

## Trophic compression of lake food webs under hydrologic disturbance

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**Abstract.** The need to protect biostructure is increasingly recognized, yet empirical studies of how human exploits affect ecological networks are rare. Studying the effects of variation in human disturbance intensity from decades past can help us understand and anticipate ecosystem change under alleviated or amplified disturbance over decades to come. Here, we use stable isotopes and an innovative analytical approach to compare the food webs of two akin lake ecosystems subject to disparate water use regimes, a pervasive, yet unappreciated stressor. We show that intensive water use (persistent, early season, rapid lake-level drawdown) can compress trophic diversity by 46%, necessitating reorganization of biostructural elements configuring lake food webs. Compression occurred over the  $\delta^{13}\text{C}$  axis indicating erosion of basal trophic diversity, but food chain length remained intact over the period and intensity of disturbance examined. This study demonstrates the potential for water use, like other disturbances (warming, eutrophication, and invasive species), to mute opportunity for benthic-pelagic coupling and benefits to lake food webs and the inherent capacity of lake ecosystems to adapt to stress. Trophically compressed lakes may be less able to adapt to intensified water use.

**Key words:** biostructure; disturbance; food web; lake ecosystems; stable isotopes; water use.

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### INTRODUCTION

Diversity maintains function and stability at multiple levels of biological organization by buffering ecological processes to environmental change, but is prone to human disturbance (Hooper et al. 2005, Tilman et al. 2006, Ives and Carpenter 2007, Greene et al. 2010). Persistent landscape-level human disturbance (e.g., fire suppression) can erode species diversity and increase the vulnerability of ecosystems to collapse or regimes shifts (Jackson et al. 2001, Kefi et al. 2007, MacDougall et al. 2013). For

exploited species exhibiting high population diversity however, stability of services to humans and other consumers within ecosystems appears less obscured by more targeted disturbance (e.g., commercial fishing, Hilborn et al. 2003, Schindler et al. 2010, 2013).

This apparent scale-dependent effect of human activity on diversity–stability relationships indicates that the nature and degree of disturbance mediate ecosystem resilience. Human activities that are dispersed over species and habitats vs. concentrated on single species with diverse life-history portfolios may be more disruptive

because “biostructure,” the network of interactions among organisms that fabricates function, but fueled by biodiversity, is more affected (McCann 2007). With expanding disturbance regimes from a growing human enterprise, we must clarify how different exploits affect biostructure to better understand and anticipate ecosystem change. So far, empirical studies are lacking.

Freshwater ecosystems are arguably the most critical life-support systems fueling humanity (DeFries and Eshleman 2004). Conceptual models (e.g., the generalist module of McMeans et al. 2016) assert that the biostructure or size-structured food webs of lake ecosystems are resilient to environmental stress because flexible feeding behavior, integration of benthic and pelagic energy pathways, and transfer of energy across habitats by mobile consumers buffer interactions from variation in lower trophic level dynamics (Vadeboncoeur et al. 2002, McMeans et al. 2016).

Despite this adaptive architecture, human activity can disrupt social-ecological goods and services in even the world’s largest lakes. For example, the invasion of *Mysis diluviana* in Flathead Lake, Montana, USA, triggered a long-term trophic cascade that culminated in the extirpation of salmon and a reduction in terrestrial consumers of salmon (Ellis et al. 2011). Long-term fisheries survey data revealed a shift toward higher dominance of eurythermal species and decline of cold-stenothermic species in a diverse suite of warming lakes across Europe which impacted commercial fishers (Jeppesen et al. 2012). Eutrophication reversed processes that promote adaptive radiation by fish (Vonlanthan et al. 2012); mechanisms that infuse lakes with stabilizing diversity (McMeans et al. 2016). Further, many lakes are exploited for water supply. Yet, the effects of altered hydrologic processes on biostructure remain underappreciated despite decades of water use (DeFries and Eshleman 2004, Oki and Kanae 2006) and growing burden on freshwater (Vorosmarty et al. 2000, Dai 2013).

Empirical tests of how human exploits affect biostructure are rare because mapping and statistically comparing ecological networks is challenging (McCann 2007), disturbances act on ecosystems interactively which can obscure

specific threats (Jeppesen et al. 2012, Rolls et al. 2017), and comparative baselines are often lacking given the long history of human modified ecosystems (DeFries and Eshleman 2004). Here, we exploit variation in human disturbance intensity of decades past to test the hypothesis that long-term water manipulation driven by irrigation practices erodes the biostructure of lakes. We use stable isotopes and an innovative analytical approach (Jackson et al. 2011) to illustrate the food webs and compare the biostructure of two akin lake ecosystems subject to disparate water use regimes.

## METHODS

### *Social-ecological system*

The study lakes, Lake Kachess (47°18'21.9" N, 121°13'52.5" W) and Lake Keechelus (47°21'05.7" N, 121°22'16.7" W), are two oligotrophic reservoirs in the Yakima River Basin, Washington, USA, a social-ecological system working toward maintaining the integrity of aquatic ecosystems while securing long-term water supply for agriculturalists. These natural lakes were impounded early in the 20th century. Their close proximity, exposure to similar climatic conditions, comparable geo- and morphometric features, identical native fish assemblages (Appendix S1: Table S1), but contrasting water use regimes (Fig. 1a) provide an excellent opportunity for determining how the structural properties of ecological networks change across a gradient of human activity (McCann 2007, McMeans et al. 2016).

Keechelus has historically been managed more intensively than Kachess based on the relative timing and magnitude of water releases (Fig. 1b, daily discharge from the dam scaled to total annual reservoir inflow), relative total active storage use (Fig. 1c, percent of total water available for irrigation and municipal use), and relative lake-level drawdown (Fig. 1d, meters below normal maximum impounded lake level), but predominantly so in recent decades. Habitat requirements of threatened salmon downstream dictated the earlier and more extensive drawdown of Keechelus during the primary growing season approximately two decades ago. As a result, Kachess remains fuller and fluctuates less during spring and summer. Thus, the benthic-littoral zone in Kachess is largely available until early autumn, but

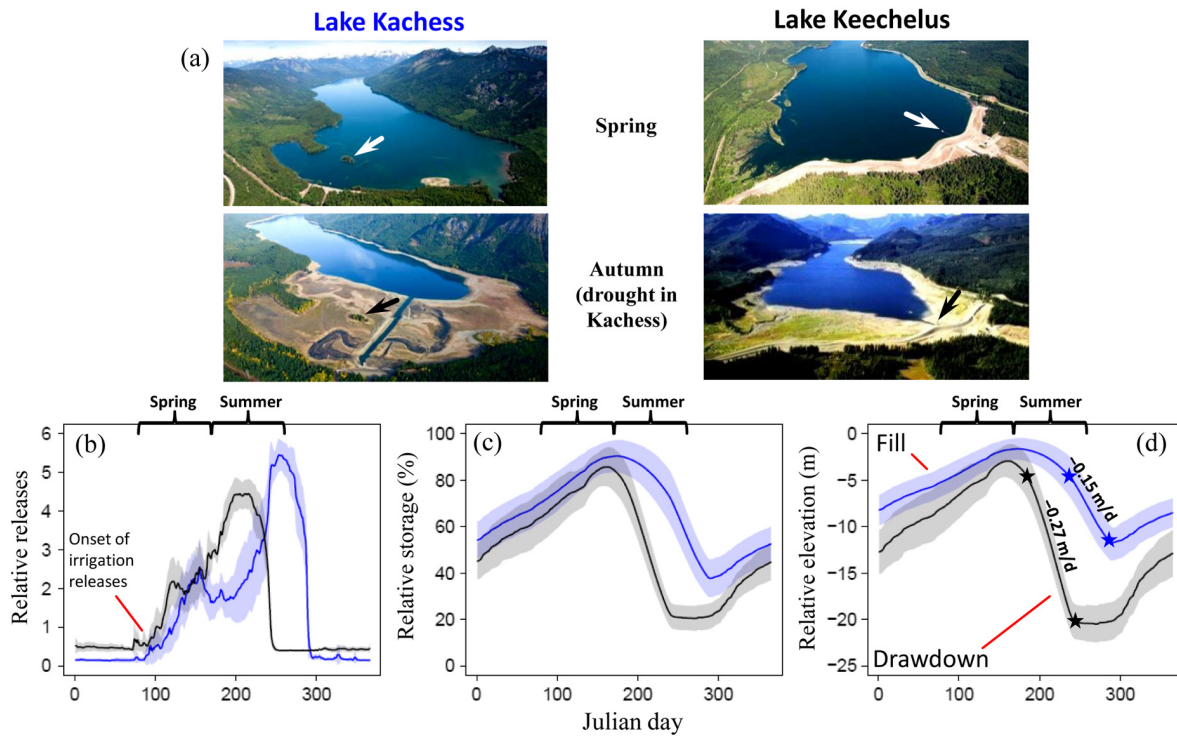


Fig. 1. Water operations (period of record: 2000–2016) and isotopic food web structure of Lake Kachess (blue) and Lake Keechelus (black). (a) Images of Kachess and Keechelus in spring prior to drawdown and in autumn after typical drawdown in Keechelus, but during drought in Kachess (only image available). De-watered habitat shown for Kachess is still largely inundated during late summer in a normal water year. Arrows denote consistent reference points. (b) Mean (solid line)  $\pm$  2 standard errors (shaded region) relative daily water releases from the dam (daily discharge scaled to total annual inflow) for each lake. (c) Corresponding mean relative daily water storage capacity (percent of total water available for irrigation and municipal use). (d) Mean relative daily surface elevation (meters below normal maximum impounded lake level). Values indicate the mean daily rate of drawdown within the periods bracketed by stars. Water operations data were freely available online from the United States Bureau of Reclamation (<https://www.usbr.gov/pn/hydro/dromet/yakima/index.html>).

disappears rapidly starting early summer and is mostly unavailable by mid-summer in Keechelus (Fig. 1d; Appendix S1: Fig. S1).

#### Analytical approach

Stable isotope ratios of nitrogen ( $^{15}\text{N}/^{14}\text{N}$ ) and carbon ( $^{13}\text{C}/^{12}\text{C}$ ) in the tissues of consumers such as fish are tightly linked to diet and trophic niche width (Bearhop et al. 2004). The value of  $^{15}\text{N}/^{14}\text{N}$  increases from prey to predator by a predictable amount indicating trophic position in the food web whereas  $^{13}\text{C}/^{12}\text{C}$  changes little from prey to predator indicating the primary energy source (e.g., benthic carbon vs. pelagic carbon in lakes) or mix thereof fueling consumers. When values

of  $^{15}\text{N}/^{14}\text{N}$  and  $^{13}\text{C}/^{12}\text{C}$  are standardized to  $\delta$ -notation and plotted in  $\delta$ -space (i.e.,  $\delta^{15}\text{N}$  vs.  $\delta^{13}\text{C}$  in per mil units [‰]), an empirical sketch of food web interactions emerges (Newsome et al. 2007); the structural components of which can be quantified and statistically compared among and within communities using robust Bayesian methods applied to the bivariate isotopic data. Specifically, we use standard Bayesian ellipses and Layman metrics (Layman et al. 2007) reformulated within a Bayesian framework (Jackson et al. 2011) to quantify and compare trophic diversity and key biostructural elements of each lake food web (see detailed description of metrics in Appendix S1).

### *Fish sampling and isotopic analysis*

We captured and sampled caudal fin tissue for isotopic analysis (Sanderson et al. 2009) from secondary, tertiary, and quaternary fish consumers (Appendix S1: Fig. S2) in Kachess ( $n = 211$ ) and Keechelus ( $n = 160$ ) spring through fall over three years (2014 through 2016). Fish were sampled with electrofishing, mid-water trawls, traps, trot-lines, and multi-meshed gill nets set at different depths and in nearshore vs. offshore habitats to subsume spatio-temporal and size-dependent variation in the isotopic values of each species and to the extent possible encompass the isotopic breadth of all fish in each lake. Fin tissue was dried at 60°C for 72 h, homogenized into a powder with a mortar and pestle, encapsulated in tins ( $0.4 \pm 0.02$  mg of material), and analyzed using a Costech Elemental Analyzer interfaced with ConFlo III and coupled with a MAT 253 mass spectrometer at the University of Washington IsoLab, Seattle, Washington, USA. Reference material was atmospheric N<sub>2</sub> for nitrogen and Pee Dee Belemnite for carbon. To avoid bias from variable lipid concentrations among samples and species, we normalized  $\delta^{13}\text{C}$  values using C:N ratios following Post et al. (2007).

Some species and size classes of fish were rare in our dataset, particularly large-bodied upper trophic level predators from Lake Keechelus (Appendix S1: Fig. S2). The rapid drawdown of Keechelus during the irrigation season limited boat access, so sampling was opportunistic, but samples were obtained during late spring and fall and from all trophic levels. Thus, to effectively apply Bayesian ellipses and Layman metrics to our unbalanced dataset, we pooled individual  $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$  values from different species ( $n = 12$ ) and sizes of fish observed into ecologically relevant trophic-groups (TG;  $n = 7$ ) and broader trophic-guilds ( $n = 5$ ) that were consistent between Kachess and Keechelus (Appendix S1: Table S2). Consolidating data into seven trophic-groups (see procedure in Appendix S1) was also most parsimonious with respect to achieving the minimum within-group sample size ( $n \geq 10$ ) needed for unbiased estimates of community-level Layman metrics without losing ecological information from single members (Jackson et al. 2011).

### *Estimation of Bayesian metrics*

We estimated community-level and trophic-group-level Bayesian isotopic metrics separately for Lake Kachess and Lake Keechelus using computational code provided in the SIBER package (Jackson et al. 2011) implemented in R version 3.2.2 (R Core Team 2016). Our analysis consisted of three phases. In phase 1, we fit a standard Bayesian ellipse to bivariate data pooled across individual consumers and used the resulting estimate of ellipse area ( $\text{SEA}_B$ ) to characterize the isotopic breadth of fish in each lake independent of biostructure (Fig. 2a). Our a priori expectation was that this metric would be most sensitive to water use and show the greatest potential degree of difference between Kachess and Keechelus because, unlike metrics constructed from the means of single members (Fig. 2b), an ellipse should incorporate more relative trophic information from uncharacteristic individuals (Fig. 2a). Thus, analysis phase 1 provided a single integrative measure of overall trophic diversity in the food web of each lake. Because water withdrawal, and in the case of Keechelus, annual, rapid dewatering of nearshore habitat early in the growing season, could affect processes contributing to diversity along the  $\delta^{15}\text{N}$  vs.  $\delta^{13}\text{C}$  axis in complex ways, the remaining analysis phases were designed to discern the specific biostructural elements and trophic-groups affected most by water use to help interpret the broadscale measure of isotopic breadth observed in Kachess vs. Keechelus.

In phase 2, we characterized the biostructural elements configuring each lake food web by estimating the suite of Bayesian Layman metrics (Appendix S1). The lake-specific convex hull area estimated during this phase represented a secondary measure of isotopic breadth, but accounted for the central trophic role of key food web constituents (Fig. 2b), a metric we refer to as the “breadth of core biostructure.” Estimating both metrics allowed us to explore whether intensive water use predominately affected peripheral trophic diversity or both peripheral and principal diversity fueling the core food web. Both degrees of trophic compression could have implications for the adaptive capacity of lake food webs (McMeans et al. 2016).

In phase 3, we fit standard Bayesian ellipses and estimated  $\text{SEA}_B$  for each trophic-group

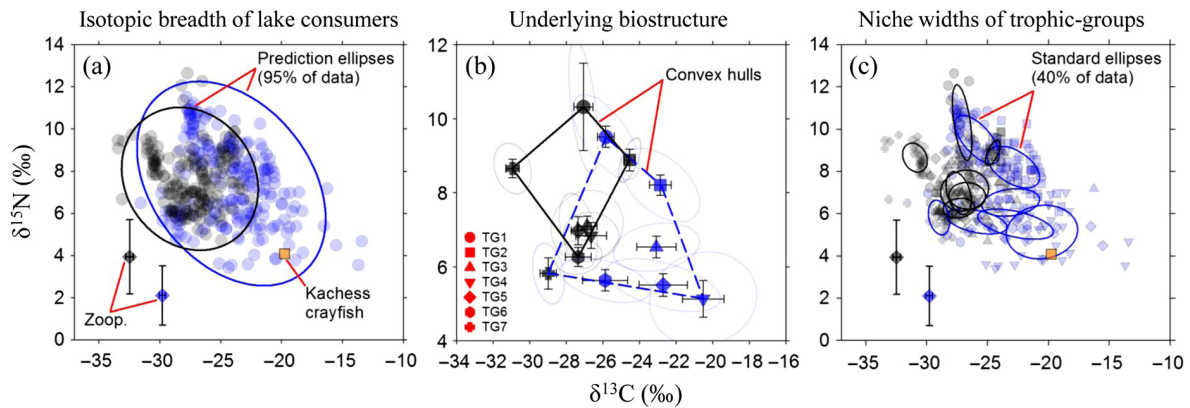


Fig. 2. (a) Bi-plot of stable isotope values from individual fish (points) sampled from each lake (blue for Kachess and black for Keechelus) independent of trophic-group. Prediction ellipses are shown for visualization purposes. (b) Mean  $\pm$  2 standard errors bivariate isotopic values for different trophic-groups in each lake—the basis for applying community-level Layman metrics and comparing the biostructural elements of each food web through Bayesian inference (Jackson et al. 2011). (c) Same bi-plot as (a), but with consumers parsed into trophic-groups (TG; symbols) and standard ellipses overlaid, the area of which, indicating trophic niche width. Note the axes on panel (b) differ from (a) and (c). The label Zoopl. on (a) stands for zooplankton.

(Fig. 2c). These metrics helped us identify possible ecological mechanisms contributing to differences in the biostructure of Kachess vs. Keechelus that stem from the interplay among the timing and magnitude of water use and the life history, behavior, and biology of organisms. Lastly, for each metric, we computed the probability that the estimated value for Kachess was greater than Keechelus and characterized the magnitude of difference between lakes (Jackson et al. 2011); the former signifying the strength of evidence for trophic compression and the latter indicating the magnitude of compression.

#### Sensitivity to differences in body size

Stable isotopes of nitrogen and carbon often change as fish grow reflecting ontogenetic shifts in habitat use and diet, and the level of change is species dependent (McIntyre et al. 2006). The distribution of body sizes of fish sampled differed between lakes for some trophic-groups (TG2, TG3, TG6, and TG7, all  $P < 0.006$ , Wilcoxon rank sum test at  $\alpha = 0.05$ , Appendix S1: Table S2), and we observed some significant linear relationships between  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  and body size within these groups, but predominately so for TG2 (warm water piscivores) and TG3 (coldwater invertivores; Appendix S1: Table S3). If TG-specific differences in body size were great

enough and size dependence in  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  strong enough, these discrepancies together could skew comparison of isotopic metrics between lakes.

To evaluate whether size discrepancies were ecologically relevant to our analysis of biostructure, we limited data from TG1, TG2, and TG3 to the body sizes of individuals that overlapped in both lakes (Appendix S1: Table S2, Fig. S3). Even though no difference in the body sizes of fish sampled in TG1 (coldwater piscivores) was observed between lakes, the range of body sizes and number of fish sampled were still notably higher in Kachess than in Keechelus (Appendix S1: Table S2), so we included TG1 in this analysis. We estimated the suite of Bayesian isotopic metrics from this reduced dataset, compared them to those estimated from the full dataset, recalculated the probability that the value estimated for Kachess was greater than Keechelus for each metric and re-characterized the magnitude of difference between lakes (Appendix S1: Table S4).

## RESULTS

The Bayesian isotopic metrics revealed distinct differences in the biostructure of Lake Kachess (relatively benign water use regime) vs. Lake

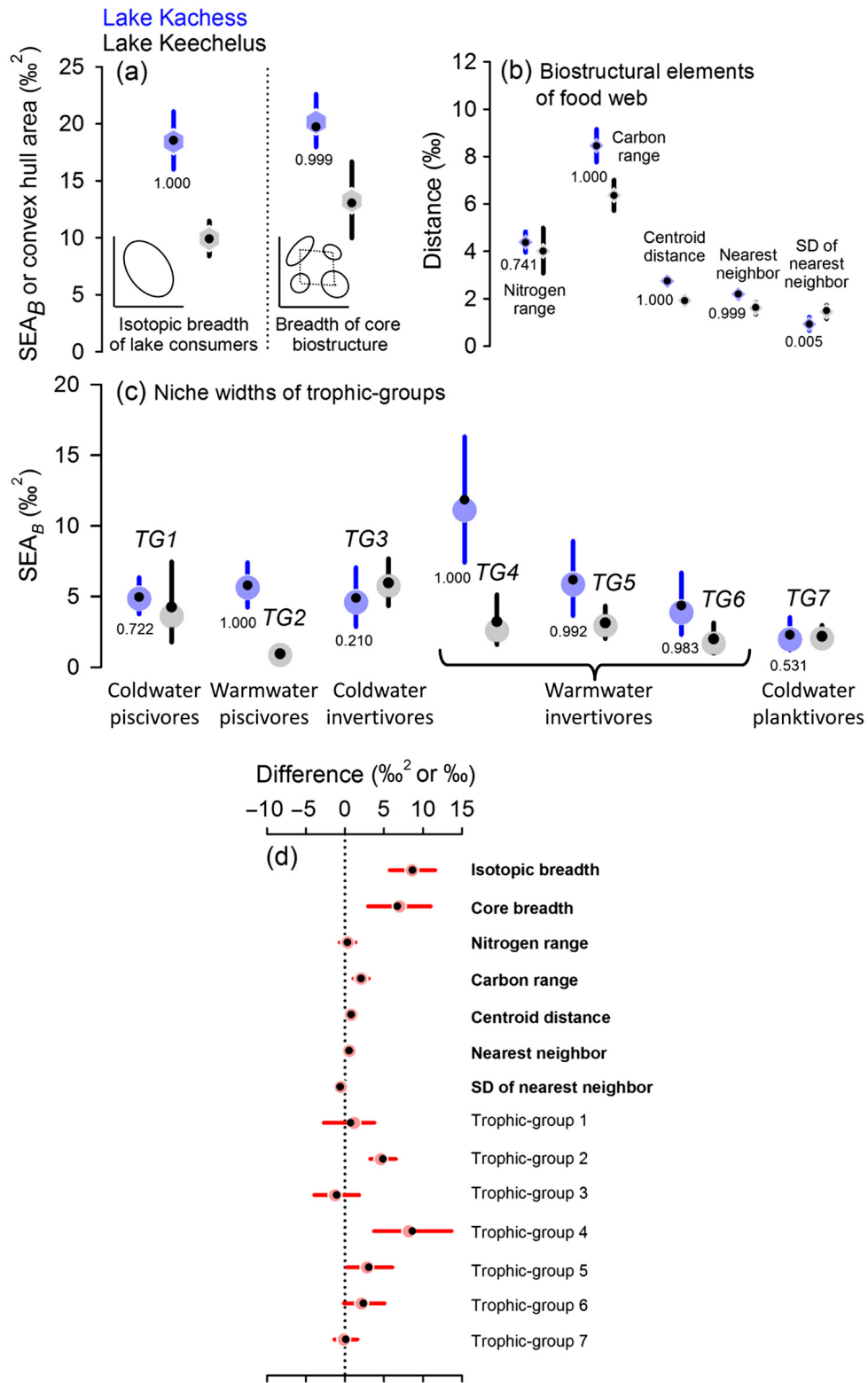


Fig. 3. Summarized posterior probability distributions (large symbols, mode; vertical bars, 95% credible intervals)

(Fig. 3. *Continued*)

for estimates of different community-level and trophic-group-level isotopic metrics characterizing the food web structure of Lake Kachess (blue) and Lake Keechelus (black). For the Layman metrics [breadth of core biostructure in (a) and biostructural elements in (b)], black dots represent maximum-likelihood estimates for comparison. For metrics based on the standard Bayesian ellipse area [ $SEA_B$ ; isotopic breadth of lake consumers in (a), and niche widths of trophic-groups (TG) within each broader trophic-guild in (c)], black dots represent the standard ellipse area estimated via maximum-likelihood corrected for small sample size (i.e.,  $SEA_C$  in Jackson et al. 2011). Numbers spanning from 0 to 1 on panels (a) through (c) represent the probability that the value of the corresponding metric estimated for Kachess is greater than Keechelus. Panel (d) shows corresponding summarized probability distributions (red symbols and bars) for the magnitude of difference between each metric estimated via Bayesian inference for each lake (i.e., Kachess–Keechelus) and corresponding differences in the maximum-likelihood estimates (black dots).

Keechelus (more intensive water use regime; Fig. 3). Collectively, the metrics and corresponding Bayesian probabilities (Kachess > Keechelus) and degrees of difference between Kachess and Keechelus also changed little after estimation from the reduced dataset (Appendix S1: Table S4), indicating that overall patterns of trophic compression were robust to discrepancies in the distribution of body sizes of fish sampled within TG1, TG2, and TG3 between lakes. Thus, we focus our presentation on metrics estimated from the full dataset (Fig. 3), but note important outcomes from the reduced dataset.

The modal isotopic breadth of lake consumers and modal breadth of core biostructure from the corresponding summarized posterior probability distributions estimated from both the full and reduced datasets were notably higher in Lake Kachess than in Lake Keechelus (Fig. 3a, d; Appendix S1: Table S4). The probability that the value of each metric from each dataset was greater in Kachess was always  $\geq 0.988$ . Based on the difference in posterior modes, overall trophic diversity was 46.2% lower in Keechelus (reduced dataset = 42.7%). Likewise, the modal difference in the breadth of core biostructure indicated that principal trophic diversity fueling the core food web was 34.3% lower in Keechelus (reduced dataset = 25.6%).

Evaluation of key biostructural elements configuring the food web of each lake showed that reduced trophic diversity along the  $\delta^{13}\text{C}$  axis, as signified by a greater carbon range in Lake Kachess (probability = 1.0), was the primary factor contributing to the compressed isotopic breadth of Lake Keechelus. The pelagic end-member was consistent between lakes (TG7), but the benthic-littoral end-member differed (TG2 one trophic level above in Keechelus vs. TG4 one trophic level

below in Kachess) due to disparate core food web configurations and greater clustering of cold and warm water invertivore trophic-groups in Keechelus. Conspecifics in Kachess were spread more evenly across the  $\delta^{13}\text{C}$  axis consistent with the structure of general aquatic food webs (McMeans et al. 2016, Fig. 2b). The modal carbon range shifted from being 32.0% greater in Kachess when using TG2 (Fig. 3b, d; Appendix S1: Table S4) to 95.2% greater when using TG4 (posterior mode = 4.34‰, 95% credible interval = 3.77–4.98‰) in computations for Keechelus. Conversely, there was little evidence for a difference in nitrogen range between lakes (probability = 0.741, Fig. 3b, d), which weakened further (probability = 0.422; Appendix S1: Table S4) after considering the more conservative dataset whereby the number of coldwater piscivores from Kachess included in the analysis was reduced. Lastly, both centroid distance and nearest neighbor distance were greater in Kachess (probability  $\geq 0.997$  across datasets), but the standard deviation of nearest neighbor distance was lower (probability  $\leq 0.050$ , Fig. 3b, d; Appendix S1: Table S4). Patterns in these remaining elements indicated that trophic diversity was compressed and food web constituents were more clustered within  $\delta$ -space in Keechelus (Fig. 2b).

Trophic niche width as signified by  $SEA_B$  varied among trophic-groups within each lake, but a clear and consistent pattern emerged when comparing the  $SEA_B$  of trophic-groups within the coldwater trophic-guild vs. the warm water trophic-guild between lakes (Fig. 3c, d). We found little evidence that the niche widths of coldwater piscivores (probability = 0.722 [0.612 from reduced dataset], TG1), invertivores (0.210 [0.718], TG2), and planktivores (0.531 [0.531], TG7) were higher in Lake Kachess or differed between lakes. Conversely, we

found strong evidence (probability  $\geq 0.983$  across datasets) that the niche width of each trophic-group within the warm water trophic-guild was compressed in Keechelus relative to Kachess (Fig. 3c, d). The degree of compression varied, but ranged from 50.0% to 84.6% across trophic-groups and datasets based on differences in posterior modes (Appendix S1: Table S4).

## DISCUSSION

The biostructure of Lake Keechelus differed in configuration compared to Lake Kachess. This outcome was likely driven by the more intensive water use regime that governed Keechelus over the past two decades. The food web of Keechelus was trophically compressed relative to Kachess and the intensity of water use in Keechelus appeared sufficient to erode peripheral and principle trophic diversity, necessitating reconfiguration of the lakes core biostructure. Trophic compression transpired primarily over the  $\delta^{13}\text{C}$  axis, but was unidirectional toward phytoplankton or phyto-detrital fueled energy pathways as indicated by more negative  $\delta^{13}\text{C}$  values reflecting those of obligate pelagic planktivores and their zooplankton prey which are primary consumers of phytoplankton. Invertivore trophic-groups that showed less negative and broader  $\delta^{13}\text{C}$  values relative to planktivores in Kachess exhibited more negative  $\delta^{13}\text{C}$  values clustered toward planktivores in Keechelus, and these shifts manifested in the Bayesian estimations of carbon range. The trophic niche widths of warm water benthic-littoral trophic-groups were largely constricted in Keechelus, whereas coldwater pelagic trophic-groups did not differ between lakes. Collectively, results support the notion that intensive water use eroded energy pathways originating from basal carbon resources, but left processes contributing to overall food chain length intact over the period and intensity of disturbance examined. Like other human disturbances (biological invasions, climate change, or eutrophication), this study demonstrates the potential for water use, an understudied yet pervasive environmental stressor, to mute opportunity for benthic-pelagic coupling and benefits to organisms, food webs, and lake ecosystem productivity (Vadeboncoeur et al. 2002).

It is possible that the reduced basal trophic diversity (i.e., a reduction in the  $\delta^{13}\text{C}$  range)

observed in Keechelus relative to Kachess was driven by a natural restriction in the benthic-littoral baseline  $\delta^{13}\text{C}$  value relative to the pelagic baseline  $\delta^{13}\text{C}$  value provided by zooplankton and not driven by more intensive water use and corresponding contraction in food web structure. We were not able to collect a sufficient number of benthic organisms of limited mobility (e.g., snails) to adequately characterize the baseline benthic algae  $\delta^{13}\text{C}$  value in either lake since they were rare within in the diets of fish (Hansen et al. 2017). Additionally, we would expect the  $\delta^{13}\text{C}$  values of omnivorous, mobile crayfish to be highly biased in Keechelus because they too have responded to the rapid dewatering of littoral habitat over the previous two decades. For these reasons, the difference between  $\delta^{13}\text{C}$  values of warm water invertivore trophic-groups and coldwater planktivores sampled in Kachess, a very similar lake to Keechelus, offered the best representation of what the range between baseline  $\delta^{13}\text{C}$  values would otherwise be in Keechelus in the absence of water use or under a less intensive water use regime.

A number of additional lines of evidence support the notion that the observed truncation in the  $\delta^{13}\text{C}$  range for Keechelus relative to Kachess was driven by intensive water use and a corresponding contraction in food web structure, not a lake-specific restriction in the breadth of basal resources unrelated to water use. First, in the absence of water use, and based on differences in lake size and shape (Appendix S1: Fig. S1), the corresponding lower depth ratio (mean depth/maximum depth, Appendix S1: Table S1) of Keechelus (0.30) vs. Kachess (0.46), and the fact that each lake is clear, moderately deep, and oligotrophic, we would expect contributions of benthic carbon to whole lake primary productivity and the resultant degree of trophic diversity stemming from all basal resources to be as great or greater in Keechelus than in Kachess according to empirical and theoretical interactions among basin morphometry, nutrients, light penetration, and benthic algal growth (Vadeboncoeur et al. 2008, Hampton et al. 2011). Second, in addition to a significantly reduced carbon range estimated for Keechelus, the niche widths of all benthic-littoral warm water invertivore and piscivore trophic-groups were compressed in Keechelus relative to Kachess, whereas the niche widths of all coldwater trophic-groups (planktivores, piscivores,



and invertivores) did not differ between lakes. If our results were driven by a natural restriction in the breadth of basal resources in Keechelus, we would expect the niche widths of all coldwater trophic-groups to be compressed relative to Kachess as well. Third, water level fluctuations on the order of 1–3 m on average modify benthic-littoral communities (Evtimova and Donohue 2016) whereas Keechelus experiences rapid fluctuations that are an order of magnitude higher. Lastly, similar patterns were observed in a flood-pulse ecosystem whereby the niche widths and isotopic values of different species of fish expanded/contracted and shifted within  $\delta$ -space during the wet (when floodplain habitat was inundated thereby increasing the range of feeding habitats and or diversity in available food resources) vs. the dry season, respectively (Pool et al. 2017).

Emerging work argues for conservation strategies that go beyond protecting biodiversity and toward protecting biostructure, the network of species interactions that supports function (McCann 2007, Gray et al. 2014, Travis et al. 2014) and enables ecosystems to act as complex adaptive systems (Levin 1998). McMeans et al. (2016) recently proposed the “generalist module” as a major food web attribute underlying the adaptive capacity of lake ecosystems that repeats itself at multiple scales. At the whole-lake scale, this model formalized how increases in body size, mobility, benthic-pelagic coupling, and propensity for generalist feeding with rising trophic level create a food web architecture with high habitat partitioning (feeding in pelagic or benthic habitat) near the base by zooplankton or zoobenthos and at intermediate trophic levels by invertivorous fish, but high coupling and omnivory by top predators. Within this framework, lower trophic level dynamics get absorbed by the capacity of predators to flexibly adapt their feeding behavior which helps maintain food web stability (McCann et al. 2005, Gross et al. 2009).

The reconfiguration of Keechelus relative to Kachess provides empirical support for the inherent capacity of lake food webs to adjust structure to maintain function while under stress. The food web of both lakes also conformed to the generalist module, but we observed more apparent coupling by invertivorous fish than originally conceptualized by McMeans et al. (2016). For example, the consistent shift toward an apparent heavier reliance on pelagic primary production observed by invertivore

trophic-groups in Keechelus suggests that these fish ate more zooplankton or fed on a similar or different suite of zoobenthos fueled more by phyto-detrital carbon and less by benthic carbon when compared to Kachess. Our study was not designed to discern these types of underlying mechanisms, but it still follows that flexible feeding behavior at low-to-intermediate trophic levels enabled adaptation to trophic compression. Thus, the ability to feed in separate macrohabitat compartments by lower trophic level consumers, not just top predators, could contribute to adaptive capacity for aquatic ecosystems and should be explored further as a more prominent component of the generalist module applied at the whole-lake scale.

Structurally, persistent or amplified trophic compression from hydrologic disturbance and concentrated feeding by lake consumers on food resources fueled by more limited basal trophic diversity could have consequences for the ability of some organisms to maintain robust populations, but community-level responses may be difficult to predict, particularly in the face of ongoing environmental change (Dai 2013, Tunney et al. 2014). We should expect complex changes in fish assemblage structure owing to the synergistic effects of warming, nutrients, and water use on surface level fluctuations, primary productivity, oxy-thermal habitat, and interactions with the life history (migration and spawning), behavior (habitat use and feeding), and thermal biology (stenothermic vs. eurythermal) of species (Jeppesen et al. 2010, 2012, Evtimova and Donohue 2016, Rolls et al. 2017), particularly by the large-bodied, mobile, upper trophic level predators. In our study, the maximum trophic position of top predators in Kachess (4.57) and Keechelus (4.56) corresponded with expectations based on the size (volume) of each lake ecosystem, a strong predictor of food chain length (Post et al. 2000). However, under persistent or amplified water use, dewatering of littoral habitat, and trophic compression, potential reductions in the productivity of different prey fishes (e.g., small-bodied benthic-littoral fish that breed near-shore in spring), concentrated feeding by top predators on alternative prey, and alterations to food web interactions could erode food chain length, a process analogous to trophic downgrading which has consequences for lake ecosystem adaptive capacity, structure, and function (Estes et al. 2011, McMeans et al. 2016).

This study builds the foundation needed for more analyses evaluating the effects of intensive water use on lake ecosystems. Direct experimental manipulations of surface water elevation that persist year-after-year would be ideal, but often not feasible given the multiple competing demands for water stored in reservoirs (e.g., irrigation, municipal supply, and threatened or endangered species conservation needs). However, the differences in water use regimes (in both the timing and magnitude of water releases and drawdown) observed between Lake Kachess vs. Lake Keechelus were unique and made this study possible. Although delayed in time when compared to Keechelus, Kachess also experiences interannual variation in water use and surface level drawdown. Thus, our estimate for overall trophic compression in Keechelus (46%) is likely conservative. We are often forced to evaluate patterns over gradients in human use intensity (McCann 2007), as was done here, and we encourage the pursuit of such opportunities to further our understanding of how pervasive human disturbances like water use affect ecosystems.

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