

Allochthonous organic matter supplements and sediment transport in a polymictic reservoir determined using elemental and isotopic ratios

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Received: 18 September 2008 / Accepted: 3 July 2009 / Published online: 21 July 2009
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Abstract Because allochthonous organic matter (OM) loading supplements autochthonous OM in supporting lake and reservoir food webs, C and N elemental and isotopic ratios of sedimenting particulate OM were measured during an annual cycle in a polymictic, eutrophic reservoir. Particulate organic C and N deposition rates were greatest during winter and lowest during spring. C:N ratios decreased through our study indicating that OM largely originated from allochthonous sources in winter and autochthonous sources thereafter. $\delta^{13}\text{C}$ were influenced by C_4 plant signatures and became increasingly light from winter through autumn. $\delta^{15}\text{N}$ indirectly recorded the OM source shift through nitrate utilization degree with maximum values occurring in May as nitrate concentrations decreased. Unlike relationships from stratified systems, $\delta^{13}\text{C}$ decreased with increasing algal biomass. This relationship suggests that minimal inorganic C fixation relative to supplies maintained photo-synthetic isotopic discrimination during productive

periods. Water column mixing likely maintained adequate inorganic C concentrations in the photic zone. Alternatively, OM isotopic composition may have been influenced by changing dissolved inorganic nutrient pools in this rapidly flushed system. $\delta^{15}\text{N}$ also recorded increased N_2 fixation as nitrate concentrations declined through autumn. Secondary sediment transport mechanisms strongly influenced OM delivery. Particulate organic C and N deposition rates were $3\times$ greater near the sediment-water interface. Isotopic ratio mixing models suggested that river plume sedimentation, sediment resuspension, and horizontal advection influenced excess sediment deposition with individual mechanisms being more important seasonally. Our findings suggest that allochthonous OM loading and secondarily-transported OM seasonally supplement phytoplankton production in productive reservoirs.

Keywords Allochthonous · Autochthonous · C:N ratios · Organic matter · Sediment resuspension · Stable isotopes

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Introduction

Organic matter (OM) produced within watersheds (allochthonous) can be transported to lakes and reservoirs where it supplements OM produced within lakes (autochthonous). The traditional paradigm of

autochthonous OM supporting aquatic food webs has recently been scrutinized. Traditional aquatic food web studies ignore large allochthonous OM loading rates of some systems or assume allochthonous OM is recalcitrant (Cole et al. 2002). Community respiration exceeds C fixation by algae in lakes worldwide (Cole et al. 1994). In these net heterotrophic systems, community respiration must be subsidized by allochthonous OM (Cole et al. 2002). Allochthonous OM supplements are thought less important in more productive systems. Algal production typically approaches or exceeds community respiration in eutrophic lakes worldwide (del Giorgio and Peters 1993, 1994). However, allochthonous OM contributions may be seasonally important in eutrophic reservoirs. Minor allochthonous contributions can maintain consumers during periods of low autochthonous production (Vander Zanden and Sanzone 2004). Temperate lake models suggest baseline respiration rates of allochthonous OM exist independently of algal production (del Giorgio et al. 1999), but bacteria rapidly respond to short periods of algal-derived DOC even in oligotrophic systems (McCallister and del Giorgio 2008). Reservoirs may receive greater allochthonous loads than lakes because of relatively large watersheds and greater inflows (Thornton 1990).

Understanding both OM transport and processing in lakes and reservoirs is critical to accurately determining global C budgets (Lehmann et al. 2002; Downing et al. 2006, 2008). Reservoir sediments accumulate 160 Tg organic C year⁻¹, roughly 4× that of natural lakes (Dean and Gorham 1998). Downing et al. (2008) estimated that medium-sized reservoirs may bury 2× more organic C than previously thought. However, little of the C fixed in lakes and reservoirs may be preserved in sediments (Meyers et al. 1984; Meyers 1994). Secondary sediment resuspension and transport mechanisms re-expose previously sedimented OM to bacterial and benthic utilization (Meyers and Eadie 1993; Meyers and Ishiwatari 1993). Therefore, C burial efficiencies of lakes and reservoirs are potentially reduced. Secondary transport of previously deposited particles complicates sediment deposition rate measurements (Bernasconi et al. 1997) and C burial calculations.

C and N elemental and isotopic ratios are routinely used to determine OM sources and biogeochemical processing in natural lakes. C:N ratio source distinctions are well-documented. Vascular land plants are

largely composed of carbohydrates, such as cellulose and lignin, for structural support though phytoplankton is not (Meyers and Ishiwatari 1993). Vascular land plants have C:N ratios ≥ 20 , whereas phytoplankton has C:N ratios between 4 and 10 (Meyers and Teranes 2001). The application of isotopic ratios to understand biogeochemical C and N cycling is complex. OM $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ have been shown to record phytoplankton productivity (Cifuentes et al. 1988; Schelske and Hodell 1995; Hodell and Schelske 1998) and nitrate utilization (Altabet and Francois 1994; Teranes and Bernasconi 2000) respectively, in marine and stratified natural lake systems. Sedimenting phytoplankton preferentially removes ^{12}C and ^{14}N from the epilimnion (Hodell and Schelske 1998). Phytoplankton becomes isotopically heavy as epilimnetic CO_2 and NO_3 concentrations are depleted because isotopic discrimination is reduced (Hodell and Schelske 1998). However, these relationships may not apply to polymictic systems due to persistent water column mixing. More studies documenting seasonal variations of OM isotopic compositions are required to understand C and N cycling (Bernasconi et al. 1997; Gu et al. 2006) particularly in polymictic systems.

Additionally, system differences between reservoirs and natural lakes may complicate application of stable isotope techniques, which were largely advanced from natural lakes, to reservoirs. Reservoirs have been called “river-lake hybrids” because they possess intermediate characteristics between rivers and natural lakes concerning morphology/hydrology, primary nutrient sources (external loading versus internal recycling), and primary OM sources (allochthonous versus autochthonous; Kimmel et al. 1990). Reservoirs tend to be more spatiotemporally dynamic than natural lakes of similar size. Reservoirs exhibit longitudinal gradients in environmental conditions resulting from morphology/hydrology with many reservoirs also displaying vertical gradients attributed to thermal stratification which predominate in natural lakes (Kennedy and Walker 1990). Often, reservoirs receive large, pulsed inflows that result in extreme, irregular water level fluctuations and rapid, variable water retention times (WRT; Wetzel 1990). Thus, models developed from natural lakes should be applied cautiously to reservoirs (Wetzel 1990). Lind et al. (1993) demonstrated difficulties associated with applying natural lake trophic-state classification

methods to reservoirs. They suggested that short WRT was likely the most important factor explaining these difficulties. Similar difficulties may complicate the use of stable isotopes to determine phytoplankton productivity. Also, stable isotope models assume that OM is primarily comprised of phytoplankton (Schelske and Hodell 1995). OM source distinctions may mask productivity relationships in reservoirs due to enhanced sediment loading from watersheds.

In this study, we investigated OM sources and secondary sediment transport mechanisms during an annual cycle in a shallow ($Z_{\text{mean}} = 6.4$ m), polymictic, eutrophic reservoir. We hypothesized that sedimenting particulate organic matter (SPOM) primarily originated from allochthonous sources in winter/spring and autochthonous sources in summer/autumn. We also hypothesized that enhanced SPOM deposition near the sediment-water interface (SWI) was more strongly influenced by surface sediment resuspension in winter/spring and horizontal advection of autochthonous OM in summer/autumn. Particulate organic C (POC) and N (PON) deposition rates, C:N ratios, and C and N stable isotopic composition of SPOM were measured to test these hypotheses. We identify and comment on complications associated with applying stable isotope techniques to reservoirs

and propose sampling strategies to account for these difficulties.

Methods

Study site

Waco Reservoir (31°34'28"N 97°13'13"W) is a eutrophic, polymictic reservoir located near the western city-limits of Waco, McLennan County, Texas, USA (Fig. 1). Morphometric and watershed characteristics are summarized in Table 1. The calculated water residence time during our study (0.47 year) was longer than the 20 years average water residence time. Chemical characteristics are summarized in Table 2. The North Bosque River watershed provides ~75% of reservoir inflow (Lind and Barcena 2003). North Bosque River discharge (USGS Gauge Station No. 08095200; USGS Water Data for USA 2008) and Waco Reservoir water surface elevation (US Army Corps of Engineers-Ft. Worth District Hydrologic Data on Ft. Worth District Lakes 2008) are displayed in Fig. 2. Additional small tributaries include the Middle and South Bosque Rivers and Hog Creek. Predominate landuses include rangeland in the North

Fig. 1 Waco Reservoir map indicating sampling stations. The upper inset map indicates McLennan County, Texas. The lower inset map with associated scale bar indicates sediment trap (circle) and sediment core (star) locations

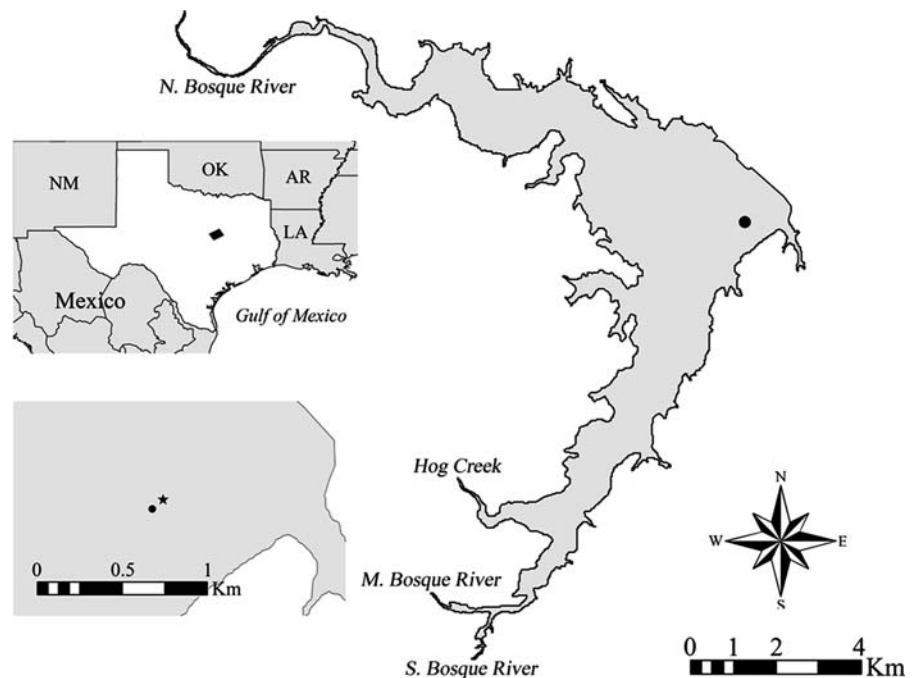


Table 1 Morphometric and watershed characteristics of Waco Reservoir, McLennan County, Texas, USA

| Characteristic | Value |
|---|--------|
| Conservation pool elevation (MSL) | 141 |
| Surface area ($\times 10^7$ m ²) | 3.53 |
| Mean depth (m) | 6.4 |
| Maximum depth (m) | 21.9 |
| Volume ($\times 10^8$ m ³) | 2.26 |
| Water residence time (year) ^a | 0.37 |
| Perimeter ($\times 10^5$ m) | 1.12 |
| Watershed area ($\times 10^3$ ha) | 423.82 |
| Watershed/water area | 120 |

^a Calculated as 20 years average (1980–2001 excluding 1990 and 1991 when river discharge was not recorded)

Table 2 Chemical characteristics of Waco Reservoir between October 2003 and September 2004

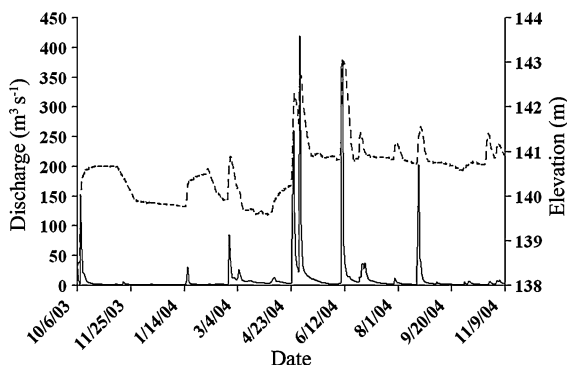
| Characteristic | Value |
|--|--|
| pH | 8.2 ^a (7.7–8.4) |
| Total alkalinity (mg CaCO ₃ l ⁻¹) | 161 ^b (119–167 ^c) |
| Total N (mg l ⁻¹) | 1.10 (0.52–1.92) |
| NO ₃ ⁻ (mg l ⁻¹) | 0.39 (0.02–1.04) |
| Total P (mg l ⁻¹) | 0.10 (0.02–0.62) |
| Chlorophyll <i>a</i> (μg l ⁻¹) | 10.8 (5.5–16.6) |
| Turbidity (NTU) | 7.5 (3.1–11.5) |

Values reported as averages and ranges (in parentheses) of monthly samples collected at sediment trap location (0.3 m depth; Scott et al. 2008)

^a Value reported as median

^b 1996 value reported by Rendón-López (1997)

^c 1976–1979 values reported by Lind (unpublished data)

**Fig. 2** North Bosque River discharge (solid line) and Waco Reservoir water surface elevation (broken line) during our study

Bosque River watershed and row-crop agriculture and rangeland in the remaining watersheds (Dworkin 2003). Numerous dairy operations occur near the North Bosque River headwaters. Six municipalities discharge treated wastewater into the North Bosque River above the reservoir. Water column mixing is holomictic (Lind 1971) although brief periods of thermal stratification have been reported (Kimmel and Lind 1972). Based on phytoplankton productivity, Waco Reservoir was classified soon after impoundment as eutrophic (Kimmel and Lind 1972) and later as mesotrophic (Lind 1986). Phosphorus has been identified as the primary limiting nutrient (McFarland et al. 2001) with short periods of N limitation occurring during late summer (Scott et al. 2008). Light limitation of phytoplankton productivity resulting from high inorganic turbidity (i.e. clays) has been reported (Lind 1986; Rendón-López 1997).

Organic matter sources

Sedimenting particulate matter was collected by buoy-carried, anchored duplicate sediment traps. Sediment traps were deployed semi-monthly or monthly for approximately 1 week duration from November 2003 to October 2004 (Fig. 1). Cylindrical sediment traps, which had a 10:1 height-to-diameter ratio, were not treated with anti-microbial agents or preservatives. Little OM (~10%) is lost through mineralization by bacteria with exposure times of 1 week (Bloesch and Burns 1980). Sediment traps were suspended at four meters, which represents the average photic depth of Waco Reservoir's lacustrine region, and at one meter above the SWI. Photic sediment traps were intended to collect primary sedimentation of autochthonous and allochthonous particles. Bottom sediment traps were intended to collect the aforementioned particles and material experiencing secondary transport within the reservoir. Secondary transport mechanisms include surface sediment resuspension, horizontal advection (i.e. sediment focusing), and river plume sedimentation (Hilton et al. 1986; Ford 1990).

Sediment slurry samples were dried at 104°C, powdered, and treated to remove inorganic carbon (i.e. calcite) prior to analyses. HCl (~1.2 N) was slowly added to dry sediments until complete removal of inorganic carbon as indicated by effervescence termination (Vreca and Muri 2006). After adequate rinsing with de-ionized water, samples were dried at

104°C until reaching constant weight. POC and PON concentrations (weight percent) and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were analyzed by an Elemental Analyzer coupled to an Isotope Ratio Mass Spectrometer (EA–IRMS). POC and PON deposition rates were calculated as the product of elemental concentrations and bulk sediment deposition rates (Teranes and Bernasconi 2000; Lehmann et al. 2004b). C:N values were reported as atomic ratios. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were reported versus the Pee Dee Belemnite carbonate standard (V-PDB) and atmospheric N_2 (AIR) respectively.

Sediment transport mechanisms

Bernasconi et al. (1997) created two-variable mixing models to determine which secondary sediment transport mechanism(s) (sediment resuspension, sediment lateral transport, and allochthonous organic matter loading) contributed to excess POC and PON deposition. Although several mechanisms may concurrently contribute to sediment deposition (Hilton et al. 1986), we were able to begin distinguishing among primary processes influencing deposition seasonally in this polymictic reservoir. We defined excess sediment deposition as bottom minus photic sediment trap deposition rates. To determine relative contributions of resuspended OM, we used the following equation:

$$\delta_{\text{Bottom}} = \delta_{\text{Photic}} \times \text{Prct}_{\text{Photic}} + \delta_{\text{Sediment}} \times \text{Prct}_{\text{Sediment}}$$

where

$$\text{Prct}_{\text{Photic}} + \text{Prct}_{\text{Sediment}} = 1$$

and δ_{Bottom} is the predicted isotopic composition in bottom sediment traps, and δ_{Photic} and δ_{Sediment} are observed isotopic compositions in photic sediment traps and surface sediments respectively. δ_{Sediment} was determined from the upper 1.5 cm of a sediment core extracted in July 2004 (Fig. 1). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were analyzed as previously described for sediment trap samples. $\text{Prct}_{\text{Photic}}$ is the percent contribution of photic to bottom sediment trap deposition (i.e. photic divided by bottom sediment trap deposition rates), and $\text{Prct}_{\text{Sediment}}$ is the percent contribution of excess sediment to bottom sediment trap deposition (i.e. [bottom minus photic sediment trap deposition rates] divided by bottom sediment trap deposition rates). Sediment resuspension influences excess material

deposition when predicted and observed SPOM isotopic compositions in bottom sediment traps are correlated. To determine relative contributions of horizontally-transported autochthonous material, we re-arranged the aforementioned equation:

$$\delta_{\text{Sediment}} = [\delta_{\text{Bottom}} - (\delta_{\text{Photic}} \times \text{Prct}_{\text{Photic}})] \times \text{Prct}_{\text{Sediment}}^{-1}$$

where variables are defined as previously stated except δ_{Sediment} is the predicted SPOM isotopic composition of surface sediments, and δ_{Bottom} is the observed SPOM isotopic composition in bottom sediment traps. In the latter equation, δ_{Sediment} and $\text{Prct}_{\text{Sediment}}$ refer to isotopic compositions and percent contributions of excess material regardless of source. Specifically, these variables refer to excess material primarily originating from autochthonous sources because we compared predicted values of excess material to observed compositions in photic sediment traps. Horizontal advection in the water column influences excess material deposition when predicted excess material isotopic compositions and observed isotopic compositions in photic sediment traps are correlated. We used the term horizontal advection to replace lateral transport as originally used by Bernasconi et al. (1997) to remove ambiguity. Lateral transport may be interpreted as material movement from the littoral to profundal zones. We defined horizontal advection as sediment movement along the reservoir's longitudinal flow axis. These mixing models assume that carbon and nitrogen isotopic compositions of SPOM are not altered (Cifuentes et al. 1988; Bernasconi et al. 1997).

Statistical considerations

We performed statistical analyses using SPSS 16.0 software (SPSS Inc.). Outliers (values outside of three standard deviations from the mean) were excluded from statistical analyses. We tested for differences between photic and bottom sediment traps for all variables using paired samples *t*-tests ($\alpha = 0.05$). Normality of data distributions were determined by the Shapiro-Wilk test statistic based on our low sample size (i.e. $N < 200$). Paired variables were transformed as required to meet normality assumptions. Mean differences and standard deviations were expressed as untransformed

variable units, while significance testing was performed using normalized variables.

Results

Organic matter sources

POC and PON deposition rates and SPOM C:N ratios are presented in Fig. 3. We identified the January sample in photic sediment traps as an outlier based on C:N ratios (16.26; Fig. 3c). Although reasons for this value are unknown, it may have been influenced by a small North Bosque River discharge peak and resulting 12 cm lake-level rise (Fig. 2). We excluded January samples from statistical analyses for POC and PON deposition rates and C:N ratios. POC deposition rates varied temporally from 388 to 2,433 and 868 to 11,231 $\text{mg C m}^{-2} \text{ day}^{-1}$ in photic and bottom sediment traps respectively (Fig. 3a). PON deposition rates varied from 47 to 266 and 118 to 1,055 $\text{mg N m}^{-2} \text{ day}^{-1}$ in photic and bottom sediment traps respectively (Fig. 3b). During winter (November–February), POC and PON deposition rates were typically greater and more variable than other seasons (Fig. 3a, b). Bottom sediment traps collected more POC and PON relative to photic sediment traps in winter. POC and PON deposition rates were typically lowest during spring (March–May) and were most similar between photic and bottom sediment traps. However, photic and bottom sediment traps collected more POC and PON in April compared to other spring samples. During summer/autumn (June–October), POC and PON deposition rates were slightly greater in photic sediment traps and 2 \times greater in bottom sediment traps relative to spring. SPOM C:N ratios varied temporally from 7.82 to 11.76 and 7.81 to 12.61 in photic and bottom sediment traps, respectively (Fig. 3c). C:N ratios generally decreased throughout the study with exponential ($r^2 = 0.59$, $p < 0.001$) and linear ($r^2 = 0.37$, $p = 0.003$) functions best describing trends in photic and bottom sediment traps respectively. April samples, which had maximum C:N ratios for both photic and bottom sediment traps, deviated from these general trends.

Sedimenting particulate organic matter (SPOM) C and N isotopic compositions are displayed in Figs. 4 and 5. $\delta^{13}\text{C}$ varied temporally from -31.92 to

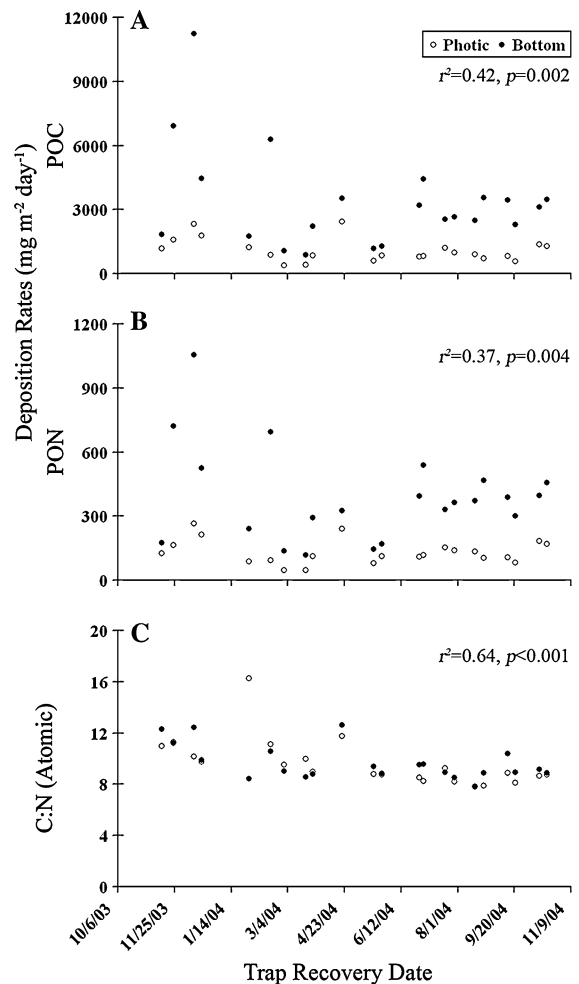


Fig. 3 Seasonal variation of **a** particulate organic carbon and **b** particulate organic nitrogen deposition rates and resulting **c** C:N ratios of sedimenting particulate organic matter in photic (open circles) and bottom (closed circles) sediment traps. Coefficients of determination and probability values for significant correlations ($p < 0.05$) between photic and bottom sediment trap data have been included. January samples were excluded from analyses because the photic sediment trap C:N ratio was identified as an outlier

-24.68‰ and -31.31 to -23.41‰ in photic and bottom sediment traps, respectively (Fig. 4a). $\delta^{15}\text{N}$ varied from 9.29 to 12.20 and 8.88 to 11.76 ‰ in photic and bottom sediment traps respectively (Fig. 4b). $\delta^{13}\text{C}$ decreased throughout the study with linear functions best describing trends in photic ($r^2 = 0.81$, $p < 0.001$) and bottom ($r^2 = 0.75$, $p < 0.001$) sediment traps (Fig. 4a). Beginning in June, $\delta^{13}\text{C}$ decreased more rapidly and reached minima in August in both photic and bottom sediment traps. $\delta^{15}\text{N}$ decreased from

November to January in both photic and bottom sediment traps (Fig. 4b). $\delta^{15}\text{N}$ increased from January to April before becoming dramatically heavier in May. Photic sediment trap $\delta^{15}\text{N}$ decreased from May to October. During this period, bottom sediment trap $\delta^{15}\text{N}$ varied widely and reached a minimum in August. Samples separated temporally based on seasonal isotopic composition differences (Fig. 5). Winter/spring samples were isotopically heavy and light for C and N respectively, whereas summer/autumn samples were isotopically light and heavy for C and N respectively. Bottom sediment trap samples from June were exceptions and clustered with winter/spring samples.

Sediment transport mechanisms

Particulate organic C (POC) and PON deposition rates were approximately $3\times$ higher in bottom sediment traps than in photic sediment traps (Table 3). Annual mean differences between bottom and photic sediment

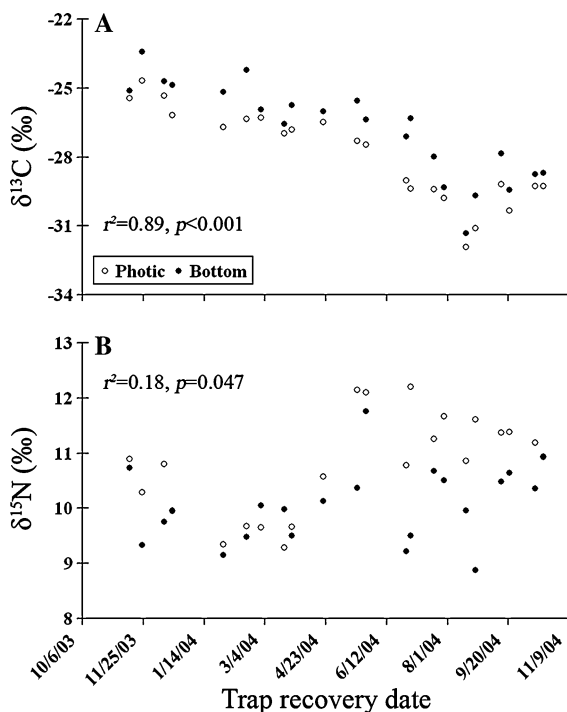


Fig. 4 Seasonal variation of **a** C and **b** N isotopic compositions of sedimenting particulate organic matter in photic (open circles) and bottom (closed circles) sediment traps. Coefficients of determination and probability values for significant correlations ($p < 0.05$) between photic and bottom sediment trap data have been included

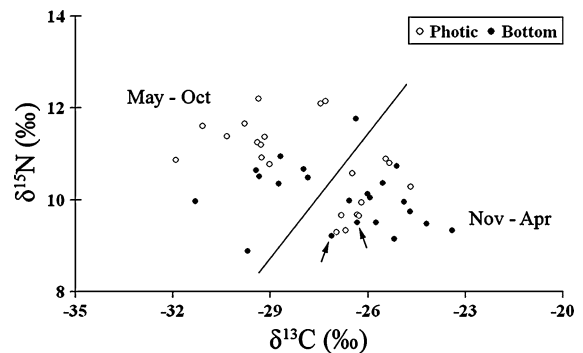


Fig. 5 Scatterplot of N versus C isotopic compositions of sedimenting particulate organic matter in photic (open circles) and bottom (closed circles) sediment traps. Winter/spring samples occurred to the right of the line, while summer/fall samples occurred to the left. The two arrowed samples from 6/28 and 7/2 were exceptions

traps were statistically significant ($p < 0.001$ for both POC and PON; Table 4). Deposition rates in photic and bottom sediment traps were significantly correlated for both POC ($r^2 = 0.42$, $p = 0.002$) and PON ($r^2 = 0.37$, $p = 0.004$; Fig. 3a, b). C:N ratios were greater in bottom sediment traps than in photic sediment traps (Table 3). C:N ratios were significantly different between paired sediment traps ($p = 0.030$; Table 4). However, annual mean differences varied greatly with respect to the mean ($\text{CV} = 198\%$). C:N ratios were significantly correlated ($r^2 = 0.64$, $p < 0.001$) in photic and bottom sediment traps (Fig. 3c).

Predicted C and N isotopic compositions in bottom sediment traps are presented in Fig. 6. Predicted $\delta^{13}\text{C}$ were significantly correlated ($r^2 = 0.80$, $p < 0.001$) to observed values in bottom sediment traps (Fig. 6a). Predicted and observed $\delta^{15}\text{N}$ in bottom sediment traps were significantly correlated ($r^2 = 0.46$, $p < 0.001$; Fig. 6b). Paired values were not significantly different between sediment traps for $\delta^{13}\text{C}$ ($t = -0.511$, $\text{DF} = 21$) and $\delta^{15}\text{N}$ ($t = -1.530$, $\text{DF} = 21$). Predicted $\delta^{13}\text{C}$ underestimated observed values during winter (November–February) but overestimated observed values during summer/autumn (July–October; Fig. 6a). There was generally close agreement between values during spring through early summer (March–June). Predicted $\delta^{15}\text{N}$ tended to overestimate observed values during winter through late summer (November–August) and underestimated observed values thereafter (Fig. 6b). The four largest

Table 3 Particulate organic carbon (POC) and particulate organic nitrogen (PON) deposition rates, C:N ratios, and C and N isotopic compositions of sedimenting particulate organic matter in photic (4 m depth) and bottom (1 m above sediment surface) sediment traps

| | Deposition rates | | C:N ^a (atomic) | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) |
|-------------|--|--|---------------------------|---------------------------|---------------------------|
| | POC ^a (mg C m ⁻² day ⁻¹) | PON ^a (mg N m ⁻² day ⁻¹) | | | |
| Photic trap | 1,080 ± 558 | 133 ± 58 | 9.3 ± 1.2 | −27.56 | 10.84 |
| Bottom trap | 3,429 ± 2,377 | 398 ± 225 | 9.7 ± 1.4 | −26.34 | 9.92 |
| Sediment | | | | −25.99 ^b | 9.83 ^b |

POC and PON deposition rates and resulting C:N ratios were calculated as annual averages ± standard deviations. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were calculated as annual weighted averages relative to POC and PON deposition rates respectively. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are reported in conventional δ -notation versus the Pee Dee Belemnite carbonate standard (V-PDB) and atmospheric N₂ (AIR) respectively

^a January samples excluded from calculations (see text for explanation)

^b Obtained from homogenized upper 1.5 cm of sediment core

Table 4 Paired samples *t*-test analyses of particulate organic carbon and particulate organic nitrogen deposition rates, C:N ratios, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for photic versus bottom sediment traps

| | Deposition rates | | C:N ^a (atomic) | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) |
|----------------|--|--|---------------------------|---------------------------|---------------------------|
| | POC ^a (mg C m ⁻² day ⁻¹) | PON ^a (mg N m ⁻² day ⁻¹) | | | |
| Mean diff. | 2,349 | 265 | 0.42 | 1.11 | −0.74 |
| SD | 2,061 | 196 | 0.83 | 0.69 | 0.87 |
| <i>p</i> value | <0.001 ^b | <0.001 ^b | 0.030 ^c | <0.001 | 0.001 |

Mean differences were calculated with respect to bottom sediment traps with positive values indicating greater/heavier values and negative values indicating lesser/lighter values

^a January samples excluded from calculations (see text for explanation)

^b Calculated using log₁₀ transformed data

^c Calculated using inverse transformed data

differences in $\delta^{15}\text{N}$ between photic and bottom sediment traps occurred from May through August.

Predicted C and N isotopic compositions of excess SPOM are displayed in Fig. 7. Excess material was defined as material collected in bottom sediment traps that was additional to material collected in photic sediment traps (i.e. bottom minus photic sediment trap deposition rates). Predicted excess material $\delta^{13}\text{C}$ and observed values in photic sediment traps were significantly correlated ($r^2 = 0.75$, $p < 0.001$; Fig. 7a). Predicted excess material was always enriched in ^{13}C compared to photic sediment trap SPOM. Predicted excess material $\delta^{15}\text{N}$ and observed values in photic sediment traps were not correlated ($\alpha = 0.05$; Fig. 7b). Predicted excess material was typically depleted in ^{15}N compared to photic sediment trap SPOM with the largest differences occurring from May through August.

Discussion

Organic matter sources

C:N ratios indicated that allochthonous sources contributed substantially to SPOM in Waco Reservoir during our study. Annual average C:N ratios and maxima in photic (9.3 ± 1.2 and 11.8 respectively) and bottom (9.7 ± 1.4 and 12.6 respectively; Table 3; Fig. 3c) sediment traps were near upper limits of typical phytoplankton C:N ratios (4–10; Meyers and Teranes 2001). For comparison, Pyramid Lake (Nevada, USA) surface sediments had C:N ratios of 6.7–11.5 in areas where algae contributed 90% of bulk organic C to the water column (Tenzer et al. 1997). We likely underestimated basin-wide allochthonous OM contributions because our sampling station was located at distance from river input (Fig. 1). OM is

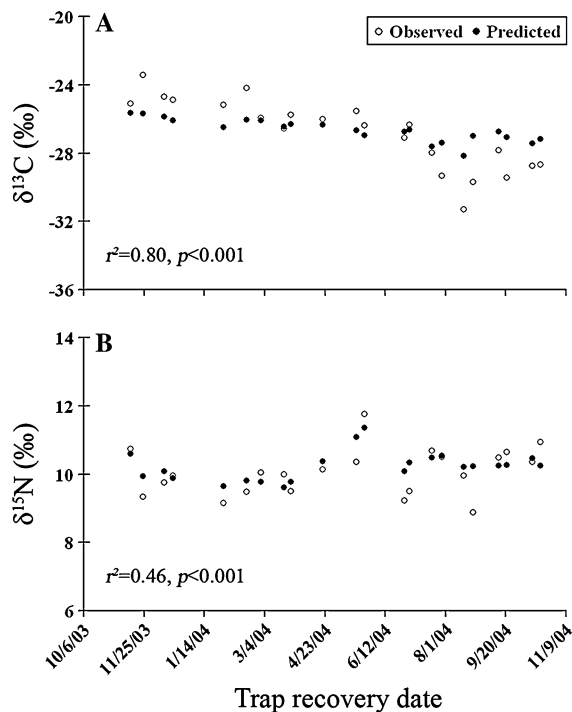


Fig. 6 Time-series of **a** C and **b** N isotopic compositions of sedimenting particulate organic matter observed in bottom sediment traps (*open circles*) and predicted isotopic compositions based on isotopic compositions of organic matter in photic sediment traps and surface sediments (*closed circles*). Coefficients of determination and probability values for significant correlations ($p < 0.05$) between observed and predicted values have been included

primarily supplied by allochthonous sources in reservoir riverine zones and by autochthonous sources in reservoir lacustrine zones (Kimmel et al. 1990). Also, surface sediments had larger C:N ratios closer to allochthonous OM input points (i.e. near shore) in Lake Victoria (East Africa; Talbot and Lærdal 2000). A sampling strategy with stations located within riverine, transition, and lacustrine zones would be required to adequately characterize allochthonous OM delivery to Waco Reservoir. Although large allochthonous OM loading indicates the potential for net heterotrophy in Waco Reservoir, we did not investigate incorporation of allochthonous organic matter into food webs.

C and N elemental and isotopic ratios supported our hypothesis that SPOM primarily originated from allochthonous sources in winter/spring and autochthonous sources in summer/autumn. Large SPOM compositional changes were implied by widely varying

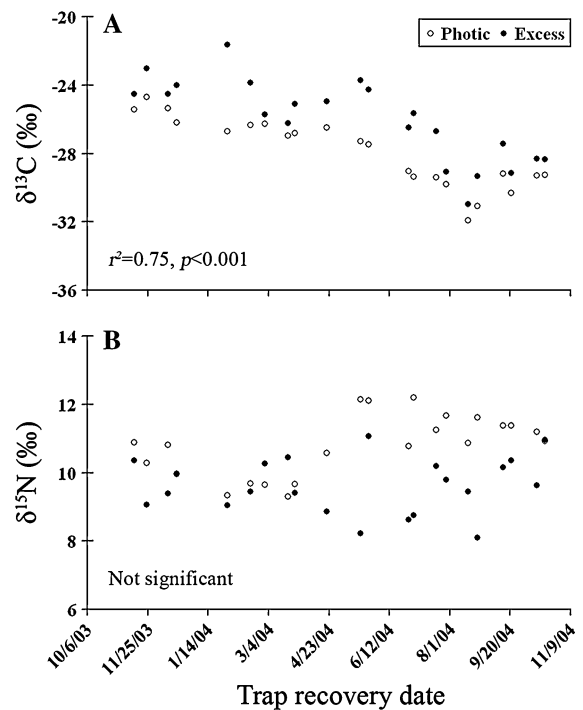


Fig. 7 Time-series of **a** C and **b** N isotopic compositions of sedimenting particulate organic matter observed in photic sediment traps (*open circles*) and predicted isotopic compositions of excess organic matter required to obtain observed values in bottom sediment traps (*closed circles*). Excess organic matter was defined as the fraction of organic matter remaining after organic matter in photic sediment traps had been subtracted. Coefficients of determination and probability values for significant correlations ($p < 0.05$) between observed and predicted values have been included

C:N ratios (7.8–12.6; Fig. 3c). Decreasing C:N ratios during our study identified a seasonal SPOM compositional shift with allochthonous OM composing more of SPOM in winter relative to autumn (Fig. 3c). C and N isotopes also suggested seasonal SPOM compositional shifts with SPOM being ^{13}C -enriched and ^{15}N -depleted in winter/spring relative to summer/autumn samples (Fig. 5). $\delta^{13}\text{C}$ generally decreased from winter through autumn with accelerated decreases beginning in June and an annual minimum in August (Fig. 4a). This trend likely tracks declining allochthonous OM contributions and associated C_4 plant signatures (isotopic shifts of -8 to -12‰) relative to the algae (isotopic shifts of approximately -20‰ ; Meyers and Ishiwatari 1993). During our study, lake-wide chlorophyll *a* concentrations increased beginning in late-March and remained

elevated from April through September (average \pm SD = $16.0 \pm 1.8 \mu\text{g l}^{-1}$) with the exception of August ($8.0 \mu\text{g l}^{-1}$; Scott et al. 2008) therefore supporting this claim. $\delta^{15}\text{N}$ indirectly recorded SPOM source shifts through water column nitrate utilization. Near-minimum $\delta^{15}\text{N}$ in January increased gradually through April before dramatically increasing in May (Fig. 4b), which coincided with a period of nitrate depletion reported by Scott et al. (2008). Algae are enriched in ^{15}N as nitrate pools are depleted and increasingly ^{15}N -enriched (Hodell and Schelske 1998). Our results counter the suggestion that $\delta^{15}\text{N}$ may not record nitrate utilization in eutrophic lakes (Lehmann et al. 2004a).

Interestingly, relationships between algal productivity and C isotopic compositions in Waco Reservoir appeared to contrast those advanced from stratified natural lakes (Bernasconi et al. 1997; Hodell and Schelske 1998; Hollander and Smith 2001; Lehmann et al. 2004a) and estuaries (Cifuentes et al. 1988). Although we lack seasonal productivity data, we know that algal biomass was elevated from April through September (Scott et al. 2008). We assumed that algal photosynthetic rates increased with increasing algal biomass, higher summer/autumn temperatures, and improved summer photic conditions. If this assumption held true, SPOM $\delta^{13}\text{C}$ became lighter with increased productivity. In stratified systems, epilimnetic DIC pools are enriched in ^{13}C as settling algae preferentially utilize and export ^{12}C to the hypolimnion (Hodell and Schelske 1998; Lehmann et al. 2004a). Algae become isotopically heavy because photosynthetic isotope fractionation decreases as CO_2 becomes limiting (Hodell and Schelske 1998; Lehmann et al. 2004a). These Rayleigh fractionation models require reactant quantities to be finite (Teranes and Bernasconi 2000) and are not valid when reactants are continuously replenished (Teranes and Bernasconi 2000). In polymictic systems, algae may continue to preferentially assimilate ^{12}C during highly productive periods because strong holomictic circulation patterns likely prevent ^{12}C draw-down. In Waco Reservoir, total alkalinity concentrations and pH indicate that DIC pools are abundant with bicarbonate as the primary DIC species (Table 2). Teranes and Bernasconi (2000) presented a similar argument in suggesting that $\delta^{15}\text{N}$ may not identify nitrate utilization degree when only small portions of DIN pools are consumed.

Alternatively, SPOM $\delta^{13}\text{C}$ may have been influenced by changing DIC isotopic compositions in Waco Reservoir. SPOM $\delta^{13}\text{C}$ decreased throughout our study (Fig. 4a) unlike the annual cycles typical of natural lakes. Because of Waco Reservoir's short water residence time (0.47 year during our study), DIC isotopic compositions may have drastically changed during our study. We cannot assume consistent DIC $\delta^{13}\text{C}$, which weakens our proposed relationships between algal productivity and OM isotopic compositions in polymictic reservoirs. In contrast, studies in Lake Ontario benefited from the assumption of conservative ion chemistry between years based on Lake Ontario's long water residence time (7 years; Schelske and Hodell 1991; Hodell and Schelske 1998). Variable DIC isotopic compositions likely complicate phytoplankton productivity relationships in most reservoirs, which are characterized by relatively short water residence times compared to natural lakes (Kennedy and Walker 1990). Future reservoir studies involving stable isotopes should measure DIC $\delta^{13}\text{C}$ concurrently with algae $\delta^{13}\text{C}$ to accurately determine photosynthetic isotopic fractionation.

Also, widely variable inflow rates and dissolved inorganic nutrient isotopic compositions may complicate stable isotope studies in reservoirs. Relatively large, irregular water level fluctuations are characteristic of reservoirs compared to natural lakes (Wetzel 1990). Waco Reservoir experienced two large North Bosque River discharge peaks (261 and $419 \text{ m}^3 \text{ s}^{-1}$) and a subsequent lake-level rise following April's sampling (Fig. 2). SPOM compositions differed seasonally along this timeframe with ^{13}C -enriched, ^{15}N -depleted SPOM during low water elevation (November–April) and ^{13}C -depleted, ^{15}N -enriched SPOM during high water elevation (May–October; Fig. 5). The only exceptions to this seasonal clustering were bottom sediment trap samples from June which clustered with winter samples (See arrowed samples, Fig. 5). June sampling was preceded by two discharge peaks (380 and $38 \text{ m}^3 \text{ s}^{-1}$; Fig. 2) which likely delivered large allochthonous OM loads to Waco Reservoir. $\delta^{15}\text{N}$ values of algae ($+8\text{‰}$) and land plants ($+1\text{‰}$) differ because they retain nitrogen source distinctions (Meyers and Ishiwatari 1993). While we hypothesize that seasonal differences resulted from differing allochthonous OM contributions, we cannot discredit

the claim that differences may have been strongly influenced by differing isotopic compositions of North Bosque River inflow. Future studies should include $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses of dissolved inorganic nutrient pools in major tributaries as well as those in the lake proper to remove this bias.

Sedimenting particulate organic matter (SPOM) N isotopic composition was likely influenced by cyanobacterial N_2 fixation during our study. Waco Reservoir experiences large seasonal cyanobacterial blooms of *Anabaena* sp. Photic sediment trap $\delta^{15}\text{N}$ decreased from May through October (Fig. 4b) suggesting increased utilization of atmospheric N_2 by algae during summer. Our observations agree with documented increased N_2 fixation rates during July through September (Scott et al. 2008). Atmospheric N_2 and DIN have $\delta^{15}\text{N}$ values of 0 and +7–10‰ respectively (Peters et al. 1978; Meyers and Ishiwatari 1993). Low algal $\delta^{15}\text{N}$ values have been attributed to N_2 fixation by cyanobacterial blooms (Gu et al. 1996, 2006; Scott et al. 2007). As summer nitrate concentrations decreased, cyanobacteria likely began fixing atmospheric N_2 to alleviate N limitation in Waco Reservoir.

Bottom sediment trap deposition rates were relatively high and variable during our study. POC and PON deposition rates in bottom sediment traps were an order of magnitude greater in Waco Reservoir ($3,429 \text{ mg C m}^{-2} \text{ day}^{-1}$ and $398 \text{ mg N m}^{-2} \text{ day}^{-1}$; Table 3) compared to Lake Lugano (Switzerland), a monomictic sub-alpine lake ($299 \text{ mg C m}^{-2} \text{ day}^{-1}$ and $30 \text{ mg N m}^{-2} \text{ day}^{-1}$; Bernasconi et al. 1997). Deposition rates varied seasonally with winter POC and PON deliveries disproportionately comprising annual POC and PON deposits. From November through February, bottom sediment traps collected 45 and 41% of annual POC and PON deposits, respectively. Elevated bottom sediment trap deposition rates and greater C:N ratios during winter (Fig. 3) suggested that allochthonous sources greatly contributed to annual POC and PON budgets. Lind (1971) demonstrated that allochthonous OM composed 22% of annual OM budgets in Waco Reservoir, which is plausible based on our findings. However, we showed that allochthonous sources supplied more OM seasonally. We anticipated our sediment trap estimates would be greater than inflow estimates of Lind (1971) because secondarily transported OM

would be biased towards more refractory allochthonous OM during sediment focusing.

Bottom sediment trap deposition rates likely poorly estimate POC and PON burial rates in Waco Reservoir. Our deposition rates likely overestimate burial rates because this location experiences strong sediment focusing. Filstrup and Lind (unpublished data) showed that 71% of total suspended solids (60% of volatile suspended solids) in bottom sediment traps were attributed to secondary sediment transport. However, deposition rates from our sampling location may underestimate basin-wide deposition rates because deposition rates typically decrease exponentially along a reservoir's flow axis (Thornton 1990). Even natural lakes can display a high degree of spatial variability concerning deposition rates. Schelske (2006) found that 70% each of total dry mass and OM was deposited on only 39% of Lake Apopka (Florida, USA) bottom area. Additional sampling stations located throughout the various reservoir regions are required to adequately estimate basin-wide burial rates. Additionally, bottom sediment trap deposition rates would need to be corrected for OM degradation at the SWI which can be significant. Hedges et al. (1988) discovered that 60 and 70% of POC and PON respectively were degraded at the SWI in Dabob Bay, Washington (USA).

Sediment transport mechanisms

Secondary sediment transport mechanisms potentially exposed OM to prolonged microbial mineralization during our study. Bottom sediment traps collected significantly more POC and PON than photic sediment traps (Tables 3, 4). Higher particulate organic nutrient deposition rates near the SWI have been reported for numerous natural lakes (Meyers and Eadie 1993; Bernasconi et al. 1997; Hodell and Schelske 1998). POC and PON deposition rates in bottom relative to photic sediment traps were an order of magnitude greater in Waco Reservoir ($\sim 200\%$ for both POC and PON; Table 3) compared to Lake Lugano (~ 10 and $\sim 21\%$ for POC and PON respectively; Bernasconi et al. 1997). Strong, frequent water column mixing, as well as relatively shallow depth, likely explained enhanced excess material deposition attributed to secondary sediment transport mechanisms in Waco Reservoir. Filstrup and Lind (unpublished data)

documented that excess total suspended solids deposition was related to maximum wind speed direction at this location. Holomictic circulation patterns were suggested by significant correlations between photic and bottom sediment traps for deposition rates and C:N ratios (Fig. 3). However, OM elemental and isotopic differences between photic and bottom sediment traps suggested that allochthonous OM composed greater proportions of SPOM in bottom sediment traps (Tables 3, 4).

Although several mechanisms likely contributed to secondary sediment transport, we hypothesized that excess POC and PON deposition was strongly influenced by surface sediment resuspension in winter/spring and horizontal advection of autochthonous OM in summer/autumn. Significant correlations between predicted and observed isotopic compositions for $\delta^{13}\text{C}$ ($r^2 = 0.80$, $p < 0.001$) and $\delta^{15}\text{N}$ ($r^2 = 0.46$, $p < 0.001$; Fig. 6) identified sediment resuspension as a primary mechanism influencing excess sediment deposition in Waco Reservoir. Although predicted and observed $\delta^{13}\text{C}$ agreed well during spring/early-summer, they did not agree as closely as we anticipated during winter (Fig. 6a). Relatively light observed values suggest that other mechanisms, including density plume sedimentation of allochthonous OM and associated C_4 plant signatures, contributed excess material during winter. Predicted and observed $\delta^{13}\text{C}$ disagreed after June with relatively heavy observed values (Fig. 6a). Predicted excess material $\delta^{13}\text{C}$ and observed values in photic sediment traps were significantly correlated ($r^2 = 0.75$, $p < 0.001$; Fig. 7a) indicating that horizontal advection of autochthonous OM influenced excess material deposition. Strong correlations between predicted and observed $\delta^{13}\text{C}$ ($r^2 = 0.92$, $p < 0.001$) during May through October and lack of correlation during November through April suggest that horizontal advection was a primary transport mechanism during summer/autumn but not during winter/spring. Predicted excess material $\delta^{15}\text{N}$ were not correlated to observed photic sediment trap values (Fig. 7b) similar to findings from Lake Lugano (Bernasconi et al. 1997). Other factors, including additional transport mechanisms and biogeochemical N cycling, likely influenced SPOM N isotopic compositions during our study.

The aforementioned models rely on stable isotopes serving as conservative tracers of autochthonous and

allochthonous OM sources (Cifuentes et al. 1988; Bernasconi et al. 1997). The ability of microbial degradation to mask OM isotopic source distinctions is debatable. Laboratory studies have demonstrated that microbial degradation can significantly alter OM isotopic composition in cultures (Macko and Estep 1984; Lehmann et al. 2002). However, several field studies have shown that C and N isotopic compositions were not largely changed by diagenesis and that sediment OM reflects original algal signals (Meyers and Eadie 1993; Meyers 1994; Schelske and Hodell 1995; Hodell and Schelske 1998). In Waco Reservoir, $\delta^{13}\text{C}$ became heavier from photic to bottom sediment traps to surface sediments whereas $\delta^{15}\text{N}$ became lighter (Table 3). The $\sim 1\text{‰}$ $\delta^{13}\text{C}$ increase with depth in Waco Reservoir (Table 4) was similar to observations from Lake Michigan (Meyers and Eadie 1993) which the authors attributed to lateral transport of autochthonous OM from highly productive coastal regions. This explanation does not seem plausible for our observations. $\delta^{15}\text{N}$ decreases with depth were highly variable (Table 4) and likely resulted from several nitrogen cycling processes. This decrease could potentially be explained by intermediate stages of OM processing which was hypothesized to explain a 1–2‰ $\delta^{15}\text{N}$ decrease with depth in Lake Michigan (Meyers and Eadie 1993). Based on greater POC and PON deposition rates in bottom sediment traps (Table 4), it seems more likely that isotopic composition changes resulted from greater allochthonous OM contributions to bottom sediment traps. Therefore, isotopic compositions served as conservative tracers.

Conclusions

Our findings suggest that allochthonous OM loads and secondarily-transported OM significantly contribute to SPOM in reservoirs. These supplements to autochthonous OM production may be important in maintaining food webs particularly during periods of low phytoplankton productivity. C and N elemental and isotopic ratios appeared to nicely record OM source differences in this reservoir. However, either mixing regime or reservoir characteristics obscured phytoplankton productivity inferences as indicated by atypical C isotope patterns. Future studies concerning stable isotope fractionation–phytoplankton

productivity relationships in reservoirs are warranted and should include isotopic measurements of DIC and DIN pools both within reservoir and in major tributaries. A stable isotope study performed in a monomictic reservoir would imply whether our observations differed from previous studies because of mixing regimes or system differences.

Acknowledgments We thank Dr. Bradley Christian and Lisa Vajdos for their help with field sampling. We thank Dr. Joseph White and Jeffrey Back for advice during manuscript preparation. We thank Tom Conry and the City of Waco (Texas) for project support. Stable isotope analyses were conducted at the Colorado Plateau Stable Isotope Laboratory. This research was funded by the Environmental Protection Agency through an ENSR, Inc. subcontract (no. 102200) to O. T. Lind, and by a grant from the Texas Water Resources Institute (TAES contract no. 570251) to J. T. Scott. Partial funding was provided by the Folmar and Gardner Graduate Student Research Grants through Baylor University Department of Biology to C. T. Filstrup. We thank an anonymous referee whose critiques greatly improved a previous manuscript version.

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