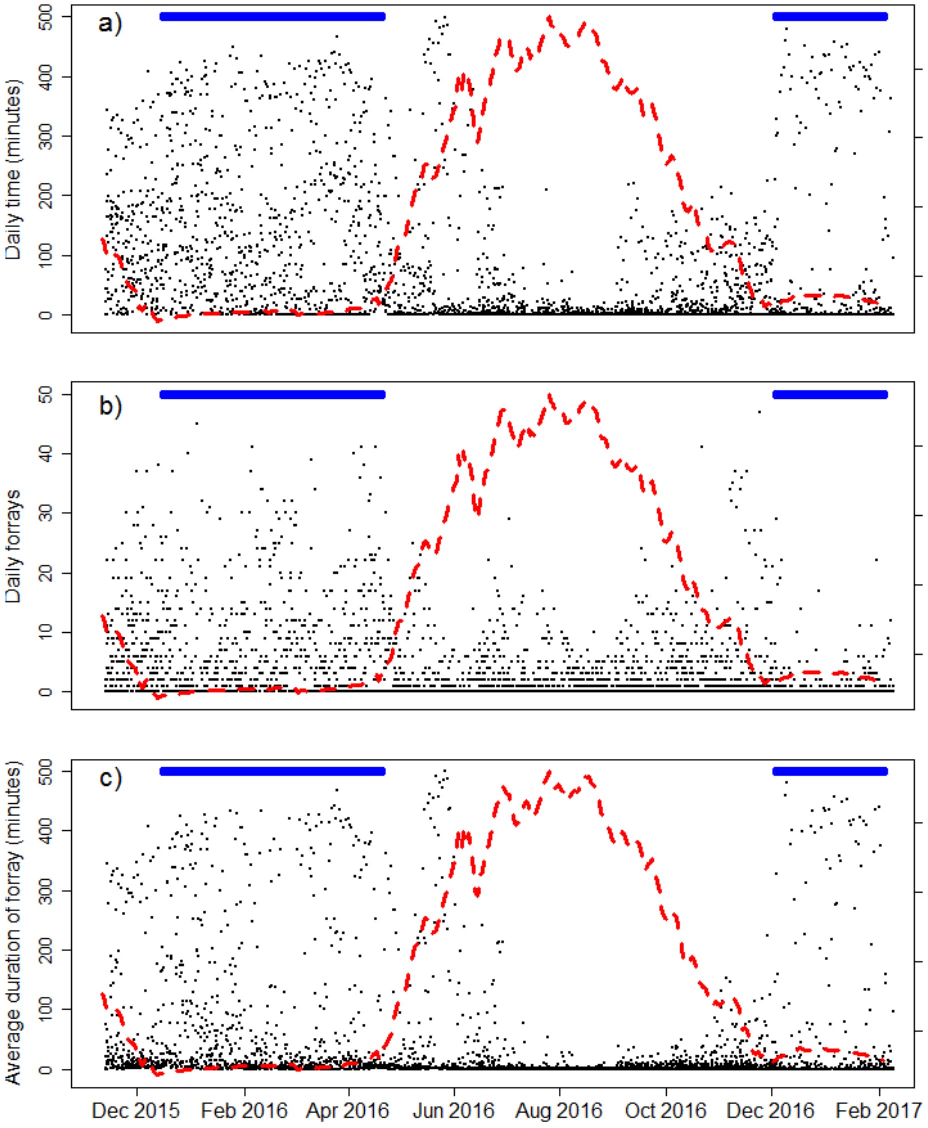

Figure 5. (a) The daily time spent in, (b) number of forays into, and (c) average duration of forays into the littoral zone for each tagged Brook Trout in Castle Lake, California. Each black dot represents an individual's daily data, blue line represents ice cover, and the red dashed line is the littoral zone water temperature. Brook Trout spent significantly (KS test, $p < 0.01$*)* more time in the littoral zone when water temperatures were above 15 °C in the littoral zone.

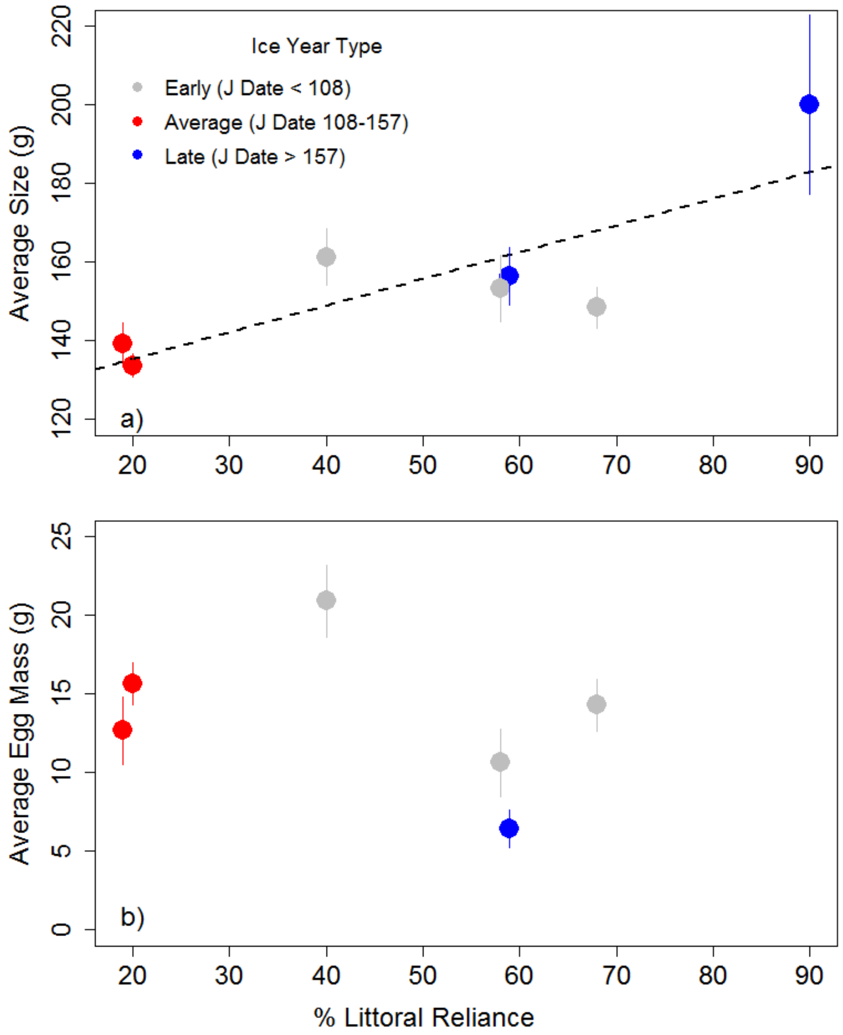

Figure 6. Average ± SE body size (a) and egg mass (b) of large (> 100 g) Brook Trout in Castle Lake, California in various ice year types related to the percent of littoral zone reliance. Dashed line indicates a significant relationship between body size and littoral reliance ($R^2 = 0.60$, $p = 0.02$), no significant relationship was detected for egg mass. Egg mass data was not available for 2010, one of the late ice break-up years

CHAPTER 3. Decreased streamflow impacts fish movement and energetics through reductions to invertebrate drift body size and abundance.

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ABSTRACT

Streamflow drives ecological processes across multiple trophic levels making it a “master variable in lotic systems. In mountain systems, especially those which are regulated, increased frequency of droughts and reductions in snowpack may alter future streamflow regimes and impact ecological processes. We monitored invertebrate drift abundance, size and diversity as a function of streamflow. We then related these variables to fish movement and energetic efficiencies in the Upper Shasta River in California, above and below a large streamflow diversion. Invertebrate drift biomass was significantly less at impaired flows compared to un-impaired flows, and average body size of invertebrates decreased with decreasing streamflow. Generally, fish movement was greater at the impaired flow site (>50% of the time fish were tracked). Fish movement at the upstream site was negatively related to the size of individual prey items and amount of prey available, while significant drivers were not detected in the flow-impaired site. Energetic efficiency was reduced by over 70% when search foraging took place, and the net rate of energetic intake was below 0 J/s for low-flow periods. Our results suggest that fish foraging behavior may be influenced indirectly by altered streamflow through changes to

amount and size of invertebrate drift. A shift to foraging behavior, coupled with low food availability, result in decreased energetic efficiency. Future prescriptions of flow rates to regulated rivers should account for changes to invertebrate drift, fish behavior and fish energetics on seasonal time scales.

INTRODUCTION

Streamflow is often described as the “master variable” in rivers (Power et al. 1995), and alteration to it may result in ecological consequences (Bunn and Arthington 2002, Poff and Zimmerman 2010). Anthropogenic and climatic changes to streamflow may cause changes to both physical, chemical and biological processes (Figure 1) in mountain systems. At the ecosystem scale, primary production may be altered due to different winter and low-flow conditions, resulting in toxic algal blooms (Power et al. 2015). At the community scale, benthic invertebrate richness often decreases at reduced flow rates (Dewson et al. 2007a). Altered flow regimes also negatively affect fish communities by reducing fish growth in streams (Harvey et al. 2006, Wenger et al. 2011, Ruhí et al. 2016, Macnaughton et al. 2017). Given the number of rivers with altered-flow (Magilligan and Nislow 2005) and the increasing risk of drought that may cause low streamflow conditions in mountain systems (Vörösmarty et al. 2000), continued impacts to ecological function are expected (Pyne and Poff 2017).

Size structure, diversity and abundance of invertebrate drift decrease in flow regulated rivers (Dewson et al. 2007a, Walters and Post 2010, Kennedy et al. 2014). Dewson et al. (2007b) observed significant declines in community richness of benthic invertebrates after experimentally reducing streamflow. Reductions in abundance and diversity in benthic habitat translates into alterations to drifting invertebrates as well (Poff and Ward 1991, Shearer et al. 2003, Kennedy et al. 2014, Naman et al. 2016). Mixed results have been observed from previous studies that relate streamflow to drift (Brittain and Eikeland 1988, Poff and Ward 1991, Robinson et al. 2004, Naman et al. 2016). For example, Poff and Ward (1991) reported that low streamflows increase drift abundance, which has been attributed to a behavioral response. The authors suggest that low streamflow decreases wetted habitat and increases competition between invertebrates, causing them to release into the water column. Alternatively, low streamflows reduce the probability of catastrophic drift (Gibbins et al. 2007) and may reduce the amount of invertebrate drift (Callisto and Goulart 2005). Contrary results are routed in the frequency or duration of flow changes, making it difficult to predict consequences of low streamflow on invertebrate drift abundance.

Reduction of abundance coupled with changes to diversity and size structure of drifting invertebrates is consequential to fish in lotic systems, but few studies have examined the cascading impacts of flow rate on invertebrate drift to fish (but see Lagarrigue et al. 2002; Miller and Judson 2014; Weber et al. 2014). Salmonids typically occupy positions in the river that maximize their access to drifting prey and minimize their swimming costs (Fausch 1984), creating a bioenergetically profitable habitat (Fausch, 2014; Hughes et al., 1990; Rosenfeld et al., 2014). However, reduction in the amount of drifting invertebrates causes a shift from drift-based to search-based foraging (Fausch et al. 1997, Harvey and Railsback 2014, Larranaga et al. 2018). A shift in feeding mode that forces salmonids to swim further distances for smaller or fewer prey items would decrease their energetic efficiency. Salmonids shift behavior when prey are completely absent (Fausch et al. 1997), but ecologists have neither identified a level of invertebrate drift abundance that induces that shift, nor how that shift may reduce energetic efficiency. Here we test a model that streamflow is related to changes (abundance/diversity/size) to invertebrate drift that affect the energetic efficiencies of trout through foraging behavior.

Stakeholders of regulated rivers are challenged with assessing rivers and prescribing streamflows that sustain human and ecological needs. A common approach assesses physical habitat (velocity, depth, substrate and cover) and applies habitat suitability curves (e.g. Physical Habitat Simulation or PHABSIM). However, short-falls of this approach exist, including exclusion of food availability, behavior shifts, and emphasis on the physical habitat at the expense of biological factors (Railsback, 2016; Rosenfeld et al., 2012; Weber et al., 2014). We quantified the diversity, size structure, and abundance of drifting invertebrates, the behavior of salmonids, and the subsequent effects on bioenergetic efficiency on the flow-impaired and flow-unimpaired sections of the Upper Shasta River in northern California. We hypothesized that drift abundance, size structure and community diversity would decrease with streamflow and be reduced in the flow-impaired reach. Consequentially, trout movement would increase, suggesting a shift from drift foraging to search foraging. Lastly, we hypothesized that energetic efficiencies would be less at the flow-impaired site than flow-unimpaired.

METHODS

Study site:

The Upper Shasta River is a tributary to the Klamath River in Northern California (N41°21'; W122°25', elevation = 991 m; Figure 1). A diversion extracts up to 0.85 m^3/s (90% of unimpaired-flow) during the spring and summer months when flow is available (McBain Associates 2015 unpublished data). Above the diversion, the river is relatively unimpaired and has one diversion (< 0.01 m^3/s) and streamflow peaks at close to 2.54 m^3/s during spring runoff and 0.20 m^3/s at summertime low-flows (McBain Associates 2015, unpublished gaging data). Peak streamflow below the diversion is approximately 1.14 m^3/s and drops to a summer time low of approximately 0.01 m^3/s. The river has several small springs that maintain similar (within

1°C) temperatures above and below the diversion. The native fish community includes Rainbow Trout (*Oncorhynchus mykiss*) and Marbled Sculpin (*Cottus klamathensis*). Non-native Brown Trout (*Salmo trutta*) were also present. Access was granted to one study location 0.4 km above the diversion referred to as upstream (control with unimpaired-flow) and one location 0.15 km downstream of the diversion, (treatment with impaired-flow), referred to as downstream. The diversion between the reaches is a large (≈ 3 m tall) concrete structure spanning the width of the river, with a small fish ladder around it and completely blocks streamflow at baseflow outside of the fish ladder. The diversion has a large forebay behind it that collects most drifting sediment (McBain Associates, unpublished data), thus there is expected to be little impact of drifting invertebrates from the upstream site and reach on the downstream site and reach. Each study location was a single riffle:run:pool unit. The upstream site's topography was heterogeneous with some large boulders (Figure 1c), while the downstream site was homogenous (Figure 1b) with cobble sized substrate (Caldwell and Chandra, 2017).

Streamflow

Streamflow was continuously measured using a HOBO pressure logger and a stage discharge rating curve located 0.4 km downstream of the study site, using standard U.S.G.S methods (Buchanan and Somers, 1969). Discharge at the upstream site was measured seven times.

Invertebrate drift:

Invertebrate drift was quantified bi-monthly between May and August 2015 at both sites to determine the change in drift as streamflow declined seasonally at impaired and unimpaired-flows. Each sample was collected with a 45 x 25 cm, 500 µm mesh drift net. To account for diurnal variation in invertebrate emergence (Brittain and Eikeland 1988, Naman et al. 2016), samples were collected 3 times daily: 1-2 hr after sun rise, solar noon ± 1 hr, and 1-2 hr before sunset. At each site the net was placed in the location most likely to contain foraging fish, determined by observation of the reach from the shoreline with polarized glasses and scanned for feeding fish. Velocity was measured with a Marsh-McBirney Flo-Mate at the center of the drift net just after setting it and just before removing it, and then averaged. After 1 hr, the contents were sieved through a 250 µm mesh, preserved in 70% ethanol. Preserved samples were sorted with a dissecting microscope (Meiji EM-20, 10X magnification). Each invertebrate was identified to family (Thorp and Covich 2010) and measured to the nearest 0.1 mm from using an ocular micrometer. Mass of invertebrates (mg dry mass) was estimated from published length to dry mass relationships (Benke et al. 1999, Sabo et al. 2002).

Individuals and biomass per m^3 were calculated by dividing the total biomass and number of individuals in each sample by the volume that passed through the net. Daily average number (individuals/m^3), biomass (mg dry mass/m^3), and size of invertebrates (mg dry mass) were computed from the three diurnal collections made at each site. To determine flux, biomass concentration was multiplied by daily discharge (m^3/day) at each site. We made the assumption that drift concentration was consistent throughout the study reach to make this calculation, which is assumed in other drift foraging models (Rosenfeld et al., 2014; Wall et al., 2016).

Fish movement:

Rainbow Trout movement was monitored using passive integrated transponders (PIT tags). Fish were captured using electrofishing and tagged over the course of 6 tagging sessions between March and April 2015. Fish were anesthetized using CO_2, and tagged in the body cavity. Each fish was weighed to the nearest 0.1 g, and fork length was measured to the nearest 0.5 mm. Tagging efforts resulted in marking 147 fish (76 at the upstream site and 71 at the downstream site). Fifty-seven fish were detected at the upstream site and the number of detections per fish ranged from 4600 – 1. At the downstream site 45 fish were detected and the number of detections ranged from 11,579 – 2 per fish. For the analysis of movement, we used fish that had more than 1,000 detections (9 at the downstream site and 6 at the upstream site) to ensure there was sufficient data to estimate movement. At the upstream site, fish masses were 3.92, 12.63, 14.46, 15.85, 19.10, 42.96 g. Fish at the downstream site were 3.60, 5.01, 5.80, 8.62, 15.00, 15.21, 17.30, 28.70, and 33.61 g.

Each study site was instrumented with a 6 antenna PIT array (Figure 1b, c). At each site, the 6 antennae were placed every 1-2 m from the head of the unit to the end of the pool and covered at least 80% of the wetted width of the river. At the upstream site, monitoring occurred from April 28, 2015 - May 17, 2015, and from June 8, 2015 - August 20, 2015. At the downstream site, monitoring occurred April 4, 2017 - May 17, 2017 and from May 31, 2015 – August 20, 2015. At both sites, high water levels resulted in unmonitored periods, which required the removal of the array. Additionally, an array malfunction lasted eight days at the downstream site from June 15, 2015 - June 23, 2015. Data for analysis was used starting on May 5, 2015 for fish movement analysis. This data overlapped with our invertebrate sampling and encompassed a wide range of streamflow.

The first and last antennae of the instrumented reach was used to determine when a fish entered and exited the instrumented area. Movement “bouts” were defined as detections at two different antennae that were < 30 min apart. Detection data were first aggregated by fish, individual movement bouts were determined by the criteria that: 1) consecutive detections were not recorded at the same antenna and were < 30 min apart; or 2) that there were no more than two consecutive detections on the same antenna less than 30 min apart. These criteria were formed to ensure that detections greater than 30 min apart were considered part of a different movement pattern, and that if two consecutive detections were made on the same antennae and within 30 minutes that it was the result of fish moving off that antenna but returning before being detected at a different antenna. The distance and time of movement bouts were summed by day for each fish. For statistical comparison with drift rates, individual fish movement was averaged for the period two days prior until two days after each drift sample.

Net Rate of Energetic Intake Modeling:

A drift feeding bioenergetic model (Hughes et al., 1990; Rosenfeld et al., 2009) was used to estimate differences in fish energetics between sites and between search based and drift based foraging methods. The bioenergetic approach was a modification of the Hughes and Dill (1990) model, similar to the Rosenfeld and Taylor (2009) implementation. The drift energetic model quantifies the amount of energy content (joules) in prey that is drifting in a volume of water flowing past the foraging fish (considered gross energetic intake; GEI) and estimates the energy expenditures based on swimming costs (Hayes et al. 2016) and is corrected for capture success with a modified Holling Disc function and probability of a fish attacking a prey (Rosenfeld et al., 2009). The energy left over (net rate of energetic intake; NREI) is available to be assimilated by the fish and used for growth or reproduction. Because drift energy was sampled at the most likely place for fish to be foraging (see above), we modeled energetics at that location (used center of drift net as fish's focal point for feeding) and converted biomass to joules (Cummins and Wuycheck 1971). The model was run for the range of fish sizes observed (7.5, 8.5, 9.5, 10.5, 11.5, and 12.5 cm) at both sites for each sampling period. For specific energetics calculations please refer to (Rosenfeld et al., 2009).

We ran the model in two modes; first assuming only drift foraging (drift model), second assuming a shift to search foraging (search model). In the search model run, to account for increased movement, we took the average percentage of time fish spent in movement patterns (determined from fish behavior section) and increased the swimming velocity by 20 cm/s, 35 cm/s, and 50 cm/s in the equation 2 (to account for swimming against current at a certain speed) for 3 model runs to incorporate uncertainty around swimming speed. We assumed that an increase in movement was the result of a shift from drift-based to search-based foraging, for which our experimental design did not explicitly test, but has been observed by others (Larranaga et al. 2018). The range of swimming speed was qualitatively estimated at both sites using underwater video footage of fish foraging filmed. We also assumed that the amount of food available to drift feeders and search feeders was equivalent. We made this assumption based on the relationships between drift and benthic invertebrates (Kennedy et al. 2014).

Statistical analysis:

Daily biomass flux, concentration and size of drifting invertebrates, and fish movement patterns were compared with analysis of covariance (ANCOVA). Streamflow was the covariate, while biomass flux, invertebrate concentration, size of invertebrates, and fish movement were the response variables; site was used as the grouping variable. Each variable was log transformed prior to analysis to better meet the assumptions of homogeneity of variances and normality.

To determine differences in family-based community structure between sites and at different levels of discharge, we used non-metric multidimensional scaling (NMDS; Kenkel and

Orlóci 1986). Bray-Curtis distances were calculated to determine community dissimilarity (Clarke 1993) between sites. Analysis of similarity (ANOSIM) was used to test for significant differences in community composition, and taxon specific differences between communities were determined using similarity of percentages (SIMPER). All drift community analysis were done using the R package ‘vegan’ (Oksanen et al. 2016).

An additive linear model was used to test for the effects of site, streamflow, invertebrate biomass, invertebrate average size, invertebrate diversity, fish size, and fish density on the movement patterns of fish. We used individual responses of movement for each fish so that individual characteristics (e.g. size) could be included as predictors. Post-hoc analysis on site specific effects was done using all variables except site and used only data from each site. The dredge function was used in the ‘MuMIn’ package in R (Barton 2013) to search for the best predictors of fish movement. The top 5 models are presented from each dredge (all data, upstream, downstream) and ranked using a combination of AICc (Burnham and Anderson 2002), R^2, adjusted R^2, and significance (p) values to evaluate effects on fish movement patterns.

RESULTS

Streamflow:

Streamflow differed significantly (Table 1) between sites. Difference between sites ranged from 0.3 to 0.6 m^3/s during May and early June, to 0.15 m^3/s from June 26, 2015 until the end of the study. Streamflow peaked on approximately May 31, 2015 at both sites, then decreased until the end of the study (Figure 2 a,b).

Invertebrate drift:

The total biomass of drifting invertebrates per day was significantly less (Table 1) at the downstream site and decreased with streamflow (Figure 2 c,d). There was no significant difference among sites in the concentration of invertebrate biomass or individuals (Tables 1-2). However, we did detect an increase biomass concentration with increasing stream flow ($F = 13.75$, $R^2 = 0.25$, $p < 0.001$). Average size of invertebrates decreased with streamflow at the unimpaired-flow site, but varied at the impaired-flow site (Figure 2 e,f). However, the variation in invertebrate size with streamflow at the impaired site was driven by large (>2 mg) Aug 10, Aug 2015 (1 individual) sampling dates. Without those individuals in the analysis, the invertebrate size decreases significantly with streamflow ($p < 0.001$, $R^2 = 0.80$).

The dominant taxa by total individuals at both sites were the midges (Diptera: Chironomidae) and mayflies (Ephemeroptera: Baetidae; Figure 3). However, terrestrial invertebrates generally made up much of the total biomass at both sites (Figure 4).

NMDS (Figure 3c) suggested groupings of invertebrates for streamflows of > 0.5, 0.5-0.01 and < 0.01 m^3/s (2D stress = 0.07), and were all significantly different ANOSIM ($R = 0.62$, $p = 0.009$). SIMPER procedures performed between sites at each sampling period indicated that diversity of invertebrates was 35% dissimilar between sites when streamflow exceeded 0.5 m^3/s at both sites, but increased to 70% during and after June 26, 2015 when flow rates at the downstream site dropped precipitously.

Fish movement:

The proportion of time spent moving by fish was significantly higher in the downstream site than in the upstream site (Table 1, Figure 3). Proportion of time spent moving was low (15% and 25% in flow-unimpaired and flow-impaired sites, respectively) in the early spring (May 4, 2017 to May 17, 2017), but increased throughout the summer at both sites (Figure 2 g,h). Both proportion of time and total distance moved by fish were estimated and were directly correlated. We elected to use proportion of time moving as opposed to distance moved to better apply to energetics foraging.

Additive linear modeling suggested that when data from both sites was grouped, site and size has the largest effect on fish movement (Table 3), where being at the upstream site and larger prey resulted in less movement by fish. The second-highest-rated model included the terms total invertebrate biomass, streamflow, site and size, where increases to biomass and streamflow both had negative effects on fish movement (Table 3). We did not detect any significant relationships between fish size and movement patterns.

To determine any site-specific patterns, we did a post hoc linear modeling exercise, which only included data from each site. At both sites, invertebrate size was related to fish movement; however, it was not a statistically significant effect at the downstream site (Table 3). At the upstream site, size of invertebrates, streamflow and biomass all had significant negative effects on fish movement (Table 3). The diversity of invertebrates, size of fish, and number of fish in each pool did not have any significant effects on fish movement, but effects for those variables were examined.

Net Rate of Energetic Intake Modeling:

The percent change in NREI between the drift model and the search model was lower at the upstream site compared to the downstream (Table 4). The highest changes in NREI in the search model occurred for the largest fish at both sites and during the later summer months (July and August). The percent reduction of NREI between the drift and search model varied with the swim speed parameter. The percent reduction of NREI between the two models from the lowest swim speed (20 cm/s) was 27% of that which was predicted by the highest swim speed (50 cm/s; Table 4).

We assumed that search model was more accurate than drift only because we monitored fish movement, thus we present NREI from that model. Additionally, we chose the middle swim speed model and assumed that it represented an average swim speed by search foraging fish.

The NREI of fish intake peaked during early spring (May 31, 2015 and June 8, 2015), at 1-2 J/s (Figure 4). For fish of all sizes and at both sites, NREI decreased precipitously with streamflow at both sites from early spring to mid- and late summer (end of June through August; Figure 5). At the downstream site NREI was negative from July 7, 2015 for fish 11.5 and 12.5 cm until the end of the study, and negative for all other sizes of fish from July 28, 2015 until the end of the study (Figure 4).

DISCUSSION

Steam ecologists recognize that changes to the flow regime can manifest across trophic levels, but it is difficult to quantify. Our results suggest that decreased streamflow can reduce the total biomass and size of invertebrate drift, which may alter fish foraging behavior and decrease energetic efficiency. These findings add to a newly formed body of data that: 1) examines the impacts of flow-altered rivers across trophic levels; and 2) suggests that managers of diverted rivers should move towards an integrated approach that examines physical habitat, biological resources and individual behavior (e.g. Harvey and Railsback 2014; Hayes et al. 2016).

Invertebrate drift:

Invertebrate drift, driven by time of day, temperature, habitat and streamflow, plays a critical role in the energetics of rivers (Brittain and Eikeland 1988, Naman et al. 2016, 2017). For example, in the Colorado River, Kennedy et al. (2014) reported increases to the concentrations of *Gammarus* and *Chironomidae* during increased streamflow. Our results were similar, and we detected a statistically significant increase in the concentration of drift biomass with increasing streamflow. We further analyzed our results in biomass flux per unit time (Naman et al. 2017) because looking at concentration alone does not account for the total amount of food available. Our findings suggest that total drift was comparable between sites at higher (> 0.75 m^3/s) streamflow. However, at lower streamflow (< 0.5 m^3/s) at the downstream site, the amount of drift decreased substantially. The mechanism causing the reduction in drift was not determined specifically in this study; however, possibilities include:1) life history timing resulted in emergence from the benthic habitat before streamflow decreased, so they can disperse effectively (Brittain and Eikeland 1988, Naman et al. 2016); or 2) that low streamflow reduces the transport potential between productive riffles and the pools where we measured drift (Naman et al. 2017). We suggest the latter, as we observed few individuals in the drift samples at low streamflow, but higher biomass concentrations that were driven by a few large individuals swept up in the drift from shoreline slackwaters (e.g. water striders, Gerridae) or terrestrial environments (e.g., ants and other Hymenoptera).

The average body size of drift can be important to fish foraging strategy and the distance at which they capture prey (Hughes and Dill 1990, Dodrill et al. 2016). Our results suggest that average body size of drift at both sites decreased with streamflow (when excluding outliers from downstream site). Naman et al. (2017) suggested that invertebrate drift in riffle habitat were significantly larger than those in pool habitat. We believe a similar mechanism may be functioning here, where the size of drifting invertebrates decreased because of a disconnection with the riffle habitat at lower streamflow.

Our results provide initial evidence to suggest that the community of drift in the Upper Shasta River differs between sites when streamflow is < 0.5 m^3/sand becomes more dissimilar as streamflow decreases. These results reinforce findings of previous studies where diversity decreased with streamflow (Wooster et al. 2016). The negative correlation between drift diversity and streamflow may be a direct reflection of species presence in the benthic habitat, which is influenced by streamflow (Dewson et al. 2007b, Walters and Post 2010, Hille et al. 2014, Kennedy et al. 2014). While numerous other mechanisms are plausible, streamflow is the underlying cause of each of them, suggesting that alterations to streamflow will typically result in changes to community diversity of invertebrate drift in rivers (Wooster et al. 2016).

Fish movement:

Drift feeding salmonids have been shown to alter feeding behavior in the absence of drifting prey, shifting from drift based to search-based foraging (Fausch et al., 1997; Harvey and Railsback, 2014) and increase movement in decreased streamflow(Larranaga et al. 2018). Our results suggest that when streamflow is similar among sites, time that fish spent moving is comparable. However, when there is decreased streamflow at the flow-impaired site, with less drifting invertebrate biomass available per day, fish movement was significantly higher (downstream vs upstream).

The average size of invertebrate drift had the most significant effect on the movement of fish. This mechanism is plausible in the Upper Shasta, as the ability of fish to detect prey items decreases rapidly with size (Hughes et al., 1990, 2003). Total available drift biomass and streamflow were also important. As total drift rate declines, drift foraging fish with previously high focal point fidelity switch to search foraging (Fausch et al. 1997). Thus, our results suggest that streamflow may impact fish movement both directly (through habitat changes) and indirectly through the reduction of flux and body size of invertebrate drift. Interestingly, invertebrate community diversity or fish size was not important in fish movement, which suggests that neither prey preference nor size based fish hierarchy is a driver for fish movement at our study sites.

As expected, all effects of size, streamflow, and biomass were significant for fish movement at the upstream site. This was similar to results from Fausch et al. (1997) and Hughes et al. (2003) where decreased or removal of invertebrate drift caused fish to alter foraging behavior to find additional food. When compared to upstream sites, fish present below the diversion moved significantly more following diversion than they did upstream. However, the drivers of fish movement were difficult to identify at the downstream site as no statistically significant effects were detected. We suggest a few possible explanations. First, while we selected sites that were as similar as possible (excluding streamflow) the downstream site's topography was more homogenous, indicating more of a pool habitat than the upstream site. Fish have been shown to forage differently among habitats (Rosenfeld et al., 2009; Vondracek et al., 1993) and causes of invertebrate drift may also vary among sites with differing geomorphology (Naman et al. 2016). Given our observed difference in drivers between sites and the important role that geomorphic patches play in river ecology (Thorp et al. 2006), we suggest that future studies should replicate fish movement/behavioral studies in multiple habitats at various streamflow to help distinguish how habitat may interact with fish movement and streamflow.

Net Rate of Energetic Intake Modeling:

NREI models are useful for identifying changes in the potential growth rates of fish as a function of food availability, velocity and depth (Fausch 2014, Piccolo et al. 2014). First, our NREI model suggests that estimated changes in movement reduce energetic efficiencies by more than 70% in the flow-impaired site. Second, our results show that NREI decreases with streamflow and season, driven by the reduction of food availability, velocity, and increased movement.

The first set of NREI modeling results suggest that search-based foraging can reduce energetic efficiencies when compared to only drift foraging at a flow-impaired site. Similar results were found in individual-based model results that included search-based foraging (Harvey and Railsback, 2014). In other research, Rosenfeld and Raeburn (2009) found increased growth rates among fish that drift foraged in riffle habitat when compared to pool habitat where the authors observed search foraging. Our results suggest that the size of invertebrate prey is a strong predictor of fish movement and decreases with streamflow and season. Therefore, we conclude that decreased streamflow can drive a smaller average size of prey, alter foraging behavior of trout and reduce energetic efficiencies.

The second set of results from our NREI modeling suggests that when streamflow is similar between sites, fish energetics are also comparable, which is related to similar movement patterns driven by food availability and food size. However, when the streamflow is reduced below natural conditions energetic efficiencies can go below zero, and is especially important in late summer baseflows when food availability is low. Food availability drives NREI models (Harvey et al., 2014; Hayes et al., 2016; Rosenfeld et al., 2009). However, the causes of its availability is not well understood (Naman et al. 2016) and varies among habitats and systems (Naman et al. 2017). We embraced this variability by including it in our model as error.

Furthermore, we determined that food availability decreases with streamflow and season, which causes negative energetic efficiencies in flow-impaired areas during the late summer. Future research questions should address how NREI varies among habitat types and seasons so that streamflow to NREI relationships may be inferred at the population level.

Drought, coupled with diversions causes stress to the ecology of headwater streams (Vörösmarty et al. 2000). Our data suggest that when streamflow is similar in impaired and non-impaired reaches food availability to fish, fish movement, and fish energetics are comparable, and it is only when significant reductions to streamflow are made to the impaired site are differences observed. We conclude that reductions in streamflow cascades across trophic levels, altering the abundance and size of invertebrate drift, which increases movement of drift foraging fish and decreases energetic efficiency of fish in flow-impaired rivers. Our data support the incorporation of food availability, energetics and behavior when prescribing flow rates (Railsback, 2016; Rosenfeld et al., 2012).

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TABLES

Table 1. Comparisons of streamflow, invertebrate biomass, invertebrate concentration, invertebrate average size, and proportion of fish movement between sites at the Upper Shasta River. Results are from ANCOVA tests, with site as the grouping variable.

Parameter	Covariate	F	df	p-value
Streamflow	Time	57.89	39	< 0.001
Biomass	Streamflow	64.9	39	< 0.001
Concentration (drymass)	Streamflow	2.34	39	0.13
Concentration (individuals)	Streamflow	0.11	39	0.74
Size	Streamflow	1.73	39	0.19
Fish Movement	Streamflow	9.71	77	< 0.001

Table 2. Concentrations of invertebrate drift biomass and individuals in the Upper Shasta River, CA at sites upstream and downstream of the diversion dam. Values are the mean and standard error (SE) of 3 samples collected each sampling day (1-2 hours after sunrise, solar noon ± one hour, and 1-2 hours before sunset). No statistical differences were detected between sites (ANCOVA, $p > 0.05$).

	Upstream			**Downstream**		
Date	**Streamflow m^3/s**	**mg drymass/m^3 ± SE**	**ind/ m^3**	**Streamflow m^3/s**	**mg drymass/m^3 ± SE**	**ind/m^3**
17-May-15	0.53	0.88 ± 0.01	2 ± 0	0.24	1.44 ± 0.56	3 ± 0
31-May-15	1.03	2.17 ± 0.43	4 ± 0	0.74	1.56 ± 0.22	4 ± 0
8-Jun-15	0.89	3.34 ± 0.7	8 ± 1	0.6	2.27 ± 0.32	8 ± 1
26-Jun-15	0.15	2.81 ± 0.73	12 ± 1	0.01	2.01 ± 0.82	29 ± 18
7-Jul-15	0.17	1.41 ± 0.13	6 ± 1	0.02	0.77 ± 0.35	5 ± 2
28-Jul-15	0.16	0.66 ± 0.04	5 ± 2	0.01	0.001 ± 0.001	0 ± 0
10-Aug-15	0.15	0.25 ± 0.15	5 ± 4	< 0.01	0.04 ± 0.02	1 ± 0

Table 3. Top predictors of the proportion of time spent moving by fish among sites and at each site in the Upper Shasta River, CA.

Model	**Intercept**	**R^2**	**R^2 Adjusted**	**AICc**	**ΔAICc**	***p***
All Data						
Site + Size	-0.1952	0.24	0.22	36.6	0	< 0.000
Biomass+Streamflow+Site+Size	0.8869	0.27	0.23	38	1.34	< 0.001
Streamflow + Site +Size	-0.1113	0.24	0.21	38.5	1.84	< 0.001
Site	-0.3769	0.2	0.18	38.8	2.21	< 0.001
Biomass+Site+Size	-0.1986	0.24	0.52	38.9	2.28	< 0.001
Upstream (Control)						
Size	-0.0914	0.2	0.17	33	0	0.01
StreamFlow	-0.9824	0.18	0.15	33.6	0.6	0.02
Biomass	0.3516	0.15	0.11	34.6	0.6	0.04
Biomass + Size	-0.0131	0.2	0.13	35.7	2.7	0.06
Streamflow+Size	-0.2258	0.2	0.14	35.7	2	0.06
Downstream (Treatment)						
Size	-0.377	0.02	0	-20.2	0	0.37
Biomass	-0.3206	0.001	0	-19.5	0.7	0.78
Streamflow	-0.368	0.001	0	-19.5	0.7	0.81
Streamflow + Size	-0.2454	0.03	0	-18.7	1.5	0.46
Biomass + Size	-0.3715	0.03	0	-18.5	1.7	0.51

Table 4. Range of percent reductions of modeled NREI between models that include search foraging and those that are drift only. Range is presented as the minimum % reduction (20 cm/s swimming speed) to the maximum % reduction (50 cm/s swimming speed).

	% Reduction in NREI (J s^{-1})							
	Date	5/17/2015	5/31/2015	6/8/2015	6/26/2015	7/7/2015	7/28/2015	8/10/2015
	Upstream							
Size (cm)	7.5	-1.9 to -7.2	-0.4 to -1.3	-0.2 to -0.7	-0.3 to -1.0	-0.6 to -2.2	-3.0 to -11.1	-7.0 to -26.0
	8.5	-1.5 to -5.5	-0.3 to -1.2	-0.2 to -0.7	-0.3 to -1.1	-0.7 to -2.5	-3.3 to -12.3	-7.8 to -29.0
	9.5	-1.2 to -4.5	-0.3 to -1.2	-0.2 to -0.7	-0.3 to -1.2	-0.8 to -2.8	-3.8 to -14.1	-9.1 to -33.9
	10.5	-1.1 to -4.0	-0.3 to -1.3	-0.2 to -0.7	-0.4 to -1.4	-0.9 to -3.3	-4.5 to -16.8	-11 to -41.1
	11.5	-1.0 to -3.6	-0.4 to -1.4	-0.2 to -0.7	-0.5 to -1.7	-1.1 to -3.9	-5.5 to -20.5	-13.9 to -51.8
	12.5	-0.9 to -3.5	-0.4 to -1.6	-0.2 to -0.8	-0.5 to -2.0	-1.3 to -4.8	-6.9 to -25.6	-13.4 to -67.8
	Downstream							
Size (cm)	7.5	-0.7 to -2.6	-1.5 to -5.8	-0.7 to -2.4	-1.3 to -5.0	-9.8 to -36.5	-25.5 to -94.9	-32.8 to -122.3
	8.5	-0.7 to -2.5	-1.2 to -4.4	-0.6 to -2.1	-1.6 to -5.9	-12.0 to -44.6	-25.5 to -94.8	-32.6 to -121.3
	9.5	-0.7 to -2.5	-1.0 to -3.6	-0.5 to -2.0	-1.9 to -7.1	-15.2 to -56.5	-25.5 to -94.8	-32.3 to -120.2
	10.5	-0.7 to -2.7	-0.9 to -3.2	-0.5 to -2.0	-2.3 to -8.6	-20.0 to -74.3	-25.5 to -94.8	-32.0 to -119.3
	11.5	-0.8 to -2.9	-0.8 to -3.0	-0.5 to -2.0	-2.8 to -10.6	-27.5 to -102.5	-25.4 to -94.7	-31.8 to -118.4
	12.5	-0.9 to -3.3	-0.8 to -3.0	-0.6 to -2.2	-3.5 to -13.2	-40.7 to -151.6	-25.4 to -94.7	-31.6 to -117.7

FIGURES

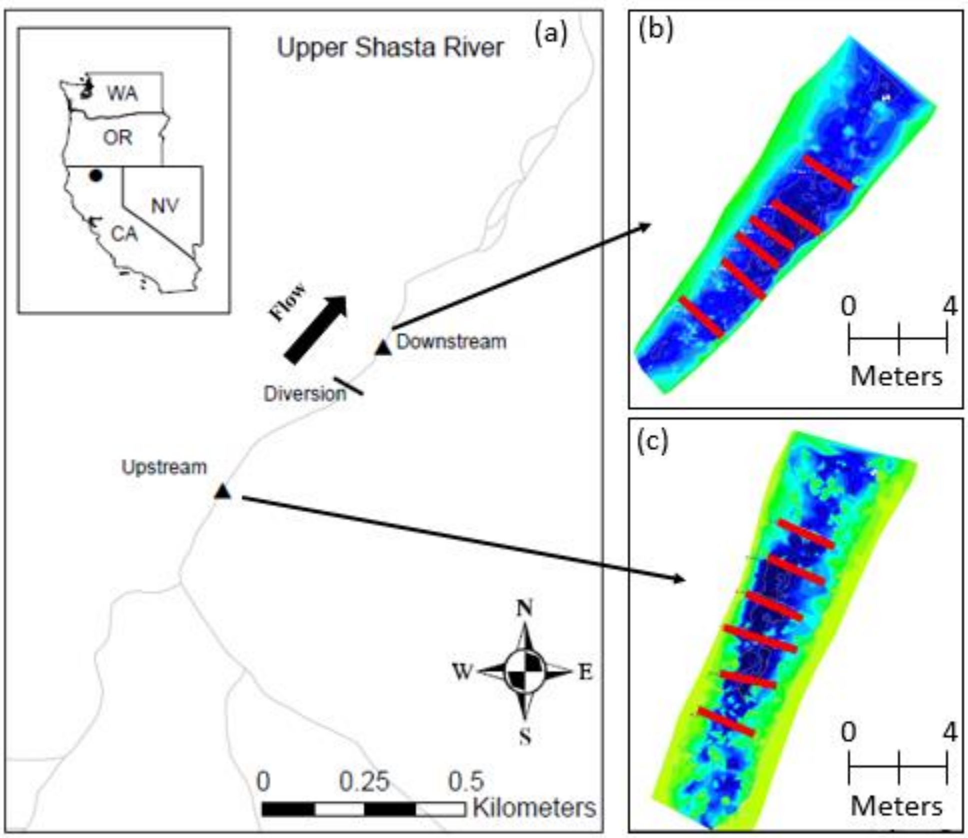


Figure 1. Panel a, Upper Shasta River, located in Northern CA. Triangles denote the location of each study site. Upstream is the unimpaired-flow site, and downstream is flow-impaired site. Panels b (downstream) and c (upstream), topographic maps of study sites and locations of PIT antennae (red lines) at each site. Darker blue is lower elevations while greener is higher elevations, these figures do not represent the wetted width of the river, rather they represent the entire topography of each site.

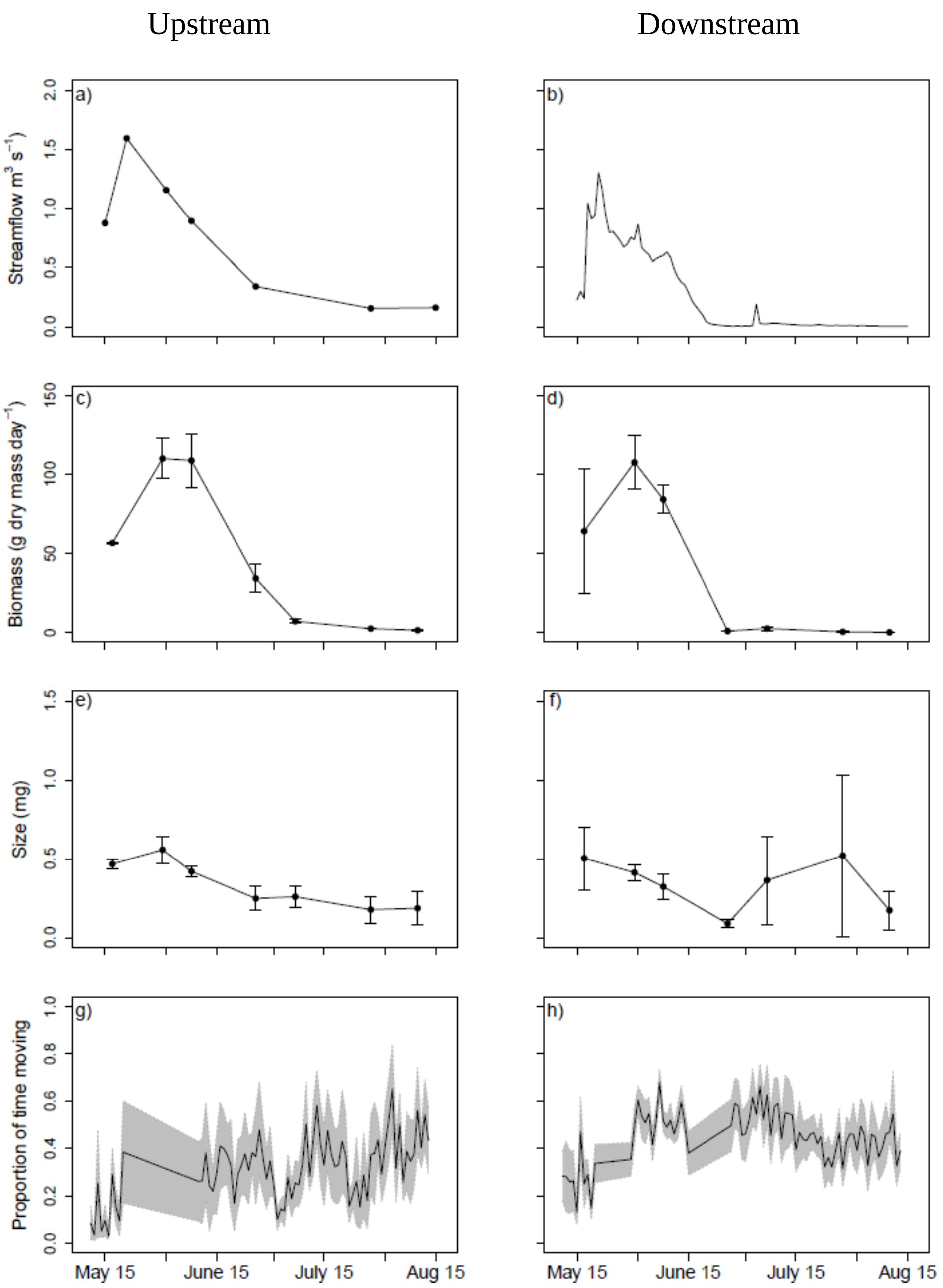


Figure 2. Streamflow (a,b), daily invertebrate drift biomass (c,d), average size of invertebrate drift (e,f), and fish movement (g,h) in the Upper Shasta River, CA during 2015. Data from upstream site is on the left-hand column and data from downstream site is from the flow impaired site is in the right-hand column. Streamflow for the unimpaired-flow site was collected periodically from at each sampling period, while streamflow from the impaired flow site (b) was monitored continuously by a stream discharge gage. Means and standard errors are presented for daily invertebrate drift biomass and average size of invertebrates. Daily average (black line) and standard error (grey shade) of the proportion of time spent moving by tagged fish, straight lines on each graph represent times that the array was malfunctioning or not in place due to high water.

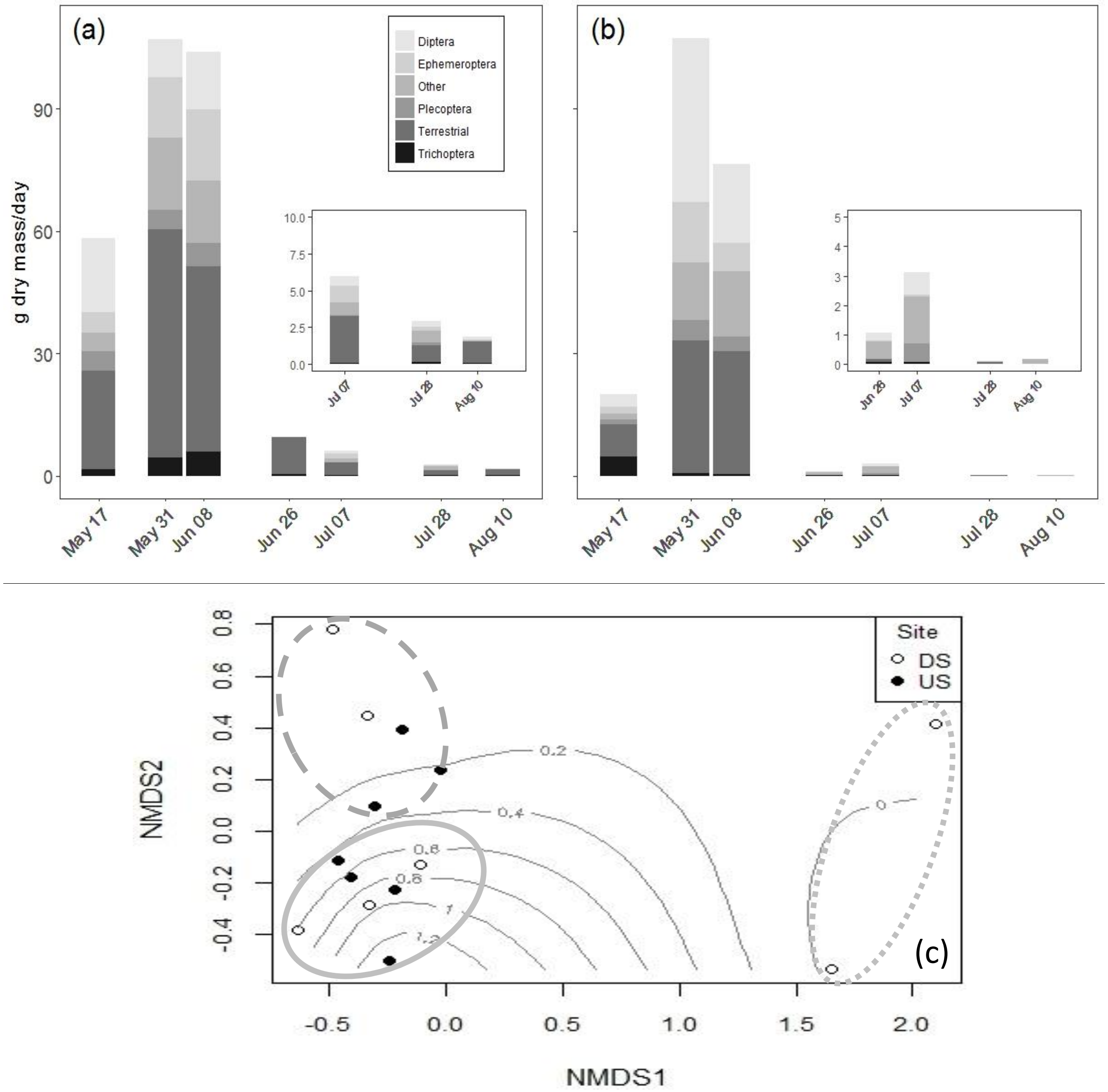


Figure 3. Invertebrate diversity in the Upper Shasta River, CA during 2015. Panel a and b: bar charts showing the contribution of each taxon to the community biomass at the: (a) upstream site; and (b) downstream site. Insets are zoomed in on the dates with low biomass for better visualization. Panel c: Non-metric multi-dimensional scaling ordination of all invertebrate drift samples by family level (2D stress = 0.07). Contours indicate the discharge (m^3/s^{-1}) that each sample was taken, groupings were made between at >0.5 (solid line), 0.5-0.01 (dashed line), and < 0.01 (dotted line) m^3/s (ANOSIM, R = 0.62, p = 0.009).

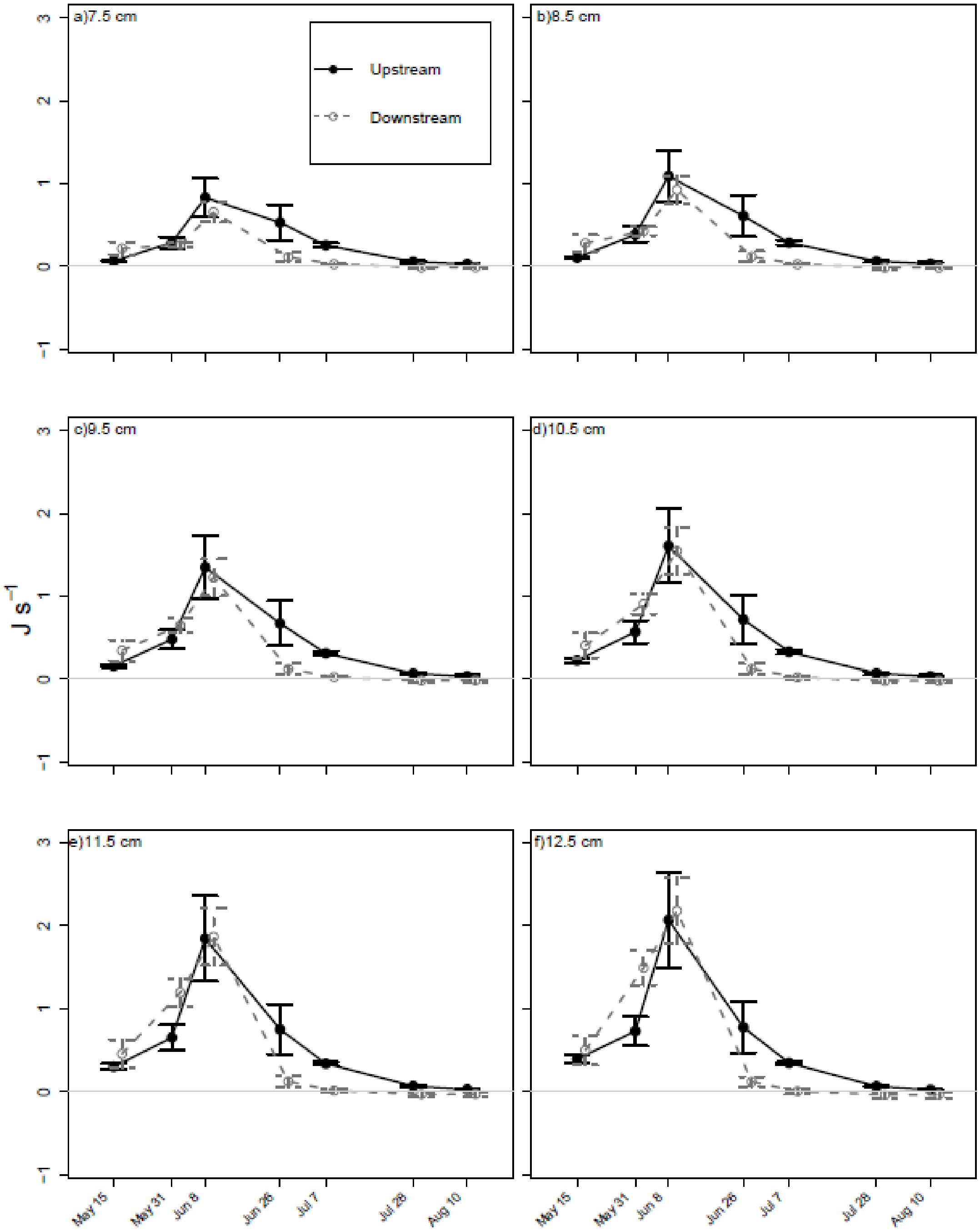


Figure 4. Net-rate of energetic intake (NREI) of fish of different sizes from unimpaired (gray dashed line) and impaired (solid line) streamflow sites in the Upper Shasta River, CA during 2015. Panels represent the size class of fish. NREI was modeled using a drift foraging model (Hughes and Dill 1990), and adjusted for shifts in fish behavior using the 35 cm/s average swimming speed model.

APPENDIX A. Chapter 1 Supplemental Material 1

METHODS

Ice formation was determined using the same remote sensing methods that were used for ice break-up on the same lake data set. Lake physical (watershed size, surface area, etc) and climatic variables (air temperature, precipitation, etc) were acquired from the U.S.G.S hydrography data set and from GRIDMET (Abatzoglou 2013), respectively. Climate data variables were summed from October 1st to December 31st, because the most commonly observed ice formation dates were in November and December. We assumed that Fall conditions would dictate ice formation based on observations by Shuter et al. (2013) and that was not logical to include climate variables that accumulate after ice formation.

Drivers of ice formation were determined using a similar approach that was used for ice break-up. A subset of lakes was randomly removed from the data set to create a training data set, while the remainder was used as test data set. Castle Lake was not used in the test data set because only 5 confirmed ice formation dates were available. A Random Forest (Breiman 2001, Liaw and Wiener 2002) algorithm was implemented using surface area, deliver ratio, elevation, latitude, watershed area, snow fraction, air temperature (summed as the total degree days below 0 °C), solar radiation, and wind speed. Predictive models for ice formation were developed using LMEM with the same stepwise model development and comparison methods that were used for ice break-up.

RESULTS

Drivers of ice formation:

Random forest identified surface area, solar radiation and snow fraction in Fall as the most important variables (Figure A1). Smaller lakes, with higher snowfall and less solar radiation drove earlier ice out dates. Elevation and delivery ratio had similar percent decrease in

MSE, compared to solar radiation (Figure A1) and the remaining variables decreased in their importance. Partial dependence plots indicated that the variables for predicting ice formation were less important than those which predicted ice break-up (Figure A2). The effect of single variable permutations effected ice formation date by a maximum of 10 days, while the same analysis effected ice break-up by a maximum of 50 days (Figure B2).

Model development and forecasting:

The base LMEM using the top 3 predictors from the Random Forest analysis (surface area, solar radiation, and snow fraction) had significant univariate and interactive effects ($p < 0.01$), but had the highest AIC score (Table S1). We added additional covariates stepwise to identify any improvements in model performance. We also added covariates to a model that included temperature, given the frequent use of temperature in other ice formation models (e.g. Gao and Stefan 1999; Shuter et al. 2013). Evaluation of all model iterations, showed that the top model included surface area, temperature, snow fraction and solar downward radiation but model iterations were within 16 AIC units of each other (Table A1). We selected the model which used surface area, snow fraction and temperature for prediction. We did not use solar radiation as a term for prediction in our model because the AIC scores were only within 1 unit of the that did not include solar radiation, and forecasting solar radiation using GCM's is not common, making the model less useful for prediction.

Model performance was evaluated using the test lake data set, and had a RMSE of 14 days, an absolute mean error (± standard deviation) of 10 ± 8 days. While the error on our model prediction was less than that of our ice break-up model, it was much higher than other models of ice formation (2 days; Shuter et al. 2013). In addition, the slope of our relationships between observed to predicted values was an average of 0.16 indicating that predictions outside of the mean were not accurate. Given our results, we did not predict ice formation dates using GCM projected climate data.

Table A1. Performance of linear mixed modeling results for ice formation, models are organized by AIC score. Fixed effects are listed in the Model column, all models included a random intercept term for lake identity. The bolded model was selected for projection of ice formation. See text for rationale on model selection.

Model	AIC	Log Likelihood	R^2 (corrected)
Surface Area*Temperature*Snow*Solar Radiation	973	-468	0.61
Surface Area*Temperature*Snow	**974**	**-477**	**0.46**
Surface Area* Temperature	977	-483	0.37
Surface Area*Temperature*Snow*Elevation	977	-471	0.36
Surface Area	985	-487	0.27
Surface Area*Snow	985	-489	0.2
Surface Area*Snow*Solar Radiation	988	-484	0.42

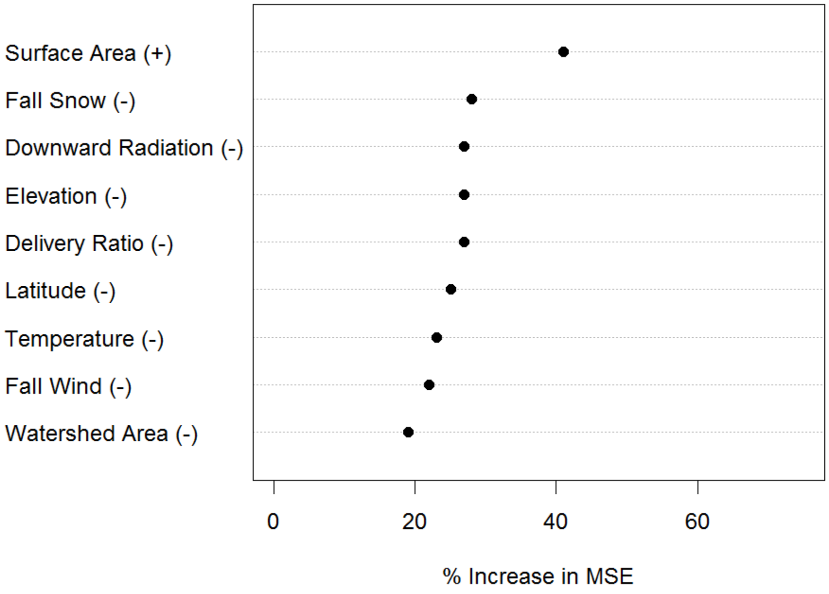


Figure A1. Variable importance plot from random forest analysis describing the drivers of ice formation in mountain lakes of the Western United States. Variables are listed in descending order of importance from top to bottom. The x-axis describes the decrease in model performance when omitting a given variable, larger values indicate higher importance. Positive signs indicate that an increase in the variable results in later ice formation date, while negatives indicate that an increase in the variable results in earlier ice formation date.

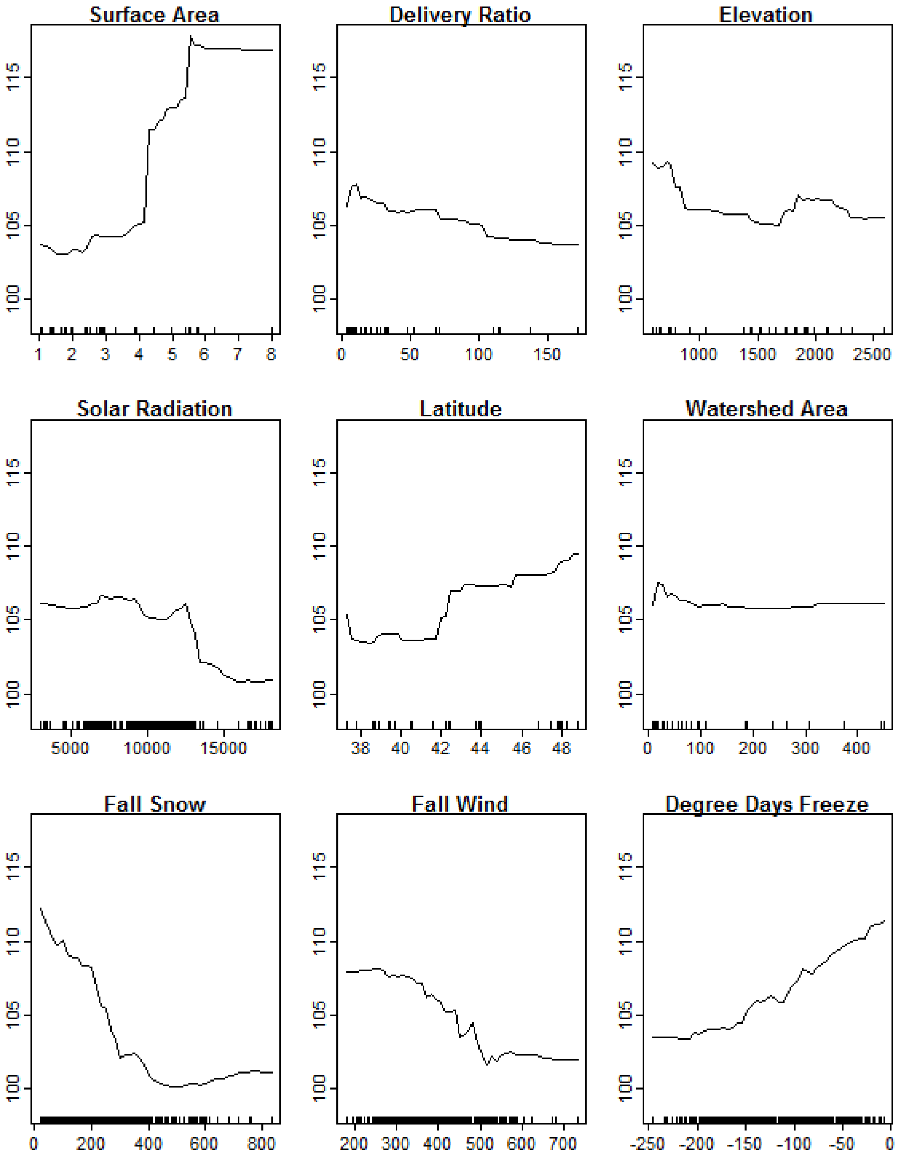


Figure A2. Partial dependence plots showing the relationships of the all predictor variables (ordered in descending order of importance left to right, top to bottom) to the ice formation days from September 1st from random forest analysis. Partial dependence plots are the results of the model if all other variables are held at their median value.

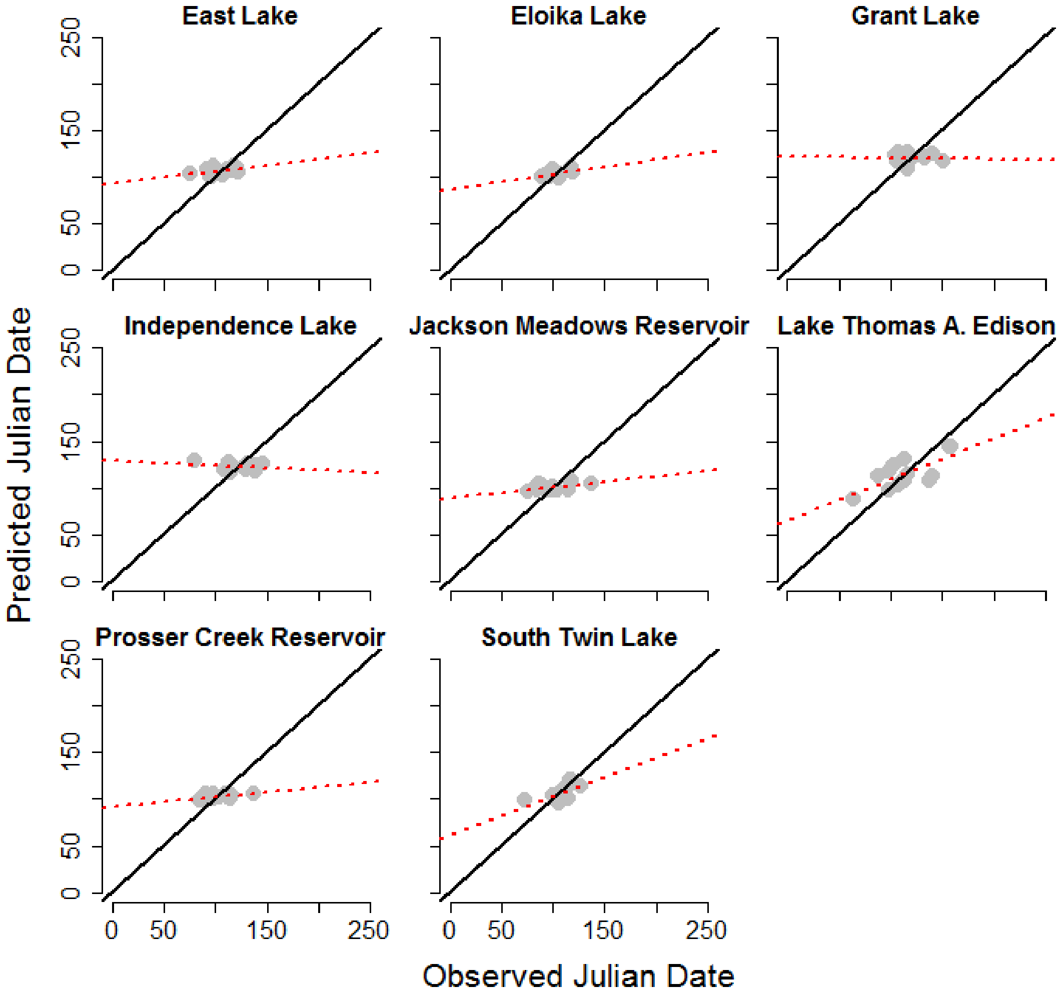


Figure A3. Regression of predicted to observed days since September 1 of ice formation from the test lakes predicted by the base linear mixed model (terms = snow fraction*temperature*surface area). The black regression is the 1:1 line. RMSE was 14 days, mean (± standard error) and were 10 ± 8 days. The mean slope was 0.16. Castle Lake was not used in the ice formation test date set due to lack of data.

APPENDIX B. Chapter 1 Supplemental Material 2

Table B1. List of lakes and lake characteristics used in identifying drivers of mountain lake ice break up, development of linear mixed effects models and projections of ice break up under climate change scenarios. Surface area in km^2, elevation in m, latitude in degrees N, mean and coefficient of variation for Julian date of ice off, inter-annual average of the sum of daily snow fraction, and inter-annual average of the sum of daily average temperature from 2001 – 2017.

Lake	Surface Area	Elevation	Latitude	Mean Ice Off	CV Ice Off	Average Snow Fraction	Average Temp
Blue Lake	1.41	649	47.4845	46	0.51	161	672
Blue Lake, Upper	1.35	2319	38.6320	150	0.13	776	142
Boca Reservoir	3.91	1597	39.4036	76	0.28	251	484
Bumping Lake	5.48	1044	46.8469	107	0.19	606	120
Calispell Lake	1.94	620	48.2735	83	0.24	122	502
Caples Lake	2.43	2222	38.6987	137	0.17	706	308
Castle Lake	0.20	1657	41.2270	130	0.22	251	130
East Lake	3.92	1945	43.7280	136	0.10	490	125
Echo Lakes	1.34	2113	38.8415	133	0.21	589	587
Eloika Lake	2.55	581	48.0195	77	0.21	139	538
Fish Lake WA	2.01	589	47.8345	86	0.18	365	419
Florence Lake	3.89	2089	37.2582	90	0.31	742	121
Fordyce Lake	2.89	1825	39.3895	136	0.17	1056	433
Fourmile Lake	2.53	1751	42.4650	142	0.10	831	274
Gem Lake	1.08	2584	37.7534	137	0.15	555	106
Gold Lake	1.96	1826	39.6779	133	0.23	594	825
Grant Lake	4.47	2032	37.8399	87	0.29	255	553
Hauser Lake	2.44	667	47.7786	72	0.29	140	611
Howard Prairie Lake	7.97	1381	42.2201	69	0.44	352	523
Huntington Lake	5.77	1980	37.2407	112	0.16	572	817
Hyatt Reservoir	3.28	1530	42.1759	86	0.35	330	651
Independence Lake	2.78	1979	39.4436	128	0.13	547	333
Jackson Meadows Reservoir	4.14	1720	39.4988	121	0.29	974	617
Juniper Lake	2.40	1920	40.4532	146	0.15	1278	287
Lake of the Woods	4.97	1511	42.3672	107	0.29	460	496
Lake Spaulding	2.80	1428	39.3360	78	0.45	562	1106
Lake Thomas A. Edison	7.43	2180	37.3794	105	0.25	699	220
Lava Lake	1.39	1446	43.9204	122	0.18	723	260
Loon Lake	4.42	726	48.0449	82	0.17	168	363
Lower Bear River Reservoir	2.95	1658	38.5425	91	0.44	431	1103
Medicine Lake	1.79	1903	41.5823	148	0.12	851	138
Newman Lake	4.45	648	47.7772	83	0.19	121	627
North Twin Lake	2.97	784	48.2873	94	0.10	157	309
Paulina Lake	5.55	1932	43.7199	106	0.19	467	87
Prosser Creek Reservoir	2.80	1637	39.3805	89	0.26	335	441
Snag Lake	1.67	1731	40.5142	122	0.23	618	315
South Twin Lake	3.75	785	48.2628	94	0.12	157	309
Spirit Lake	6.27	744	47.9414	86	0.18	214	372
Swan Lake	2.71	647	47.4690	54	0.53	199	557
Upper Priest Lake	5.42	743	48.7846	101	0.12	251	208
Waptus Lake	1.03	904	47.5034	138	0.12	1043	39

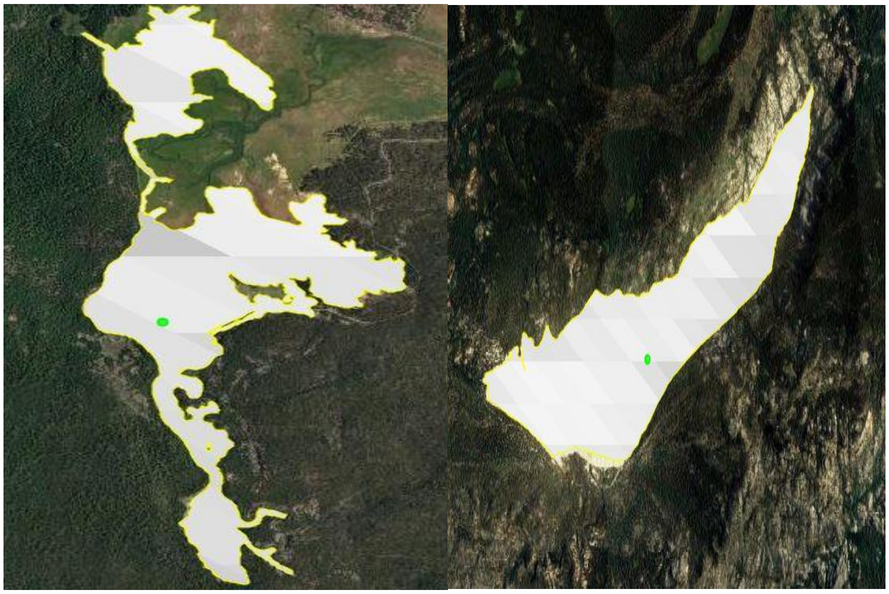


Figure B1. Example of QA/QC procedure for accuracy of MODIS pixels on lakes to identify ice-break up. A composite image that took the highest NDVI recorded from January 1, 2017 to March 31, 2017 MOD10A1 grid was overlaid onto lake polygons and the data extraction point (green dot). If the extraction pixel (pixel with green dot on) overlapped any portion of the land, the lake was omitted form the data set to reduce any error associated with snow on the land when quantifying lake ice break-up. Left panel is an example of lake where no pixels were usable, while the right panel is a lake with multiple usable pixels.

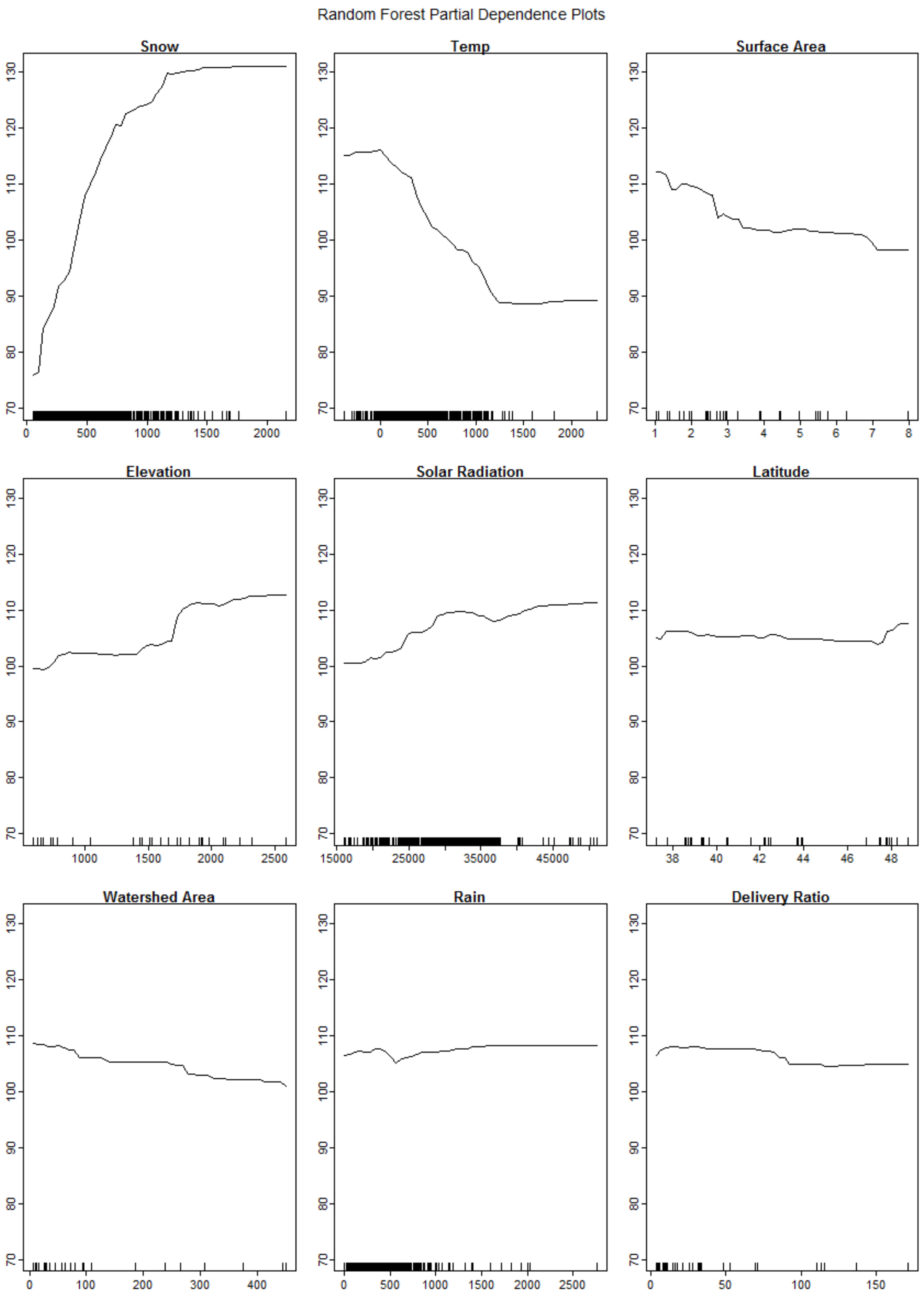
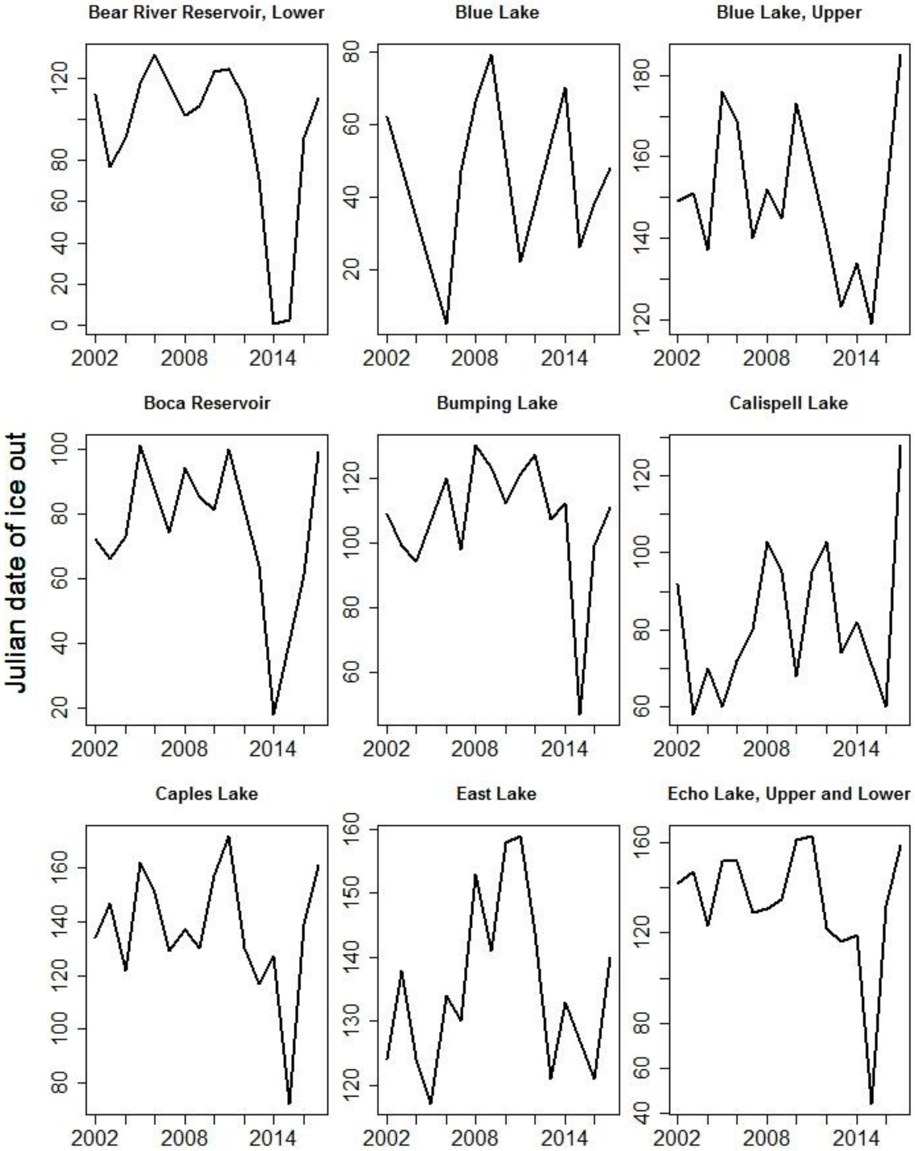
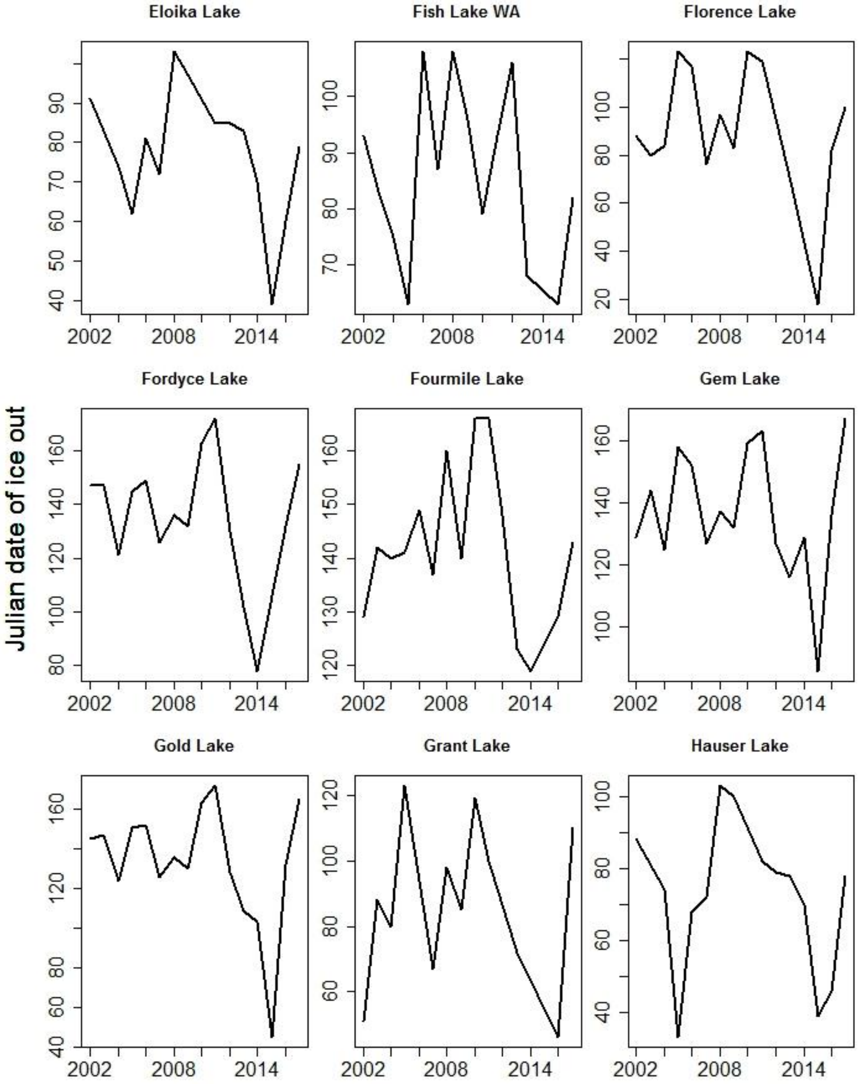


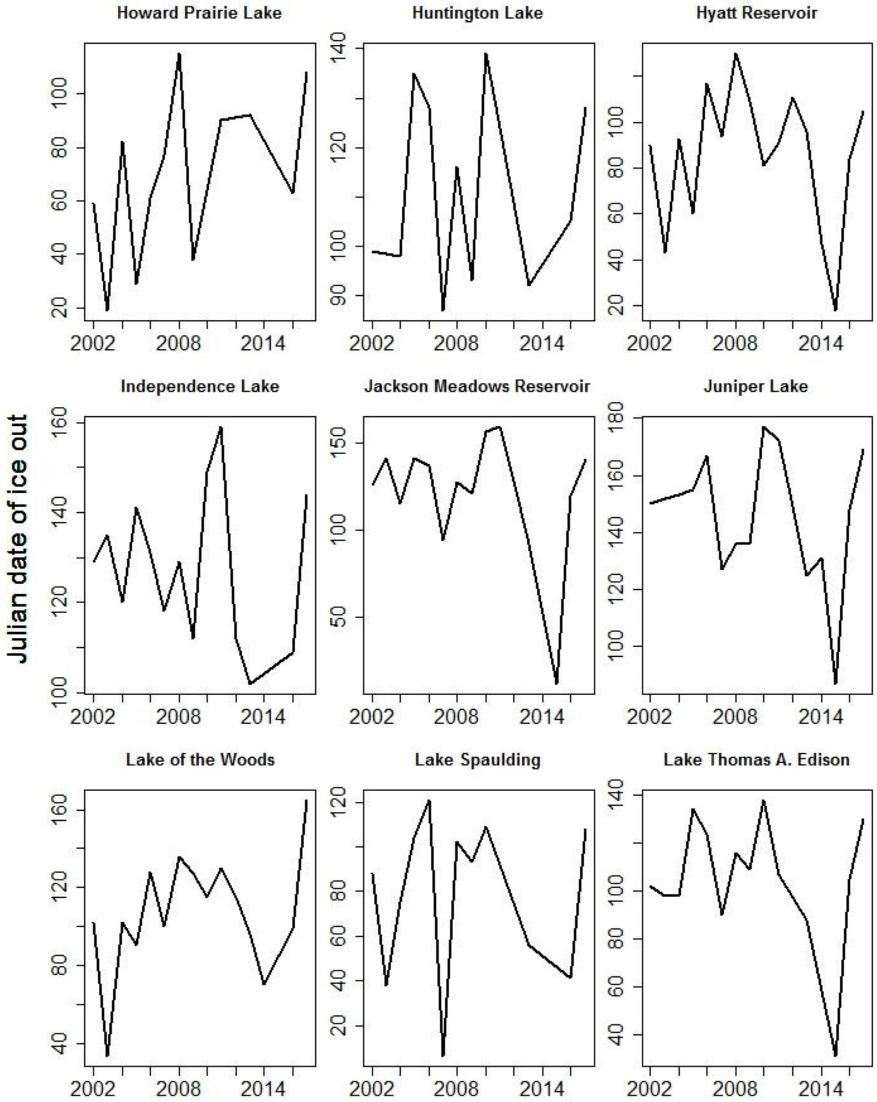
Figure B2. Partial dependence plots showing the relationships of the all predictor variables (ordered in descending order of importance left to right, top to bottom) to the ice break-up Julian date from random forest analysis. Partial dependence plots are the results of the model if all other variables are held at their median value.

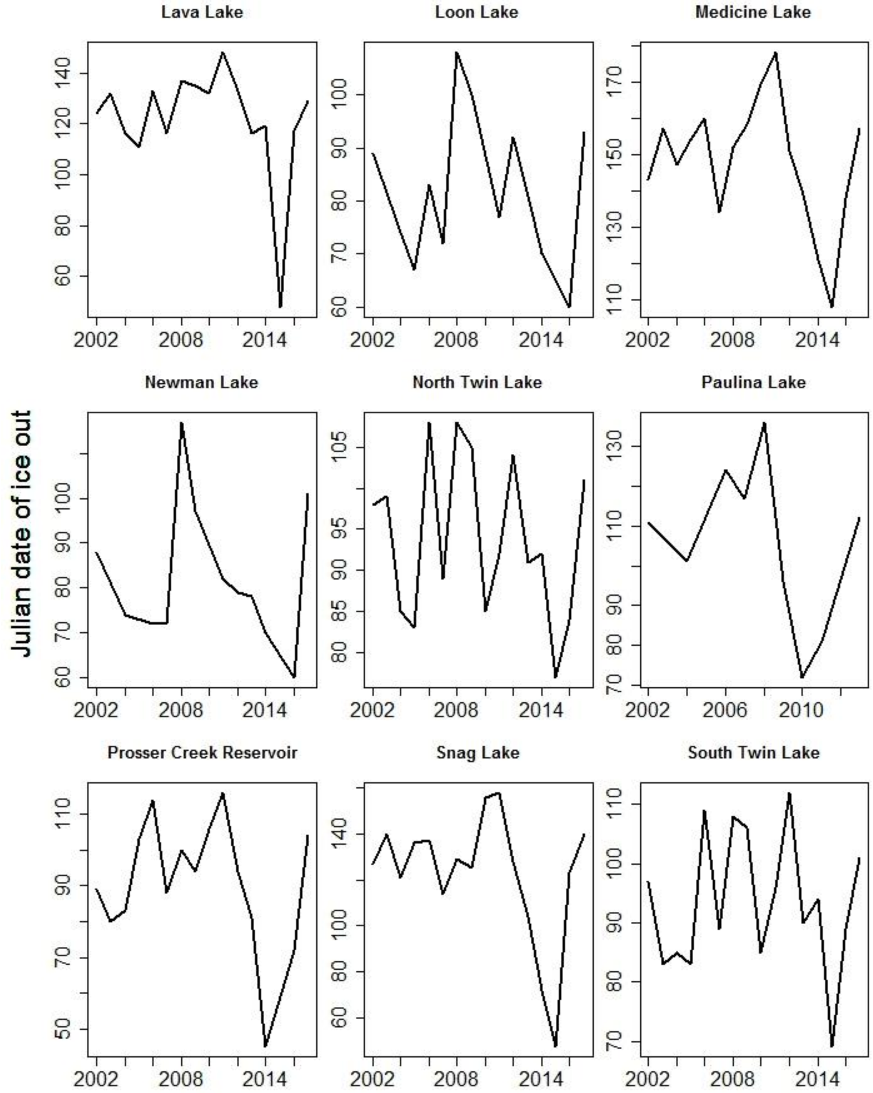

Bear River Reservoir, Lower
Blue Lake
Blue Lake, Upper
Boca Reservoir
Bumping Lake
Calispell Lake
Caples Lake
East Lake
Echo Lake, Upper and Lower
Julian date of ice out
2002
2008
2014

2307


Eloika Lake
Fish Lake WA
Florence Lake
Fordyce Lake
Fourmile Lake
Gem Lake
Gold Lake
Grant Lake
Hauser Lake
Julian date of ice out
2002
2008
2014
40
50
60
70
80
90
100
120
140
160
20

2308


Howard Prairie Lake
Huntington Lake
Hyatt Reservoir
Independence Lake
Jackson Meadows Reservoir
Juniper Lake
Lake of the Woods
Lake Spaulding
Lake Thomas A. Edison
Julian date of ice out
2002
2008
2014


Lava Lake
Loon Lake
Medicine Lake
Newman Lake
North Twin Lake
Paulina Lake
Prosser Creek Reservoir
Snag Lake
South Twin Lake
Julian date of ice out
2002
2008
2014
2006
2010

2310

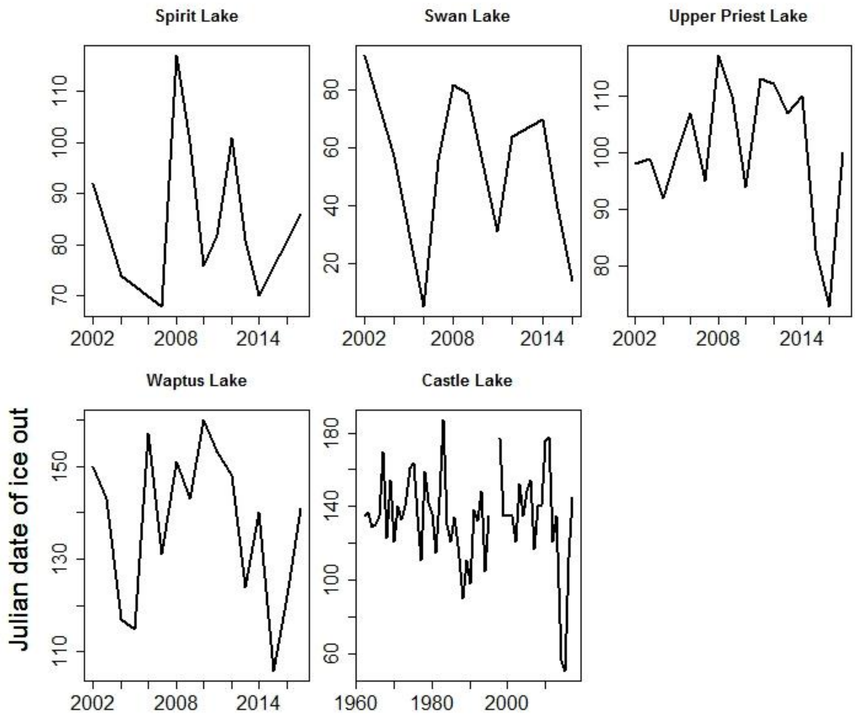


Figure B3. Julian date of ice break-up for each lake listed alphabetically. Refer to Table B1 for locations and descriptive statistics that correspond to lake name. All lake ice break updates were determined using remote sensing, except for Castle Lake which was observed visually or with a digital camera (1996 and 1997 were not observed at Castle Lake.

APPENDIX C. Chapter 2 Supplemental Material 1

Table C1. Raw isotopic (δ^{13}C and δ^{15}N) data for habitat (littoral vs. pelagic) contributions to fish consumers. Values with NA indicate there was not enough material to obtain and accurate signal. Early season was taken from June and July, late season is from September and October. Locations are PML = pool mixed layer (0,3,5 m) for zooplankton, spring, dock correspond to fish sampling locations, littoral, profundal and sub=littoral correspond to areas which zoobenthic species were sampled.

Month	Day	Year	Ice Type	Season	Location	Habitat	Group	Species	d15N	d13C
6	1	2008	avg	early	PML	Pelagic	zoops	Zoop	NA	NA
7	1	2008	avg	early	PML	Pelagic	zoops	Zoop	2.3	-31.7
8	1	2008	avg	late	PML	Pelagic	zoops	Zoop	2.9	-31.4
9	1	2008	avg	late	PML	Pelagic	zoops	Zoop	3.8	-27.8
6	12	2009	avg	early	Spring	lake	fish	BT	8.142339	-26.07
6	12	2009	avg	early	Dock	lake	fish	BT	8.460326	-24.98
6	12	2009	avg	early	Dock	lake	fish	BT	7.8383097	-22.17
6	12	2009	avg	early	Dock	lake	fish	BT	8.4802498	-21.82
7	19	2009	avg	early	Spring	lake	fish	BT	9.1274713	-23.7
6	1	2009	avg	early	PML	Pelagic	zoops	Zoop	2.2	-31.3
7	1	2009	avg	early	PML	Pelagic	zoops	Zoop	3.1	-30
8	1	2009	avg	late	PML	Pelagic	zoops	Zoop	3.4	-28.2
9	1	2009	avg	late	PML	Pelagic	zoops	Zoop	3.2	-24
6	1	2010	late	early	Littoral	Littoral	ben_invertes	Oligo/Chiro	2.1	-25.2
7	1	2010	late	early	Littoral	Littoral	ben_invertes	Oligo/Chiro	2.6	-23.8
6	1	2010	late	early	Littoral	Littoral	ben_invertes	Trichoptera	4.4	-26.9
7	1	2010	late	early	Littoral	Littoral	ben_invertes	Trichoptera	2.2	-23.8
7	1	2010	late	early	Profundal	Profundal	ben_invertes	Oligo/Chiro	4	-21.5
6	26	2010	late	early	T2	lake	fish	BT	8.2330731	-23.77
7	1	2010	late	early	Spring	lake	fish	BT	9.2198444	-25.53
7	1	2010	late	early	Spring	lake	fish	BT	9.3082615	-20.99

7	1	2010	late	early	Dock	lake	fish	BT	8.6210824	-22.97
7	1	2010	late	early	Dock	lake	fish	BT	9.4039716	-20.68
8	17	2010	late	late	Dock	lake	fish	BT	8.6462796	-20.66
8	17	2010	late	late	Dock	lake	fish	BT	7.9596333	-24.09
8	20	2010	late	late	Dock	lake	fish	BT	8.4523433	-22
8	20	2010	late	late	Dock	lake	fish	BT	7.2472417	-28.01
8	20	2010	late	late	Dock	lake	fish	BT	8.5802542	-23.14
8	20	2010	late	late	Dock	lake	fish	BT	7.8901635	-22.42
8	20	2010	late	late	Dock	lake	fish	BT	7.3918112	-26.63
8	20	2010	late	late	Dock	lake	fish	BT	7.5047439	-29.05
8	20	2010	late	late	Dock	lake	fish	BT	8.0273432	-24.84
8	20	2010	late	late	Dock	lake	fish	BT	7.4610039	-26.35
8	20	2010	late	late	Dock	lake	fish	BT	9.7549138	-21.4
8	20	2010	late	late	Dock	lake	fish	BT	10.263186	-21.45
8	20	2010	late	late	Dock	lake	fish	BT	9.0747025	-24.23
6	1	2010	late	early	PML	Pelagic	zoops	Zoop	2.9	-25.8
7	1	2010	late	early	PML	Pelagic	zoops	Zoop	1.8	-32.6
8	1	2010	late	late	PML	Pelagic	zoops	Zoop	3.3	-28.2
9	1	2010	late	late	PML	Pelagic	zoops	Zoop	2.5	-30.7
7	1	2011	late	early	Littoral	Littoral	ben_invertes	Oligo/Chiro	1.4	-26.1
7	1	2011	late	early	Littoral	Littoral	ben_invertes	Trichoptera	2.7	-24.4
7	1	2011	late	early	Profundal	Profundal	ben_invertes	Oligo/Chiro	2.9	-34.4
9	1	2011	late	late	Littoral	Littoral	ben_invertes	Oligo/Chiro	1.7	-26.3
9	1	2011	late	late	Profundal	Profundal	ben_invertes	Oligo/Chiro	2	-40
6	21	2011	late	early	Dock	lake	fish	BT	8.7	-28.2
6	21	2011	late	early	Dock	lake	fish	BT	8.5	-25
6	21	2011	late	early	Dock	lake	fish	BT	8.7	-27.8
6	21	2011	late	early	Dock	lake	fish	BT	9	-25.5
9	16	2011	late	late	Spring	lake	fish	BT	8.3	-22.8
9	16	2011	late	late	Dock	lake	fish	BT	9	-25.1
9	16	2011	late	late	Dock	lake	fish	BT	9	-28.1

9	16	2011	late	late	Dock	lake	fish	BT	8.8	-27
7	1	2011	late	early	PML	Pelagic	zoops	Zoop	NA	NA
9	1	2011	late	late	PML	Pelagic	zoops	Zoop	2.9	-27.8
6	1	2012	avg	early	Littoral	Littoral	ben_invertes	Oligo/Chiro	1	-26
6	1	2012	avg	early	Littoral	Littoral	ben_invertes	Trichoptera	2.9	-27.6
6	1	2012	avg	early	Profundal	Profundal	ben_invertes	Oligo/Chiro	3	-37.7
9	1	2012	avg	late	Littoral	Littoral	ben_invertes	Oligo/Chiro	2.7	-24.3
9	1	2012	avg	late	Littoral	Littoral	ben_invertes	Trichoptera	2.2	-26.1
9	1	2012	avg	late	Profundal	Profundal	ben_invertes	Oligo/Chiro	3.8	-36.9
7	18	2012	avg	early	Dock	lake	fish	BT	7.8	-26.2
7	18	2012	avg	early	Dock	lake	fish	BT	8	-23.1
7	18	2012	avg	early	Dock	lake	fish	BT	8	-24.6
7	18	2012	avg	early	Dock	lake	fish	BT	7.7	-27.1
9	15	2012	avg	late	Spring	lake	fish	BT	9.1	-29
9	15	2012	avg	late	Dock	lake	fish	BT	7.9	-28.9
9	15	2012	avg	late	Dock	lake	fish	BT	7.9	-23.2
9	15	2012	avg	late	Dock	lake	fish	BT	8	-30.5
8	1	2012	avg	late	PML	Pelagic	zoops	Zoop	NA	NA
6	1	2013	avg	early	Littoral	Littoral	ben_invertes	Oligo/Chiro	0.8	-26.4
6	1	2013	avg	early	Littoral	Littoral	ben_invertes	Trichoptera	1.8	-26.3
6	1	2013	avg	early	Profundal	Profundal	ben_invertes	Oligo/Chiro	4	-33.4
9	1	2013	avg	late	Littoral	Littoral	ben_invertes	Oligo/Chiro	2.2	-20.8
9	1	2013	avg	late	Profundal	Profundal	ben_invertes	Oligo/Chiro	3.2	-32.3
6	13	2013	avg	early	Dock	lake	fish	BT	7.6	-29.1
6	13	2013	avg	early	Dock	lake	fish	BT	7.4	-23.1
6	13	2013	avg	early	Dock	lake	fish	BT	8.2	-30.6
6	14	2013	avg	early	Spring	lake	fish	BT	8.1	-27.7
9	1	2013	avg	late	Dock	lake	fish	BT	8.2	-22.1
9	1	2013	avg	late	Dock	lake	fish	BT	7.2	-30.6
9	1	2013	avg	late	Dock/Deep	lake	fish	BT	6.9	-26.6
9	1	2013	avg	late	Dock	lake	fish	BT	7.3	-28.6

6	1	2013	avg	early	PML	Pelagic	zoops	Zoop	2.1	-28.4
7	1	2013	avg	early	PML	Pelagic	zoops	Zoop	4.6	-30
8	1	2013	avg	late	PML	Pelagic	zoops	Zoop	4	-28.3
9	1	2013	avg	late	PML	Pelagic	zoops	Zoop	3.9	-29.2
9	1	2013	avg	late	PML	Pelagic	zoops	Zoop	2.7	-26.2
6	1	2014	early	early	Littoral	Littoral	ben_invertes	Oligo/Chiro	3.2	-20.5
6	1	2014	early	early	Littoral	Littoral	ben_invertes	Trichoptera	2.7	-20.6
6	1	2014	early	early	Profundal	Profundal	ben_invertes	Oligo/Chiro	1.1	-35.4
9	1	2014	early	late	Littoral	Littoral	ben_invertes	Oligo/Chiro	2.5	-19.8
9	1	2014	early	late	Littoral	Littoral	ben_invertes	Trichoptera	3.8	NA
9	1	2014	early	late	Profundal	Profundal	ben_invertes	Oligo/Chiro	2.7	-27.2
6	10	2014	early	early	Dock	lake	fish	BT	7.2	-23.5
6	10	2014	early	early	Dock	lake	fish	BT	6.7	-25.5
6	10	2014	early	early	Dock	lake	fish	BT	8	-25.9
6	10	2014	early	early	Dock	lake	fish	BT	7.4	-24.3
9	6	2014	early	late	Spring	lake	fish	BT	7.2	-22.6
9	6	2014	early	late	Dock	lake	fish	BT	7.6	-30.3
9	6	2014	early	late	Dock	lake	fish	BT	7.6	-25.5
9	6	2014	early	late	Dock	lake	fish	BT	7.9	-28.9
6	1	2014	early	early	PML	Pelagic	zoops	Zoop	NA	NA
7	1	2014	early	early	PML	Pelagic	zoops	Zoop	3.3	-27.6
7	1	2014	early	early	PML	Pelagic	zoops	Zoop	NA	NA
8	1	2014	early	late	PML	Pelagic	zoops	Zoop	2.9	-27.7
9	1	2014	early	late	PML	Pelagic	zoops	Zoop	NA	-18
6	1	2015	early	early	Littoral	Littoral	ben_invertes	Oligo/Chiro	2.8	-23.7
6	1	2015	early	early	Littoral	Littoral	ben_invertes	Trichoptera	-0.7	-25.7
6	1	2015	early	early	Profundal	Profundal	ben_invertes	Oligo/Chiro	1.6	-34.4
9	1	2015	early	late	Littoral	Littoral	ben_invertes	Oligo/Chiro	1.4	-20.7
9	1	2015	early	late	Profundal	Profundal	ben_invertes	Oligo/Chiro	2.3	-32
6	2	2015	early	early	Dock	lake	fish	BT	7.9	-28.4
6	2	2015	early	early	Dock	lake	fish	BT	8	-28.7

6	2	2015	early	early	Dock	lake	fish	BT	8	-29.1
6	2	2015	early	early	Dock	lake	fish	BT	7.8	-30.1
9	12	2015	early	late	Dock	lake	fish	BT	7.8	-28.1
9	13	2015	early	late	Dock	lake	fish	BT	7.8	-27.6
9	13	2015	early	late	Dock	lake	fish	BT	7.6	-26
9	13	2015	early	late	Dock	lake	fish	BT	7.7	-27.4
6	1	2015	early	early	PML	Pelagic	zoops	Zoop	3	-28.3
6	1	2015	early	early	PML	Pelagic	zoops	Zoop	NA	NA
7	1	2015	early	early	PML	Pelagic	zoops	Zoop	2.3	-27.9
8	1	2015	early	late	PML	Pelagic	zoops	Zoop	1.2	-28.1
9	1	2015	early	late	PML	Pelagic	zoops	Zoop	NA	-18
6	1	2016	avg	early	Littoral	Littoral	ben_invertes	Oligo/Chiro	1.7	-25.6
6	1	2016	avg	early	Littoral	Littoral	ben_invertes	Trichoptera	1.2	-25.6
6	1	2016	avg	early	Profundal	Profundal	ben_invertes	Oligo/Chiro	2.7	-33.1
9	1	2016	avg	late	Littoral	Littoral	ben_invertes	Oligo/Chiro	2.3	-22
9	1	2016	avg	late	Littoral	Littoral	ben_invertes	Trichoptera	2.7	-21.8
9	1	2016	avg	late	Profundal	Profundal	ben_invertes	Oligo/Chiro	3.3	-32.9
6	21	2016	avg	early	Spring	lake	fish	BT	7.4	-25.4
6	21	2016	avg	early	Spring	lake	fish	BT	7.7	-27.4
6	21	2016	avg	early	Spring	lake	fish	BT	7.6	-23.5
6	21	2016	avg	early	Dock	lake	fish	BT	7	-26.7
9	10	2016	avg	late	Dock	lake	fish	BT	8.2	-22.9
9	10	2016	avg	late	Dock	lake	fish	BT	8.4	-28.2
9	11	2016	avg	late	Dock	lake	fish	BT	8	-27.4
9	11	2016	avg	late	Dock	lake	fish	BT	7.5	-24.3
6	1	2016	avg	early	PML	Pelagic	zoops	Zoop	3.7	-30
7	1	2016	avg	early	PML	Pelagic	zoops	Zoop	3.8	-27.1
8	1	2016	avg	late	PML	Pelagic	zoops	Zoop	NA	NA
9	1	2016	avg	late	PML	Pelagic	zoops	Zoop	NA	NA

Tables C2: Averages raw compound-specific amino acid isotope data used in the FRUITS model for computations of autochthonous vs allochthonous carbon contributions to fish energetics. Averages are from 2 replicates per fish.

Month	Day	Year	Location	Species	Ala	Asp	Glu	Gly	Ile	Leu	Lys	Met	Phe	Pro	Thr	Val
9	16	2011	Dock	BT	-21.66	-19.23	-20.71	-11.82	-26.78	-32.24	-23.17	-29.63	-32.08	-18.54	-15.89	-28.33
9	16	2011	Dock	BT	-25.38	-22.58	-23.63	-16.02	-29.90	-35.52	-25.61	-33.06	-35.27	-22.63	-19.29	-31.51
9	16	2011	Dock	BT	-26.19	-22.41	-23.24	-17.41	-30.13	-35.75	-24.69	-32.62	-34.11	-23.70	-19.14	-32.13
6	21	2011	Dock	BT	-25.52	-23.32	-24.00	-14.22	-30.13	-35.98	-26.32	-32.22	-35.05	-22.16	-17.74	-32.19
6	21	2011	Dock	BT	-21.91	-20.87	-19.78	-11.71	-26.95	-32.71	-23.00	-29.30	-32.08	-18.80	-14.95	-28.69
6	21	2011	Dock	BT	-25.48	-21.92	-23.13	-15.22	-29.86	-35.72	-24.73	-32.07	-34.90	-22.37	-18.16	-31.81
6	21	2011	Dock	BT	-23.34	-21.35	-20.58	-13.84	-27.99	-33.82	-24.01	-30.40	-33.18	-20.56	-18.37	-29.70
6	2	2015	Dock	BT	-28.84	-23.38	-26.06	-21.48	-34.50	-39.05	-29.29	-36.53	-36.25	-26.24	-23.03	-37.30
6	2	2015	Dock	BT	-26.88	-22.65	-26.20	-17.00	-30.78	-36.99	-28.14	-34.36	-36.35	-23.37	-22.26	-33.59
6	2	2015	Dock	BT	-29.49	-26.93	-26.36	-21.21	-33.98	-39.18	-29.94	-36.99	-37.13	-26.50	-21.34	-36.62
6	2	2015	Dock	BT	-24.64	-22.91	-25.67	-15.34	-29.48	-35.80	-26.23	-38.42	-35.59	-22.35	-22.41	-31.60
6	21	2016	Dock	BT	-21.80	-22.09	-21.09	-11.31	-28.46	-33.71	-25.24	-32.12	-34.27	-20.44	-22.95	-29.97
7	18	2012	Dock	BT	-22.96	-22.34	-21.43	-12.32	-28.50	-33.83	-23.30	-31.88	-33.01	-20.04	-16.96	-29.64
7	18	2012	Dock	BT	-19.51	-18.45	-18.88	-9.65	-25.45	-30.48	-20.83	-28.20	-30.68	-17.47	-15.06	-26.68
7	18	2012	Dock	BT	-21.21	-19.04	-20.32	-12.03	-26.65	-32.32	-23.03	-29.69	-32.88	-19.11	-16.10	-28.26
7	18	2012	Dock	BT	-24.31	-22.98	-22.34	-13.63	-29.47	-34.81	-25.49	-32.32	-34.57	-21.90	-18.98	-31.07
9	15	2012	Dock	BT	-27.56	-25.10	-26.51	-17.03	-31.41	-37.26	-27.87	-34.51	-36.00	-25.22	-19.44	-33.25
9	15	2012	Dock	BT	-20.63	-18.72	-18.98	-11.69	-25.40	-31.20	-22.22	-28.49	-30.33	-19.77	-16.14	-27.23
9	15	2012	Dock	BT	-28.85	-27.21	-27.80	-19.13	-34.93	-40.45	-28.38	-36.90	-38.41	-28.04	-26.50	-37.00
9	1	2013	Dock	BT	-17.06	-16.34	-18.28	-8.34	-23.86	-29.69	-19.62	-29.62	-29.01	-16.43	-16.35	-25.32
9	1	2013	Dock	BT	-25.28	-24.65	-24.84	-15.19	-32.22	-38.08	-28.02	-40.07	-37.40	-24.46	-23.86	-34.07
9	1	2013	Dock	BT	-24.96	-20.68	-23.40	-16.87	-31.49	-36.31	-24.36	-32.99	-34.28	-24.14	-19.61	-34.00
9	1	2013	Dock	BT	-24.59	-23.30	-21.90	-14.09	-30.15	-35.91	-26.30	-31.87	-34.95	-22.86	-20.11	-31.64
9	6	2014	Dock	BT	-26.02	-24.38	-25.18	-16.12	-31.66	-37.87	-27.09	-33.61	-36.76	-23.15	-26.43	-33.48
9	6	2014	Dock	BT	-24.96	-22.00	-22.77	-15.47	-30.50	-35.32	-24.75	-32.87	-33.85	-21.74	-16.96	-33.06
9	6	2014	Dock	BT	-26.29	-23.65	-24.70	-16.20	-30.55	-36.97	-26.25	-32.77	-35.85	-22.92	-24.34	-32.86

9	12	2015	Dock	BT	-25.57	-23.31	-24.35	-15.33	-30.49	-36.26	-26.38	-33.31	-35.81	-22.13	-19.22	-33.09
9	11	2016	Dock	BT	-24.17	-22.25	-23.65	-12.69	-29.90	-35.61	-25.92	-32.13	-35.15	-21.55	-19.79	-31.58
9	11	2016	Dock	BT	-20.61	-19.38	-19.90	-11.05	-26.79	-32.22	-22.52	-29.40	-31.96	-18.63	-25.12	-28.75
6	13	2013	Dock	BT	-25.51	-24.32	-24.61	-15.38	-30.95	-36.99	-26.71	-32.81	-36.53	-24.36	-21.88	-32.95
6	13	2013	Dock	BT	-19.43	-18.97	-19.41	-9.11	-24.98	-30.56	-22.45	-27.61	-30.06	-18.42	-16.18	-26.56
6	13	2013	Dock	BT	-27.03	-23.71	-27.97	-18.25	-34.28	-39.03	-28.01	-37.46	-37.21	-27.70	-22.89	-36.15
6	10	2014	Dock	BT	-19.33	-17.22	-18.38	-11.56	-25.85	-31.34	-21.31	-28.05	-30.44	-17.46	-15.41	-27.50
6	10	2014	Dock	BT	-21.73	-17.63	-21.12	-14.01	-27.86	-33.03	-23.63	-28.26	-32.16	-19.44	-19.49	-30.04
6	10	2014	Dock	BT	-23.79	-20.00	-22.48	-13.20	-28.04	-33.66	-24.49	-30.72	-32.88	-20.59	-18.79	-30.17
6	10	2014	Dock	BT	-21.19	-20.07	-20.50	-14.19	-27.12	-32.62	-22.62	-28.68	-32.00	-19.29	-18.14	-29.39
9	13	2015	Dock	BT	-26.18	-22.63	-23.27	-16.19	-30.82	-35.96	-26.53	-35.35	-35.31	-23.13	-20.66	-32.89
9	13	2015	Dock	BT	-23.72	-23.11	-23.15	-13.06	-28.47	-33.72	-26.24	-31.57	-33.65	-20.66	-17.95	-30.79
9	13	2015	Dock	BT	-24.12	-23.14	-22.87	-12.97	-29.33	-35.41	-25.60	-32.18	-34.66	-21.23	-25.73	-31.13
9	10	2016	Dock	BT	-19.50	-18.20	-18.21	-8.53	-25.73	-31.17	-21.35	-30.79	-30.37	-17.85	-22.86	-27.19
9	10	2016	Dock	BT	-25.74	-24.20	-24.31	-13.95	-30.92	-36.01	-26.62	-34.61	-35.70	-23.26	-18.13	-32.66
9	16	2011	Spring	BT	-21.17	-16.50	-20.49	-11.90	-28.26	-32.70	-21.22	-32.73	-30.57	-19.08	-17.31	-29.72
6	14	2013	Spring	BT	-24.00	-22.04	-23.25	-14.84	-29.17	-34.81	-25.19	-32.21	-33.75	-20.82	-21.14	-30.59
6	21	2016	Spring	BT	-22.99	-20.98	-23.59	-12.78	-27.36	-32.92	-24.44	-32.83	-33.20	-20.47	-17.95	-30.09
6	21	2016	Spring	BT	-24.51	-22.73	-22.12	-14.61	-29.21	-35.20	-25.78	-33.56	-35.15	-21.88	-21.97	-31.66
6	21	2016	Spring	BT	-22.04	-20.06	-23.69	-12.12	-28.19	-33.54	-23.17	-32.16	-32.23	-20.10	-23.32	-30.78
9	15	2012	Spring	BT	-26.38	-23.07	-25.16	-15.40	-31.57	-37.73	-27.23	-34.30	-35.62	-22.95	-22.54	-33.22
9	6	2014	Spring	BT	-18.60	-16.59	-18.17	-9.61	-24.11	-29.47	-21.66	-26.73	-30.00	-16.08	-17.82	-26.33

Table C3: Standard deviations of raw compound-specific amino acid isotope data used in the FRUITS model for computations of autochthonous vs allochthonous carbon contributions to fish energetics.

Month	Day	Year	Location	Species	Ala	Asp	Glu	Gly	Ile	Leu	Lys	Met	Phe	Pro	Thr	Val
9	16	2011	Dock	BT	0.04	0.07	0.29	0.09	0.03	0.05	0.41	0.43	0.05	0.46	0.10	0.04
9	16	2011	Dock	BT	0.06	0.25	0.29	0.10	0.08	0.03	0.30	0.07	0.27	0.23	0.07	0.20
9	16	2011	Dock	BT	0.27	0.00	0.55	0.10	0.05	0.09	0.13	0.01	0.05	0.04	0.43	0.09
6	21	2011	Dock	BT	0.31	0.18	0.06	0.17	0.17	0.11	0.61	0.21	0.08	0.09	0.11	0.05

6	21	2011	Dock	BT	0.10	0.13	0.19	0.05	0.03	0.10	0.52	0.23	0.16	0.17	0.06	0.09
6	21	2011	Dock	BT	0.02	0.10	0.27	0.25	0.00	0.12	0.18	0.08	0.11	0.14	0.37	0.05
6	21	2011	Dock	BT	0.05	0.20	0.06	0.08	0.05	0.07	0.05	0.09	0.08	0.07	0.02	0.05
6	2	2015	Dock	BT	0.14	0.13	0.23	0.21	0.07	0.13	0.30	0.28	0.03	0.15	1.48	0.13
6	2	2015	Dock	BT	0.07	0.04	0.35	0.18	0.20	0.22	0.49	0.02	0.01	0.19	0.63	0.10
6	2	2015	Dock	BT	0.22	0.53	0.16	0.62	0.08	0.24	0.31	0.51	0.07	0.09	1.24	0.65
6	2	2015	Dock	BT	0.41	0.20	0.06	0.62	0.28	0.17	0.06	0.10	0.07	0.11	0.23	0.20
6	21	2016	Dock	BT	0.52	0.09	0.11	0.48	0.30	0.32	0.39	0.06	0.08	0.32	0.67	0.42
7	18	2012	Dock	BT	0.08	0.13	0.01	0.58	0.22	0.14	0.01	0.21	0.05	0.51	0.30	0.21
7	18	2012	Dock	BT	0.18	0.24	0.04	0.12	0.01	0.15	0.19	0.00	0.15	0.04	0.08	0.07
7	18	2012	Dock	BT	0.24	0.13	0.41	0.05	0.03	0.13	0.61	0.39	0.32	0.24	0.11	0.03
7	18	2012	Dock	BT	0.16	0.02	0.25	0.16	0.20	0.12	0.00	0.33	0.03	0.02	0.14	0.05
9	15	2012	Dock	BT	0.10	0.24	0.16	0.01	0.09	0.06	0.17	0.40	0.19	0.25	0.55	0.26
9	15	2012	Dock	BT	0.19	0.36	0.77	0.20	0.11	0.07	0.30	0.58	0.33	0.02	0.57	0.14
9	15	2012	Dock	BT	0.29	0.34	0.25	0.15	0.02	0.19	0.20	0.46	0.01	0.09	0.11	0.07
9	1	2013	Dock	BT	0.15	0.05	0.15	0.23	0.21	0.15	0.14	0.29	0.09	0.11	0.45	0.20
9	1	2013	Dock	BT	0.19	0.27	0.41	0.21	0.08	0.03	0.07	0.60	0.07	0.00	0.08	0.04
9	1	2013	Dock	BT	0.54	0.45	0.42	0.29	0.06	0.03	0.41	0.05	0.14	0.12	0.61	0.03
9	1	2013	Dock	BT	0.04	0.18	0.19	0.30	0.11	0.10	0.06	0.01	0.22	0.03	0.49	0.14
9	6	2014	Dock	BT	0.00	0.16	0.07	0.36	0.00	0.14	0.26	0.04	0.30	0.04	1.03	0.34
9	6	2014	Dock	BT	0.24	0.07	0.08	0.00	0.04	0.20	0.35	0.16	0.07	0.21	0.14	0.09
9	6	2014	Dock	BT	0.09	0.01	0.27	0.10	0.15	0.09	0.02	0.03	0.12	0.10	0.54	0.52
9	12	2015	Dock	BT	0.14	0.47	0.27	0.12	0.02	0.12	0.43	0.69	0.03	0.01	0.85	0.06
9	11	2016	Dock	BT	0.12	0.22	0.14	0.34	0.06	0.11	0.12	0.02	0.06	0.06	0.47	0.03
9	11	2016	Dock	BT	0.03	0.35	0.21	0.14	0.06	0.27	0.01	0.39	0.18	0.07	1.06	0.02
6	13	2013	Dock	BT	0.15	0.14	0.37	0.52	0.10	0.06	0.64	0.28	0.62	0.13	0.92	0.14
6	13	2013	Dock	BT	0.02	0.64	0.30	0.04	0.02	0.13	0.45	0.14	0.28	0.05	0.36	0.24
6	13	2013	Dock	BT	0.38	0.12	0.01	0.17	0.10	0.22	0.04	0.14	0.13	0.15	0.75	0.43
6	10	2014	Dock	BT	0.06	0.32	0.26	0.01	0.02	0.09	0.98	0.23	0.05	0.04	1.13	0.31
6	10	2014	Dock	BT	0.16	0.11	0.53	0.31	0.15	0.06	0.48	0.25	0.20	0.15	1.69	0.04
6	10	2014	Dock	BT	0.05	0.21	0.11	0.10	0.07	0.04	0.43	0.26	0.36	0.00	0.27	0.15

6	10	2014	Dock	BT	0.24	0.04	0.16	0.06	0.04	0.04	0.19	0.14	0.06	0.06	0.12	0.03
9	13	2015	Dock	BT	0.26	0.13	0.03	0.14	0.08	0.15	0.29	1.26	0.35	0.09	0.02	0.23
9	13	2015	Dock	BT	0.19	0.22	0.01	0.14	0.22	0.17	0.15	0.29	0.08	0.17	0.18	0.24
9	13	2015	Dock	BT	0.12	0.05	0.24	0.13	0.27	0.10	0.13	1.15	0.05	0.18	0.87	0.19
9	10	2016	Dock	BT	0.15	0.51	0.16	0.09	0.18	0.89	0.17	1.07	0.13	0.08	0.29	0.12
9	10	2016	Dock	BT	0.01	0.15	0.22	0.06	0.02	0.11	0.17	0.23	0.08	0.06	0.72	0.05
9	16	2011	Spring	BT	0.23	0.19	0.17	0.67	0.39	0.22	0.39	0.37	0.42	0.13	0.01	0.19
6	14	2013	Spring	BT	0.13	0.03	0.29	0.60	0.13	0.19	0.10	0.36	0.28	0.02	0.62	0.15
6	21	2016	Spring	BT	0.08	0.11	0.03	0.39	0.21	0.13	0.01	0.02	0.06	0.04	0.34	0.21
6	21	2016	Spring	BT	0.07	0.13	0.48	0.23	0.07	0.64	0.90	0.49	0.14	0.15	0.20	0.04
6	21	2016	Spring	BT	0.29	0.81	0.11	0.44	0.04	0.00	0.02	1.22	0.05	0.11	1.44	0.33
9	15	2012	Spring	BT	0.20	0.20	0.06	0.21	0.23	0.23	0.41	0.01	0.03	0.05	0.59	0.14
9	6	2014	Spring	BT	0.14	0.28	0.36	0.39	0.20	0.22	1.21	0.32	0.58	0.15	0.12	0.13

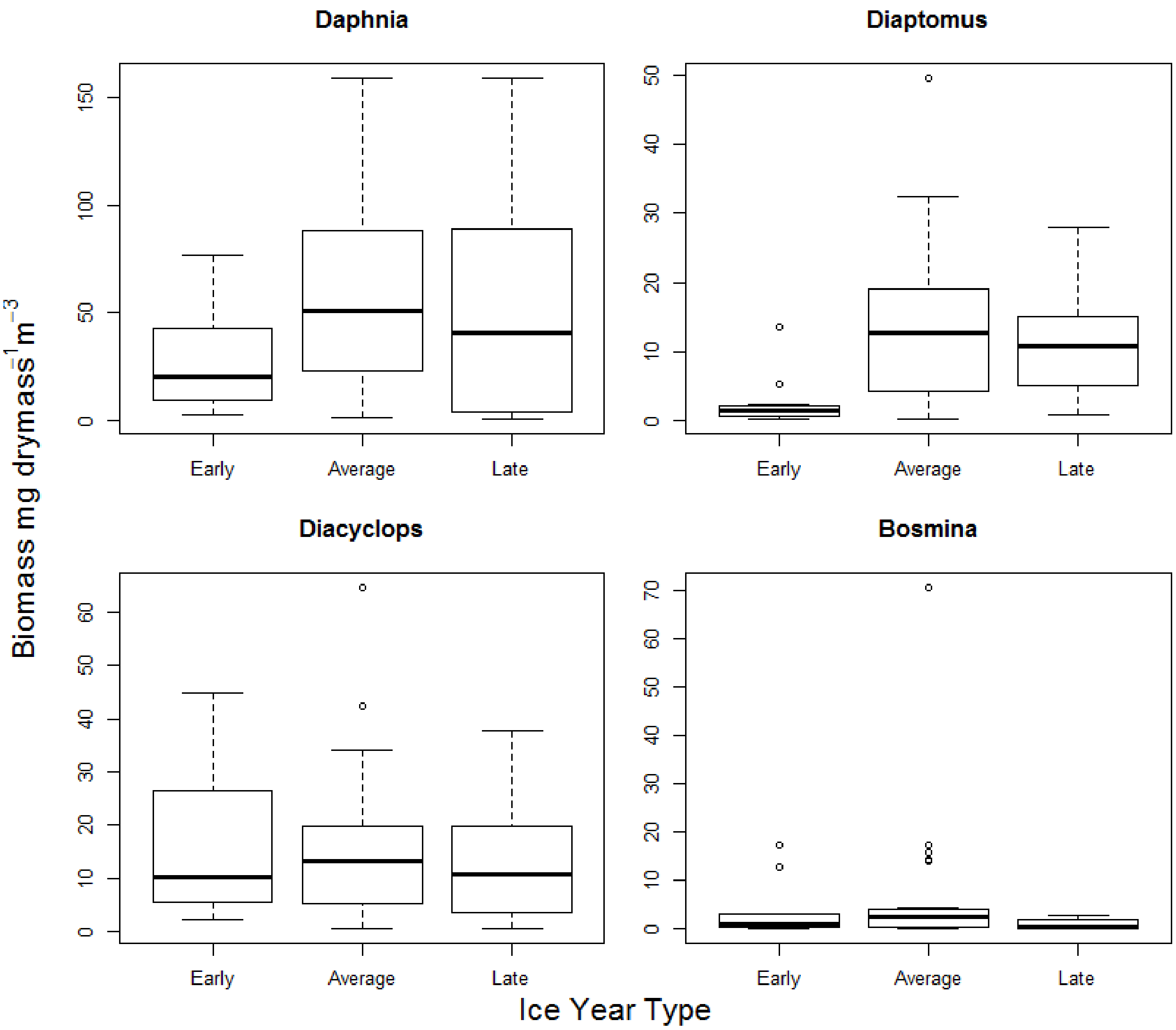


Figure C1. Biomass (mg drymass-1 m-3) for all zooplankton species in Castle Lake, California. Boxplots are of monthly (June-October) means calculated from weekly samples from 2008-2016 across different ice year types.

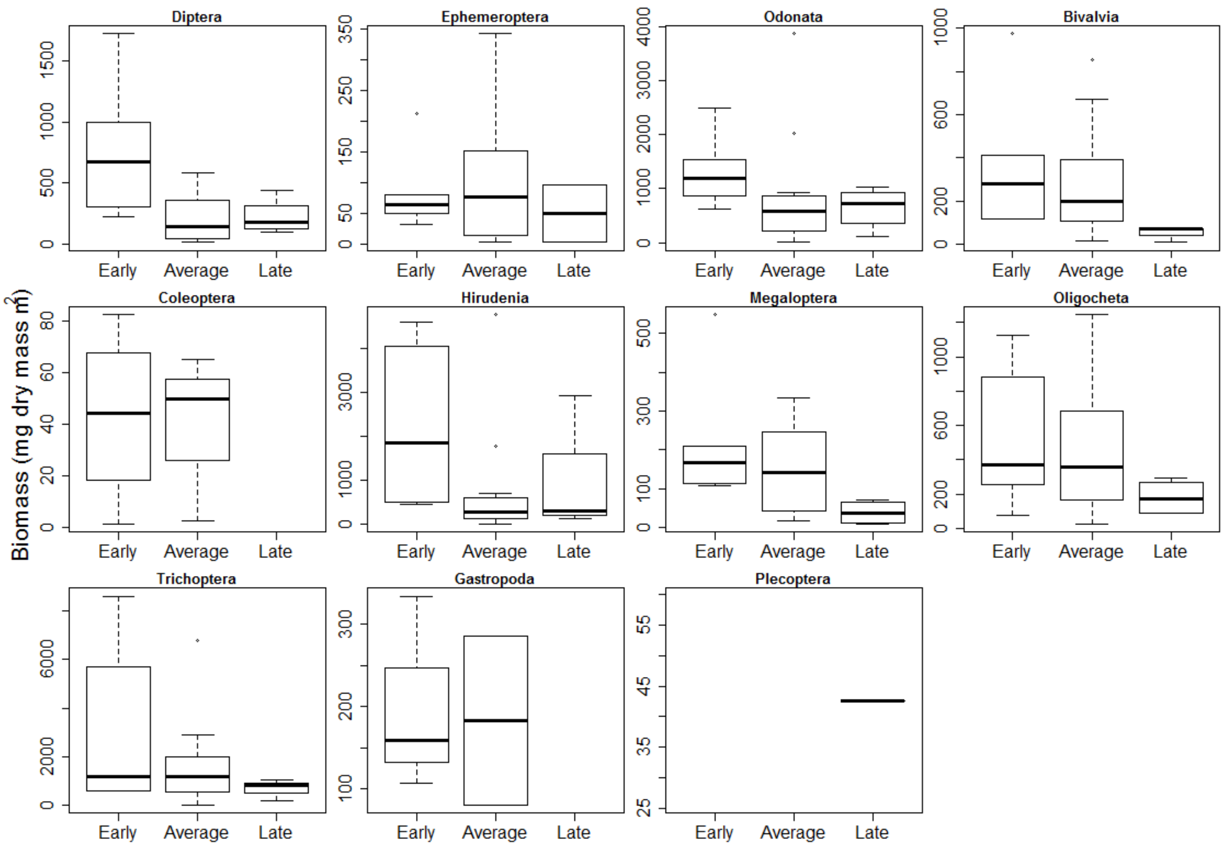


Figure C2. Taxon specific biomass of littoral benthic invertebrates in Castle Lake, CA. Boxplots are of monthly (June, July and September) means calculated from 4 sample sites in littoral zone at different ice year types.

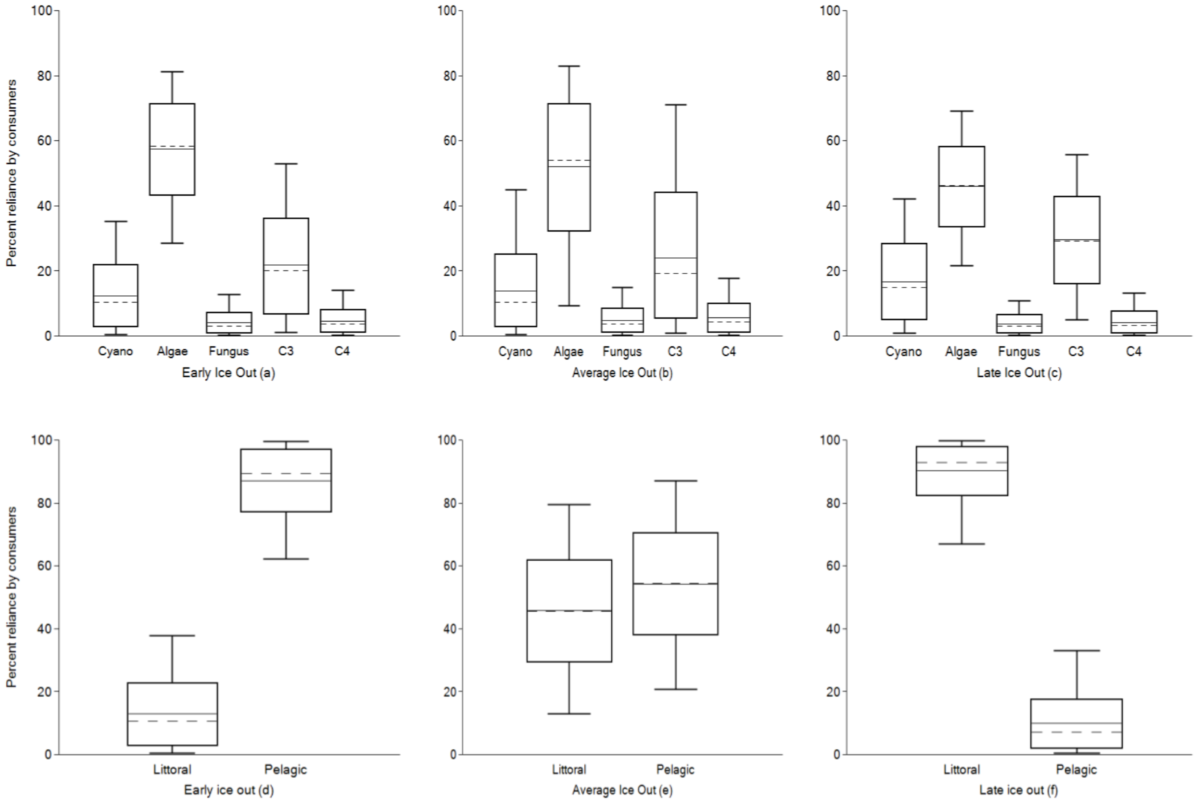


Figure C3. Percent reliance by consumers on both terrestrial and aquatic resources (a, b, c) and within lake habitat resources (d,e,f). Boxplots are of posterior distributions of estimates from the FRUITS Bayesian isotopic mixing model. Dashed line and solid line represent the median and mean of the posterior distribution, respectively.