


Use of allochthonous resources by zooplankton in reservoirs

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Abstract Aquatic food webs are supported by primary production from within the system (autochthony) as well as organic matter produced outside of and transported into the system (allochthony). Zooplankton use allochthonous resources, especially in systems with high terrestrial loading and moderate to low internal primary production. We hypothesized that due to high terrestrial loads and remnant submerged terrestrial material, allochthonous resource use by zooplankton would be significant in all reservoirs and would decline along an increasing reservoir age gradient. Using hydrogen stable isotopes and a Bayesian mixing model, we estimated the contribution of allochthonous sources to organic matter pools and crustacean zooplankton biomass for ten reservoirs. Dissolved organic matter (DOM) in all systems was dominated by allochthonous sources (posterior distribution median >92% allochthonous), while particulate organic matter (POM) composition varied (2–68% allochthonous) and had a lower allochthonous fraction in older reservoirs. There was no relationship between zooplankton allochthony and

reservoir age. Crustacean zooplankton allochthony varied among systems from 26 to 94%, and *Chaoborus* allochthony, measured in four reservoirs, was similarly variable (33–94%). Consumer allochthony was higher than POM allochthony in some reservoirs, potentially due to terrestrial DOM pathways being important and/or algal resources being inedible (e.g., cyanobacteria). As with many lakes, in the reservoirs we studied, allochthonous inputs account for a significant fraction of the organic matter of basal consumers.

Keywords Reservoirs · Zooplankton · *Chaoborus* · Deuterium · Allochthony · Bayesian mixing model

Introduction

In fresh water systems, resources for aquatic consumers have two origins: carbon that is fixed within the system by primary producers such as algae (autochthonous carbon) and carbon that is fixed by terrestrial plants within the watershed and transported into the aquatic environment (allochthonous carbon). While the magnitude and importance of allochthonous inputs have been studied in both lakes and streams (Rasmussen, 2010; Cole et al., 2011; Marcarelli et al., 2011; Cole & Solomon, 2012; Roach, 2013), allochthonous resource use in reservoir food webs has received less attention (but see Babler et al., 2011; Wilk-Woźniak et al., 2014), although a recent study

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using stable isotopes identified a positive and nearly 1:1 relationship between zooplankton and POM $\delta^{13}\text{C}$ (Jeayong et al., 2013). Use of allochthonous resources by consumers in lakes is variable but tends to be correlated with allochthonous resource availability (Solomon et al., 2011; Wilkinson et al., 2013a; Berggren et al., 2014; Tanentzap et al., 2014; Berggren et al., 2015). It is unclear if the patterns of allochthony observed in lakes are applicable to reservoirs.

Globally, the number of inland water ecosystems is increasing rapidly due to reservoir creation (Downing et al., 2006; Chao et al., 2008). A key difference between lakes and reservoirs is age as most natural lakes are thousands of years old, while most reservoirs are <100 years old (Kalff, 2002). When a reservoir is created through impoundment, the valley floods and drowns the terrestrial landscape. Greenhouse gas emissions are significantly higher in reservoirs following impoundment compared to lakes because of microbial degradation of the drowned terrestrial material (Tremblay et al., 2005; Barros et al., 2011; Brothers et al., 2012; Mendonça et al., 2012; Venkiteswaran et al., 2013). Given the patterns observed in carbon dioxide and methane emissions following impoundment, there is also potentially a relationship between consumer terrestrial resource use (consumer allochthony) and reservoir age that has not been previously explored. Terrestrially derived organic matter may be the predominant carbon source in a young reservoir, whereas over time, nutrient loading and/or eutrophication from riverine inputs may enhance the role of autochthonous primary production (Abril et al., 2005).

In addition to a difference in origin, lakes and man-made reservoirs differ in many other key characteristics which could influence terrestrial organic matter availability and use by the aquatic food web. In North America, the catchment:lake area ratio of reservoirs is three times higher than natural lakes (Kalff, 2002). The increased catchment area could potentially deliver more terrestrial material to the reservoir and also provide more opportunities for degradation and processing in the watershed (Berggren et al., 2010; Guenet et al., 2010). Reservoirs also generally receive more particulate inorganic matter than lakes from the watershed (Vorosmarty et al., 2003), which could occlude organic matter as well as decrease autochthonous production through light limitation (Knoll et al., 2003; Vanni et al., 2006). Reservoir

morphometric characteristics may also differ from natural lakes and therefore potentially control the availability and use of allochthonous material.

Organic matter in aquatic ecosystems includes particulate organic matter (POM) which can vary in composition, and a larger pool of dissolved organic matter (DOM) which is usually dominated by allochthonous material (Jaffe et al., 2008; Wilkinson et al., 2013b). Assimilation of allochthonous organic matter by bacteria is a means whereby this material becomes available to higher consumers (Karlsson et al., 2003; Jansson et al., 2007; Wilk-Woźniak et al., 2014). Direct consumption of bacteria by zooplankton is one pathway for allochthonous organic matter support of higher consumers (Cole et al., 2006; Persaud & Dillon, 2011; Taipale et al., 2014). Zooplankton can also directly consume allochthonous POM that either entered the lake in particulate form or was formed through flocculation of allochthonous DOM (von Wachenfeldt & Tranvik, 2008).

In order to assess the degree of consumer allochthony in reservoirs, we measured hydrogen stable isotopes of pelagic consumers in ten reservoirs in central Virginia along an age gradient from 23- to 88-years old. Specifically, we measured the hydrogen isotope ratios of allochthonous and autochthonous organic matter sources as well as the POM, DOM, and zooplankton which comprise a mixture of these two end members. Given the reservoir age gradient sampled, we hypothesized that zooplankton allochthony (1) would be as variable as lake ecosystems (Marcarelli et al., 2011; Wilkinson et al., 2013a) but (2) would vary along the age gradient with greater allochthonous support of zooplankton in younger reservoirs.

Materials and methods

Site description

We sampled ten reservoirs located in central Virginia (latitudinal range 37.7815–38.1639N and longitudinal range 78.7428–78.2011W) one time each in early autumn of 2013 (Table 1). At this time of year, transport of carbon from the land may be higher due to deciduous tree leaf fall, while phytoplankton production begins to decline due to colder temperatures. The dominant land cover type in the watersheds was forest and pasture.

Organic matter and consumer collection

POM samples were collected by filtering an integrated water sample of three different depths in the upper mixed layer from a central location in each reservoir. The water samples were combined for analysis to represent the surface mixed layer of the reservoirs. The upper mixed layer was defined as the depth over which the water temperature does not change by $>0.5^{\circ}\text{C}$ per meter. Particles were concentrated onto a MicroSep filter (nominal pore size = $0.8\ \mu\text{m}$), back rinsed using deionized water, and dried at 60°C . For the DOM samples, filtrate from the particle collection was acidified with $0.1\ \text{M HCl}$ and subsequently evaporated in glass petri dishes and then dried at 60°C . The POM and DOM samples were ground to a fine powder for isotopic analysis.

Zooplankton were collected from nine of the ten reservoirs by horizontally towing an $80\text{-}\mu\text{m}$ conical mesh net through the surface mixed layer. The samples consisted of a mixture of crustacean zooplankton of the order *Cladocera* (dominated by the families *Daphniidae* and *Bosminidae*) and the subclass *Copepoda* (order *Cyclopoida* and *Calanoida*) but were dominated by *Copepoda*. In four of the reservoirs, the larval stages of the dipteran *Chaoborus* spp. were present and were analyzed separately from the zooplankton sample. Net tow contents were combined with deionized water for overnight gut clearance. Samples were inspected under a dissecting microscope, and visible algal, detrital, and sediment particles were removed. *Chaoborus* were also separated from the rest of the bulk sample at this time. Both the *Chaoborus* and bulk zooplankton samples were dried at 60°C and ground to a fine powder for isotopic analysis.

End-member collection

The two end members considered in this analysis were allochthonous material and phytoplankton. The single autochthonous end member was used in this study due to the low abundance of macrophytes in these systems. For the allochthonous end member, fresh leaves from the two most common deciduous tree species (*Acer* spp. and *Liriodendron tulipifera* L.; same for all reservoirs) surrounding each reservoir were collected, dried for 48 h at 60°C , and ground to homogenize for

isotopic analysis. Leaves were collected over a small geographic range, so variability due to precipitation and other factors was likely unimportant. Other hydrogen stable isotope studies have demonstrated that fresh leaf samples from the watershed are isotopically representative of terrestrial material entering the reservoir based on comparisons with groundwater dissolved organic carbon (DOC) and leaf detritus (Solomon et al., 2011; Yang et al., 2014). The distribution of leaf values among all reservoirs was then used as the allochthonous end member in the Bayesian mixing model described below. The algal (autochthonous) end member ($\delta^2\text{H}_A$) was calculated individually for each reservoir using the equation:

$$\delta^2\text{H}_A = \delta^2\text{H}_2\text{O} + \varepsilon_H, \quad (1)$$

where $\delta^2\text{H}_2\text{O}$ is the hydrogen isotope value of the surface water in a given reservoir and ε_H is the hydrogen isotope discrimination factor. The water samples for $\delta^2\text{H}_2\text{O}$ were filtered and stored in 20-ml borosilicate vials with no headspace and refrigerated until isotopic analysis. ε_H , the isotopic discrimination factor, is determined by calculating the difference between a sample of algae and the inorganic substrate which the algae fractionates against. The ε_H used in this study was drawn from the distribution of values in Solomon et al. (2009) and Yang et al. (2014) with additional ε_H values calculated from three of the reservoirs we sampled. The three ε_H values were calculated from isolated phytoplankton samples from reservoirs in this study when phytoplankton dominated samples collected in net tows. These samples were visually inspected under a dissecting microscope and confirmed to be composed of almost entirely phytoplankton. ε_H values were calculated for the three samples using the directly measured hydrogen isotope value of the phytoplankton and $\delta^2\text{H}_2\text{O}$ (Hondula et al., 2014). The mean and standard deviation of all ε_H values ($n = 17$) were used in Eq. 1 to calculate a reservoir specific autochthonous end member for the consumer isotope mixing model. Overall, this approach combined the fractionation values from our study with literature values from other freshwater, lentic systems that used various methods of isolating phytoplankton samples. This allowed us not only to include a more robust estimate of ε_H in our model but also to include all possible information about the uncertainty in that estimate, thereby strengthening our analysis.

Hydrogen isotope analysis

Samples were analyzed for $\delta^2\text{H}$ at the Colorado Plateau Stable Isotope Laboratory (CPSIL) at Northern Arizona University. CPSIL uses the benchtop equilibration method for solid samples as described in Doucett et al. (2007). Standards include keratin, caribou and cow hoof, kudo horn, moose, bear and elk hair, baleen, feathers, and chitin, as well as *Cladophora* spp. (an alga). The analytical precision for dried organic matter replicate samples at CPSIL is 2‰ for $\delta^2\text{H}$ (M. Caron, CPSIL, Mar 2013, pers. comm.). Reported $\delta^2\text{H}$ values represent the non-exchangeable H-isotope ratio and are relative to the international standard Vienna Standard Mean Ocean Water (VSMOW). The consequences of possible differential H-exchange of measured values for the organic sources evaluated in this study is a source of variability, but this variation is likely small relative to other sources (Yang et al., 2014). $\delta^2\text{H}$ in water samples was analyzed by CPSIL using cavity ring-down laser spectroscopy.

Bayesian mixing model

A Bayesian mixing model written in R and JAGS (Just Another Gibbs Sampler), modified from Wilkinson et al. (2013a), was used to determine the contribution of allochthonous (ϕ_T) and autochthonous (ϕ_A) material to the POM, DOM, bulk zooplankton, and *Chaoborus* pools in each reservoir. For consumers, ϕ_T and ϕ_A were calculated as

$$\begin{aligned} \delta^2\text{H}_{\text{Mix}} &= (\phi_T \times \delta^2\text{H}_T + \phi_A \times \delta^2\text{H}_A) \\ &\times (1 - \omega) + \omega \times \delta^2\text{H}_2\text{O}, \\ 1 &= \phi_T + \phi_A, \end{aligned} \quad (2)$$

where $\delta^2\text{H}_{\text{Mix}}$ is the hydrogen isotope value of the mixture (either POM, DOM, bulk zooplankton or *Chaoborus*) in a given reservoir, $\delta^2\text{H}_T$ is the hydrogen isotope value of the terrestrial end member, and $\delta^2\text{H}_A$ is the hydrogen isotope value of the algal end member. The ω terms in Eq. 2 are the correction for the environmental water which is the contribution of $\delta^2\text{H}$ to consumer tissues (Solomon et al., 2009) from the surrounding environment ($\delta^2\text{H}_2\text{O}$). The ω correction values for the bulk zooplankton and *Chaoborus* (0.20 ± 0.04 and 0.14 ± 0.06 , respectively) were

from Solomon et al. (2009). We assumed that the trophic position of *Chaoborus* was 2 above primary producers and 1 for bulk zooplankton. For POM and DOM, ω was assumed to be 0. In all model runs of Eq. 2, the prior distributions of ϕ_T and ϕ_A were center log ratio transformed following Semmens et al. (2009) and Solomon et al. (2011).

Physical and chemical analyses

Physical, chemical, and biological parameters of each reservoir were also measured. Temperature and dissolved oxygen profiles were taken with a YSI ProODO handheld sensor to determine the depth of the upper mixed layer (temperature change of $<0.5^\circ\text{C}$ per meter). Water samples from the upper mixed layer were then collected for chlorophyll *a*, dissolved organic carbon (DOC), pH, color (absorbance at 440 nm), total nitrogen (TN), and total phosphorus (TP) concentrations. Chlorophyll *a* samples were filtered onto 47 mm Whatman GF/F filters and frozen. The samples were then extracted in methanol and analyzed fluorometrically (Holm-Hansen & Riemann, 1978). A portion of the filtrate was acidified with 200 μl of 0.1 M H_2SO_4 and analyzed for DOC and another portion of the filtrate was refrigerated and analyzed for color (absorbance at 440 nm). Unfiltered water was preserved with H_2SO_4 and analyzed for TN and TP after persulfate digestion. DOC, TN, and TP samples were analyzed on a Lachat QuikChem 8000 (Hach Corporation, Loveland, CO, USA) flow injection analyzer.

Reservoir depth, capacity, and age were gathered from public records and water agency personnel. Reservoir and watershed size was determined in ArcGIS using elevation data (National Elevation Data, <http://ned.usgs.gov/>), and land cover (Homer et al., 2004) in each watershed was extracted. These variables along with the chemical and biological variables described above were used in a linear regression analysis performed in R (R Core Development Team) to examine relationships between the allochthonous proportion of all carbon pools and consumers (POM, DOM, bulk zooplankton, *Chaoborus*) and the various water chemistry, physical characteristics, and watershed land cover composition measurements. All variables were examined individually.

Results

End member isotope values

The potential end members contributing to the four organic matter pools (POM, DOM, bulk zooplankton, and *Chaoborus*) were phytoplankton for the autochthonous resource and deciduous tree leaves for the allochthonous resource. The hydrogen isotope value of the allochthonous resource ($\delta^2\text{H}_T$) was $-117.6 \pm 12.23\text{‰}$ ($n = 8$). The mean and standard deviation of ϵ_H values for the three reservoirs of this study, the algal values from Solomon et al. (2009), and the isolated phytoplankton samples from Yang et al. (2014) were $-167.02 \pm 23.87\text{‰}$. In our model, we used the prior information of ϵ_H from the two previously mentioned studies in combination with the three values we measured to calculate the algal end member, specific to each reservoir based on the $\delta^2\text{H}_2\text{O}$ of epilimnetic waters. The mean $\delta^2\text{H}$ of the autochthonous end member for the ten reservoirs ranged from -206.9 to -197.2‰ .

Organic matter mixture isotope values

DOM samples were isolated for all ten reservoirs, POM and bulk (i.e. mixed crustacean) zooplankton for nine reservoirs, and *Chaoborus* for four reservoirs

(Table 2). DOM values ranged from -94.2 to -129.1‰ , POM from -147.6 to -203.6‰ , bulk zooplankton from -123.2 to -151.9‰ , *Chaoborus* from -119.3 to -144.3‰ , and water from -30.2 to -39.9‰ (Table 2). Plotting the $\delta^2\text{H}$ values of POM, DOM, zooplankton, and *Chaoborus* versus the end members (recognizing the algal end member changes with surface $\delta^2\text{H}_2\text{O}$) allowed for visual estimation of source contributions to the mixtures (Mohamed & Taylor, 2009; Fig. 1). The $\delta^2\text{H}$ values of POM were quite variable and fell between the allochthonous and autochthonous end members (mean \pm SD), while DOM $\delta^2\text{H}$ values fell near the allochthonous end member (Fig. 1a). The $\delta^2\text{H}$ values of both the bulk zooplankton and the *Chaoborus* were also quite variable and fell between the end members suggesting mixed resource use (Fig. 1b). These consumer values were used in a Bayesian mixing model to determine the contributions of allochthonous and autochthonous resources after correcting for the influence of environmental water on tissue $\delta^2\text{H}$.

Mixing model results

The fractional allochthonous contribution (ϕ_T) to both pools of organic matter, dissolved ($n = 10$) and particulate ($n = 9$), was estimated using Eq. 2. These values, hereafter reported as percentages, are the

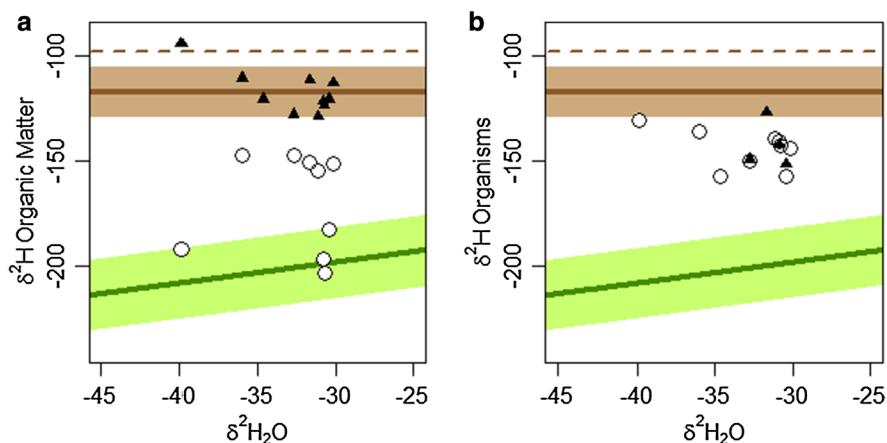


Fig. 1 The $\delta^2\text{H}$ value of POM and DOM and the mixing model end members from the ten reservoirs (abbreviations as in Table 1) versus $\delta^2\text{H}_2\text{O}$ of the surface water. **a** The algal end member (dark green line) has a slope equal to the mean ϵ_H value as algae isotopically discriminate $\delta^2\text{H}$ from $\delta^2\text{H}_2\text{O}$. The light green polygon surrounding the algal end member line is the standard deviation of the end member distribution. The

terrestrial end member (mean \pm SD; dark brown line and tan polygon) does not change with $\delta^2\text{H}_2\text{O}$ and is therefore constant across watersheds. Triangles are DOM samples and circles are POM. **b** Bulk zooplankton (circles) and *Chaoborus* (triangles) $\delta^2\text{H}$ values versus $\delta^2\text{H}_2\text{O}$. The consumer values have been corrected for environmental water

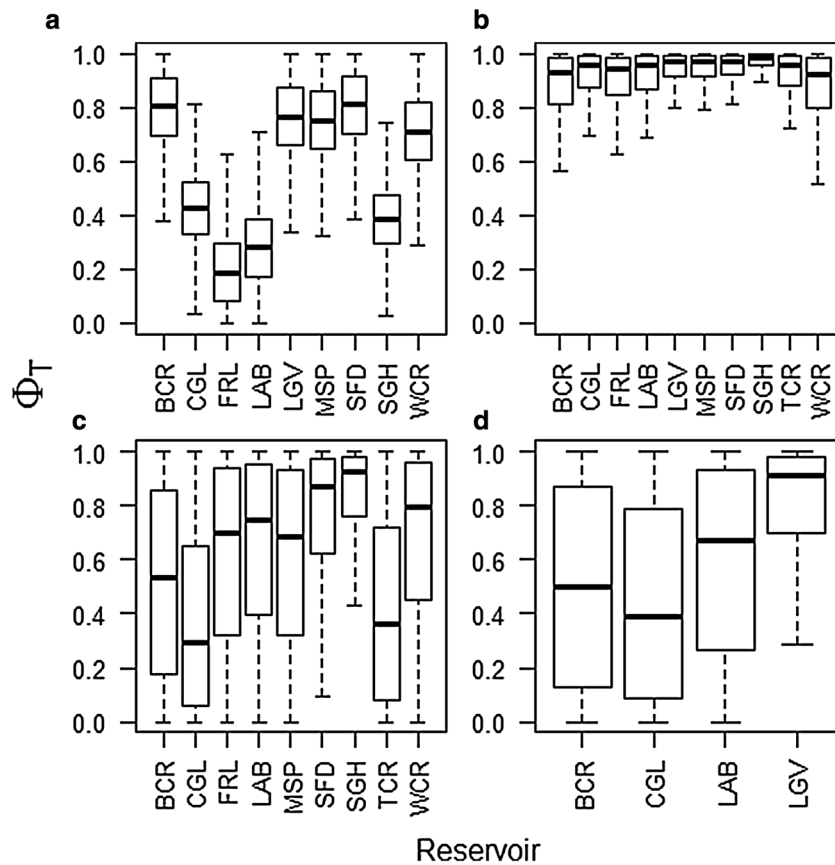


Fig. 2 Box plots of posterior distributions of modeled ϕ_T for **a** POM, **b** DOM, **c** bulk zooplankton, and **d** *Chaoborus*. Reservoir codes are given in Table 1

medians of the posterior distributions estimated by the model, though all quantiles of the posterior distribution are provided in Fig. 2. The allochthonous contribution to the POM pools of nine reservoirs ranged from 2 to 68% (Fig. 2a). There was a much smaller variation in the ten ϕ_T values of the DOM ranging from 92 to 99% (Fig. 2b). Bulk zooplankton ϕ_T values for nine reservoirs varied between systems, ranging from 26 to 94% (Fig. 2c). *Chaoborus* ϕ_T from four reservoirs also had a broad range of 33–94% (Fig. 2d).

Regression analysis

A regression analysis was performed using the biological and physical parameters measured for each reservoir (Table 1) and the median values of ϕ_T for the four organic matter pools. POM ϕ_T was marginally related to reservoir age with the hypothesized negative slope (Fig. 3; $R^2 = 0.37$, P value = 0.06,

$y = -0.01x + 0.89$). The data were too limited for further statistical regression analysis with multivariate methods. The ϕ_T of POM remained relatively constant between the ϕ_T values of 0.6–0.8 at the lower end of the reservoir age gradient, beyond which ϕ_T decreased to values ranging between 0.15 and 0.2 in older reservoirs (Fig. 3). However, we did not observe a relationship between zooplankton allochthony and the reservoir age gradient. The decrease in DOM ϕ_T with increasing surface water temperature was a significant relationship ($R^2 = 0.83$, P value < 0.001, $y = -0.005x + 1.06$). The range on DOM ϕ_T , however, was small (0.92–0.99).

POM ϕ_T was not significantly related to bulk zooplankton ϕ_T or *Chaoborus* ϕ_T (Fig. 4). Nine of the thirteen consumer estimates fell along or near the 1:1 line, indicating that in most cases POM ϕ_T was similar to consumer ϕ_T (either bulk zooplankton or *Chaoborus*). Four of the thirteen consumer ϕ_T estimates were

Table 1 Biological, chemical, and physical variables for the 10 reservoirs used in the regression analysis

Reservoir	Code	Age (years)	Surface area (ha)	Mean depth (m)	Mean capacity (m ³)	Secchi (m)	pH	Chl <i>a</i> (µg l ⁻¹)	Color (m ⁻¹)	DOC (mg l ⁻¹)	TN (µmol l ⁻¹)	TP (µmol l ⁻¹)
Beaver Creek	BCR	49	42.1	12	1.97E+06	3.2	6.8	5.1	1.2	3.2	48	0.7
Chris Greene	CGL	46	96.7	14.3	1.02E+06	2.75	7.4	4.5	1.6	3.5	28.3	0.4
Fluvanna Ruritan	FRL	57	20.2	11.4	1.10E+06	1.5	6.5	6.8	2.6	5.3	54.4	1.5
Lake Albemarle	LAB	75	14.2	7.3	4.56E+05	1.25	7.1	9.6	2.8	4.4	48.4	0.9
Lake Gordonsville	LGV	43	30.4	7	6.83E+05	0.75	6.4	11.1	7	4.4	34.2	8.9
Mint Springs	MSP	52	3.2	7.8	5.67E+04	3	6.8	6.9	1.4	4.1	23.7	0.6
S. Fork Rivanna	SFD	47	182.1	NA	NA	1.5	7	6.2	0.9	1.8	22.6	0.7
Sugar Hollow	SGH	88	19	21.9	1.63E+06	1.5	6.8	6.4	0.4	1.8	7.7	0.4
Totter Creek	TCR	42	26.7	7.3	1.08E+06	0.75	7	9.7	1.8	2.7	50.1	1.1
Walnut Creek	WCR	23	18.2	9.1	1.18E+06	1.5	7.2	5.3	1.5	3.4	20.5	0.5

Age indicates the number of years since the reservoir was inundated. For the chemical measurements, the values are means of three samples for chlorophyll *a* and pH and are individual sample results for color, DOC, TN, and TP

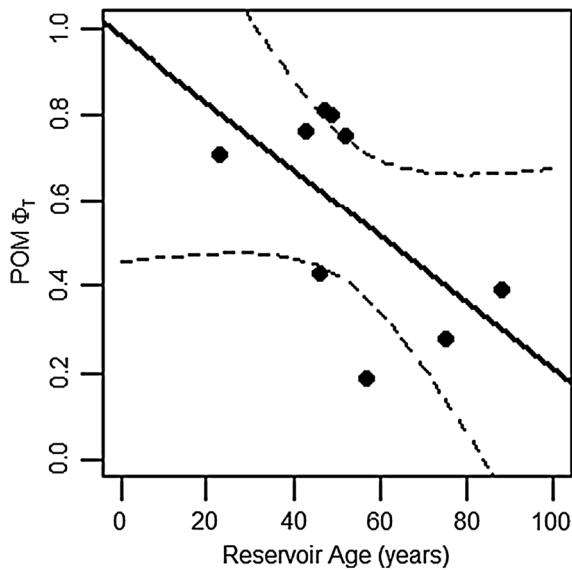


Fig. 3 Linear regression results of POM ϕ_T and reservoir age. Best-fit line (solid) and 95% confidence interval (dashed) shown. $R^2 = 0.37$, P value = 0.06, $y = -0.01x + 0.89$

substantially higher than the corresponding POM ϕ_T estimate for that system, indicating that the consumers were more allochthonous than the POM pool.

Discussion

Variability in resource and consumer allochthony

Resource use in reservoirs is relatively unexplored compared to resource use in lakes. Intersystem variability may be higher than lakes due to these systems receiving large inputs of terrestrial material in some cases while in other instances being quite eutrophic. The allochthony of consumers and organic matter in ten central Virginia reservoirs was higher than the autochthonous contribution in many cases, and similar to what has been observed in northern temperate and boreal lakes with relatively undisturbed watersheds (Cole et al., 2011; Solomon et al., 2011; Wilkinson et al., 2013a; Berggren et al., 2014; Kelly et al., 2014; Berggren et al., 2015), supporting our first hypothesis that allochthony in reservoirs is variable and similar to lakes. Three of the four pools of organic matter considered in this study—POM, bulk zooplankton, and *Chaoborus*—exhibited varying levels of allochthony, also supporting the first hypothesis.

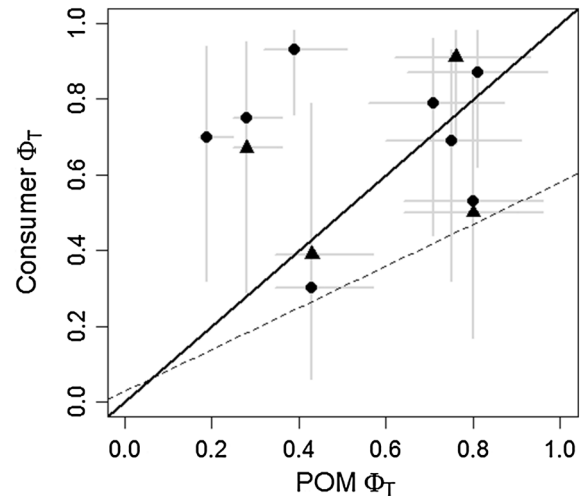


Fig. 4 The allochthonous fraction of resource pool (POM ϕ_T) versus the allochthonous fraction of the consumers (Zooplankton ϕ_T and *Chaoborus* ϕ_T ; circles and triangles, respectively). The gray lines extend from the 25% to the 75% quartiles of the posterior distributions. The solid line is the 1:1 line and the dotted line is the relationship between POM ϕ_T and *Chaoborus* ϕ_T from Wilkinson et al. (2013a) for comparison to the pattern often observed in lake ecosystems

Allochthonous organic matter contributed to over 50% of the POM in five of the nine reservoirs. The range of median values (0.02–0.68) demonstrates the variability of this pool. Similarly, POM ϕ_T is also highly variable in lakes (Pace et al., 2007; Mohamed & Taylor, 2009; Wilkinson et al., 2013b). Conversely, the allochthonous material was the dominant contribution to the DOM pool and variability among systems was low. This is similar to the allochthonous dominance of DOM in lake and riverine systems (Stets et al., 2010; Tank et al., 2011; Wilkinson et al., 2013b).

The reservoir age gradient spanned 65 years. There was a marginally significant relationship between POM allochthony and the reservoir age gradient where the allochthonous contribution to the POM pool decreased with increasing reservoir age. The POM pool in younger reservoirs is more allochthonous, potentially due to remaining material from the inundation of terrestrial habitat after dam construction in younger reservoirs and to older reservoirs having more significant sources of autochthonous organic matter (Abril et al., 2005). This pattern is also observed with respect to carbon emissions from reservoirs, which decrease over time as the initial flooded biomass pool is degraded (St. Louis et al., 2000; Barros et al., 2011; Brothers

et al., 2012; Venkiteswaran et al., 2013). The pattern among reservoir age and POM composition partially supports our second hypothesis but is based on a limited sample size and a marginal statistical test ($P = 0.06$). Further investigation is needed to examine if this pattern holds in a larger number of systems and to elucidate the source of the allochthonous material (originating in the watershed or inundated terrestrial material). There was no relationship between reservoir physical or biological characteristics and zooplankton or *Chaoborus* ϕ_T . There was a significant relationship between surface temperature and the allochthonous contribution to the DOM pool, as DOM ϕ_T was higher later in the autumn. Reservoir sampling prior to and during initial autumnal leaf drop could have influenced the magnitude and form of allochthonous organic matter entering the reservoirs, although this effect was likely small. The processing of leaf litter in the watershed leads to transport of dissolved allochthonous carbon into reservoirs (Mulholland & Hill, 1997; Berggren et al., 2010; Tanentzap et al., 2014).

The allochthonous fraction of zooplankton was variable but usually >50% in all but two reservoirs. The zooplankton in the CGL reservoir were similar isotopically to the algal POM pool, indicating POM as the likely uptake pathway (Fig. 2). Clear water systems like CGL also have lower terrestrial resource use (BCR is similar in this regard). TCR is a more eutrophic system (Table 1), and zooplankton utilize a lower allochthonous fraction in this reservoir (Fig. 2). Similarly, the four estimates of the allochthonous contribution to *Chaoborus* tissue were also all near or above 50%. The high degree of consumer allochthony as well as the variability among systems is consistent with several lake survey studies (Karlsson et al., 2003; Wilkinson et al., 2013a; Berggren et al., 2014) though not all (Mohamed & Taylor 2009; Francis et al., 2011). However, while other studies have found relationships between ecosystem size and consumer allochthony in lakes (Pace et al., 2007; Zigah et al., 2012; Wilkinson et al., 2013a) and reservoirs (Babler et al., 2011), there was no relationship in this study between zooplankton ϕ_T and any of the physical, chemical, or biological variables we measured.

Although each reservoir was sampled once over the course of this study, a wide range of conditions were captured among the various reservoirs, providing significant contrasts even with a lack of temporal sampling. Primary production was probably high in several systems as substantial algal blooms were observed during

sampling. In reservoirs with a notable algal presence, consumers preferentially consumed allochthonous organic matter in some and autochthonous organic matter in others. Algae in some of the reservoirs were likely inedible. Sample collection began on September 25, 2013 and was completed after 40 days. Although sampling occurred during the autumn season, a majority of the sampling was completed prior to the start of leaf fall, so it is unlikely that allochthonous inputs during sampling were significantly higher than during other seasons. Zooplankton tissues reflected the available resource pool from recent weeks given the likely turnover time.

Consumer allochthony pathways

POM is a complex pool of potentially available resources for zooplankton (Cole et al., 2006; Jansson et al., 2007). In many lake ecosystems, POM allochthony is greater than or equal to the allochthony of the zooplankton consumers (Wilkinson et al., 2013a; Berggren et al., 2014; Taipale et al., 2014). Similarly, Jeayong et al. (2013) identified a relationship between zooplankton and POM $\delta^{13}\text{C}$ in several reservoirs. In some of the reservoirs we studied (e.g. FRL, LAB, SGH) as well as in some of the systems summarized by Marcarelli et al. (2011), the consumers are substantially more allochthonous than the POM pool. Consumer allochthony that exceeds POM allochthony (points above the 1:1 line in Fig. 4) may occur for several reasons, including preferential use of the DOM pathway or preferential assimilation of allochthonous POM while avoiding inedible autochthonous POM. Zooplankton resource use is dependent not only on the availability of resources but also on the quality.

Dominance of a microbially mediated DOM pathway is possible (Jansson et al., 2007), as has been observed before in other lakes and reservoirs (Karlsson et al., 2003; Persaud & Dillon, 2011; Wilk-Wozniak et al., 2014). There are many possible pathways for DOM to be incorporated into the pelagic food web. For example, labile allochthonous DOM can fuel microbial growth (Jansson et al., 2007; Berggren et al., 2014) or flocculate (Von Wachenfeldt, 2008) and be grazed directly by microzooplankton and other larger taxa. In addition, raptorial feeders such as cyclopoid copepods likely exploit the DOM pathway via consumption of bacterial feeding protists (Berggren et al., 2014). Regardless of the mechanism by which DOM is being incorporated into the pelagic

Table 2 $\delta^2\text{H}$ values for surface waters and the four organic matter groups in each reservoir (NA = data not available)

Reservoir code	$\delta^2\text{H}_2\text{O}$	POM $\delta^2\text{H}$	DOM $\delta^2\text{H}$	Bulk zooplankton $\delta^2\text{H}$	<i>Chaoborus</i> $\delta^2\text{H}$
BCR	−32.7	−147.6	−128.2	−143.8	−141.4
CGL	−30.4	−182.7	−120.7	−151.9	−144.3
FRL	−30.8	−203.6	−123.7	−136.8	NA
LAB	−30.8	−196.8	−121.7	−135.1	−134.9
LGV	−31.7	−151.2	−111.9	NA	−119.3
MSP	−30.2	−151.5	−112.9	−138.2	NA
SFD	−36	−147.8	−110.6	−129.2	NA
SGH	−39.9	−192.1	−94.2	−123.2	NA
TCR	−34.7	NA	−120.8	−150.8	NA
WCR	−31.1	−155.2	−129.1	−133.5	NA

Consumer $\delta^2\text{H}$ values are not corrected for environmental water influence

food web, the DOM pool in the reservoirs was 92% or greater derived from terrestrial material, and therefore, any utilization of this carbon pool by consumers could substantially contribute to high allochthony.

The three reservoirs that were furthest from the 1:1 line (Fig. 4) were also the systems from which we were able to isolate nearly pure phytoplankton samples. These phytoplankton were large, filamentous cells, and may have been difficult for the zooplankton to ingest, thereby effectively decreasing the autochthonous POM pathway in favor of a terrestrial DOM pathway. We also observed that the POM in two of these reservoirs (LAB and SGH) was dominated by cyanobacteria (specifically heterocyst *Anabaena* spp.). Cyanobacteria are not as nutritious of a resource for zooplankton and can be inedible due to size and shape as well as being distasteful or toxic (DeMott et al., 1991; Ghadouani et al., 2003; Jeayong et al., 2013). Zooplankton and *Chaoborus* in these reservoirs enriched with cyanobacteria may have been impeded from utilizing this abundant, yet largely unsuitable resource.

As previously mentioned, seasonality may have had an impact on allochthony estimates in our study. A recent study by Wilk-Woźniak et al. (2014) identified an increase in allochthonous resource use with availability, as promoted by reservoir inflow. The availability of both allochthonous and autochthonous organic matter in reservoirs is potentially controlled by seasonal factors (temperature, light, etc.) and events such as high or low inflows from the surrounding terrestrial watershed (i.e. precipitation events). Besides the previously discussed potential difference

in pathways among reservoirs, seasonal differences during the time of sampling could contribute to the lack of an observed relationship between consumer allochthony and the physical, biological, and chemical parameters of the reservoirs. There is the potential for zooplankton resource use to change seasonally, such as from high allochthonous use in the fall and winter to autochthonous use with increased algal production in spring and summer (Grey & Jones, 2001; Taipale et al., 2008; Kankaala et al., 2010). This seasonality has been observed in the stable isotope values of consumers and their resource pools, and in some cases even indicates a decoupling between the two (Matthews & Mazumder, 2005, 2006). Isotope values of resources may turnover more rapidly than zooplankton tissue (Grey & Jones, 1999); however, there is limited knowledge of isotopic turnover rates for zooplankton and POM in natural systems (Matthews & Mazumder, 2005).

Sampling in this study was focused on among reservoir differences in resource use, not variability over time. Similar studies in lake ecosystems have identified the utility in examining carbon resource use across gradients (Karlsson et al., 2003; Lennon et al., 2006; Mohamed & Taylor, 2009; Wilkinson et al., 2013a). More recently, Berggren et al. (2014) documented both temporal and among-system variability in resource use. Although our study does not account for changes over time, such as increased autochthony with algal blooms, we do highlight that the differences among reservoirs are potentially large even over the small geographic range we considered (Table 2).

Conclusion

Allochthony of resources and consumers in temperate Virginia reservoirs was significant and similar to lakes in both magnitude and variability. For most reservoirs the four pools of organic matter considered in this study (POM, DOM, zooplankton, *Chaoborus*) were over 50% allochthonous. There was a marginally significant negative relationship between the allochthonous contribution to POM and the reservoir age gradient. This is possibly explained by the combination of a greater watershed:lake area ratio for reservoirs and the inundation of the terrestrial landscape during the creation of reservoirs. Younger reservoirs had proportionally more available allochthonous carbon for consumers to utilize, a pattern which warrants further exploration. However, we did not find the similar hypothesized relationship for consumers. Nevertheless, support of aquatic food webs by terrestrial inputs is a significant feature of these and likely other reservoir systems.

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