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Carbon sink to source: longitudinal gradients of planktonic P:R ratios in subtropical reservoirs

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Abstract Spatial patterns of planktonic production and respiration in the surface mixed layer were examined in eight Texas, USA reservoirs to test the hypothesis that P:R ratios are lowest in upreservoir inflow zones and highest in downreservoir open-water zones, as predicted by the heuristic reservoir zonation model. We measured summer planktonic metabolism with light–dark bottles and physical–chemical conditions in epilimnetic water at 85 sites distributed among sixteen longitudinal transects within the eight reservoirs (2 transects per reservoir). Volumetric production and plankton biomass were lowest in the open-water zones and increased upreservoir; however, that pattern was reversed for areal production due to greater photic depths at open-water sites. Volumetric respiration was similar in the three zones; however, corresponding planktonic P:R ratios in the surface mixed layer were significantly lower at open-water sites, which is opposite than hypothesized. Based on linear regressions of production and respiration rates on chlorophyll *a*, open-water sites were net heterotrophic during the summer regardless of trophic state; whereas inflow and mid-reservoir zone sites were heterotrophic when chlorophyll concentrations were respectively less than 9.5 and 35 mg m^{-3}. Although variation among reservoirs was high, five of the eight reservoirs had inflow zones that were net carbon sinks while seven had open-water zones that were carbon sources. Mean (±standard error) carbon flux rates of inflow, mid-reservoir, and open-water zones were -0.22 ± 0.12 (C sink), 0.39 ± 0.44 (moderate C source), and 1.33 ± 0.50 (strong C source) g C m^{-2} day^{-1} respectively. Inflow and mid-reservoir zones comprised approximately 45% of the total reservoir area studied. Therefore, omitting their contribution as often done when a single open-water site is sampled may substantially overestimate reservoir carbon flux.

Keywords Production: respiration ratios · Carbon flux · Reservoir zones · Longitudinal gradients · Heterotrophy

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Introduction

The volume of water held by reservoirs worldwide has increased by a factor of ten in recent years (Dean and Gorham 1998) and although the damming of rivers has created many ecological challenges (Kingsford et al. 1998), reservoirs can also provide important ecosystem services such as drinking water, flood control, and regulation of biogeochemical cycles. For example, reservoirs may bury two times more organic carbon than the world's oceans, despite having a global surface area four orders of magnitude less (Dean and Gorham 1998). Both natural lakes and reservoirs capture large quantities of organic matter (Harrison et al. 2009), a portion of which is metabolized within the water body. Reservoirs in agricultural areas can be particularly strong carbon sinks (Downing et al. 2008), and significant quantities of nitrogen (Harrison et al. 2009) and phosphorus (Alexander et al. 2008) can also be sequestered in these systems. Presumably much of this C, N, and P storage results from autochthonous production (Dean and Gorham 1998), but the metabolic balance (P:R ratio) of reservoirs has not been adequately described, particularly in subtropical latitudes.

Reservoirs have been described as lake–river hybrids with channel morphometry, greater hydrologic forcing, and larger watershed areas than natural lakes (Thornton 1990). Reservoir zonation theory (*see* Thornton et al. 1990) predicts that riverine zones of reservoirs have light-limited phytoplankton production, primarily allochthonous organic matter and nutrients, and respiration rates that exceed production rates (i.e. P:R < 1). Thornton et al. (1990) also predicted that as light limitation relaxes downreservoir, the compensation point between autochthonous production and processing of allocthonous organic matter will occur in the transition zone (i.e. P:R ≈ 1). Finally, conditions in the lacustrine zone with higher plankton production resulting from clearer water and less available allochthonous carbon to full microbial respiration should allow production to exceed respiration (i.e. P:R > 1). In contrast, analyses based on carbon dioxide emissions indicate that natural lakes worldwide exhibit net heterotrophy (i.e. P:R < 1; Cole et al. 1994). Carbon dioxide emissions from reservoirs have been shown to occur in temperate and tropical reservoirs as well (St. Louis et al. 2000); however, we are not aware of any studies that have measured both production and respiration along longitudinal gradients in subtropical reservoirs. One recent study on temperate reservoirs found that gross primary production rates were generally higher at upreservoir sites (Bott et al. 2006), however respiration data were not reported. Knoll et al. (2003) found that in 12 Ohio reservoirs, inflow sites had higher volumetric primary production, higher total phosphorus, and greater light attenuation than outflow sites near the dam.

Our study examined plankton metabolism and related chemical and physical features within eight reservoirs located in Texas, United States of American (USA) to evaluate spatial trends in planktonic production and respiration. Based on reservoir zonation theory, we hypothesized that P:R ratios would be lowest near the river inflow, near unity in the mid-reservoir, and highest in the open-water zone. We also tested the hypothesis previously evaluated on northern lakes by del Giorgio and Peters (1993) that both production and respiration are positively related to trophic state as measured by chlorophyll *a* concentrations. We applied this approach to evaluate whether the relationship between chlorophyll and production and respiration was dependent on location within the reservoir. Finally, we calculated the net carbon flux (i.e. the difference between production and respiration) from our reservoirs by summing the individual contributions of the inflow, mid-reservoir, and open-water zones. As the surface area of reservoirs continues to increase worldwide, our results provide more accurate estimates of carbon contributions by subtropical reservoirs to the global carbon balance.

Methods

This study is a comparative spatial analysis of production and respiration along longitudinal gradients within eight Texas reservoirs (Fig. 1). The reservoirs are likely monomictic, although occasional polymixis may occur. Portions of the study have been published elsewhere: maximum planktonic production and nitrogen fixation rates, nutrient data, and watershed analysis appear in Forbes et al. (2008). Four reservoirs (Aquilla, Conroe, Lewisville, and Cedar Creek) were sampled twice, once in summer 2005 and again in summer 2006; four additional reservoirs (Buchanan, Canyon, Stillhouse Hollow, and Texana) were sampled once in summer 2006.

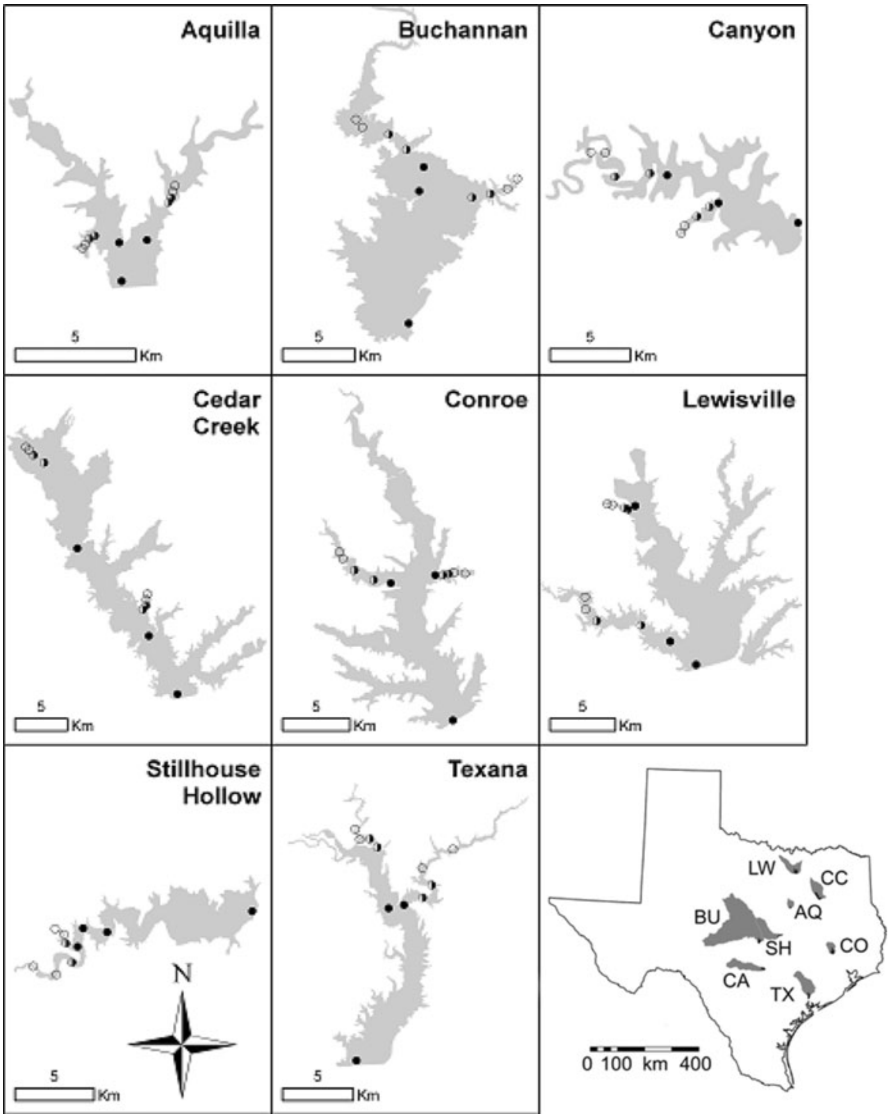

Fig. 1 Location of sample sites along longitudinal transects in A and B arms and open-water zones of eight Texas reservoirs. Note that 2006 sample sites in Aquilla were further downreservoir than 2005 sites due to low 2006 water levels. *Solid circles* are inflow, *semi-solid circles* are mid-reservoir, and *open circles* are open-water sites

We treated the different year samples as separate observations (85 sites, 120 observations). Demonstrating spatial gradients in reservoirs is needed in regions where reservoirs are regulated as lakes and authorities apply the same water quality standards to riverine arms that are applied to open water zones.

We sampled two arms of each reservoir. Typically, one arm represented a major river inflow to the reservoir and the second arm represented a smaller tributary. Sample sites were distributed along the longitudinal gradient from upreservoir to downreservoir (Fig. 1). Sites were designated inflow (I), mid-reservoir (M), or open-water (OW) depending on their relative positions. Although our sites would likely be categorized by most limnologist as ‘riverine’, ‘transition’ and ‘lacustrine’, we have avoided the use of those terms since our zone assignments are based exclusively on morphometric characteristics and ignore the variability in zonation which occurs with changing flows.

At each site, width and depth were measured along a transect established perpendicular to the longitudinal flow. Cross sectional areas were calculated as the product of mean depth and transect width. Morphometric parameters were generalized from field coordinates overlaid on existing maps and GIS information. Upstream distance (km), upstream shoreline perimeter (km) and upstream area (km^2) were calculated from the sample site upreservoir to the conservation pool elevation. Shoreline density (Dsl, m ha^{-1}) was computed as the ratio between shoreline length and impounded area (Osgood 2005).

Temperature sensors (Onset, HOBO® Water Temp Pro, Pocasset, MA, USA) were deployed at each site at 1-m depth intervals from surface to bottom, logging temperature every 5 min and continuing for at least 24 h. Depth to persistent daily stratification (if any) based on temperature was estimated from the 06:00 h profiles and defined as the depth interval where water temperature changed by at least 1°C m^{-1} (Wetzel 2001). The depth of the surface mixed layer (Z_{MIX}) was computed as the depth of the water column to the sediment surface or to the depth of persistent daily stratification (if present) as evidenced by the pre-dawn temperature profile. Vertical profiles of water temperature, pH, specific conductance, and photosynthetically active radiation (PAR) were also measured once between 10:00 and 15:00 h. The light extinction coefficient (n) and photic depth (Z_{EU}, defined as the depth with 1% surface illumination) were computed from the light profile (Lind 1985).

Water samples were collected from a depth of 0.3 m for plankton metabolism and nutrient analyses. Samples were stored in acid-rinsed containers and kept on ice (nutrient samples) or in the dark within a larger container filled with reservoir water to maintain ambient temperature (plankton metabolism). Samples were transported immediately to the laboratory. Turbidity was measured with a Hach Company (Loveland, Colorado, USA) 2100 N bench top turbidimeter. Seston was trapped onto a filter and chlorophyll *a* was extracted with acetone and determined spectrophotometrically after correction for pheophytin-a (Wetzel and Likens 2000). Total nitrogen and phosphorus samples were digested using the persulfate method, soluble reactive phosphorus samples were filtered and all nutrients analyzed with a Lachat Quickchem 8500 Flow Injection Autoanalyzer using standard colorimetric techniques (American Public Health Association 1998).

Planktonic photosynthetic parameters of P_{MAX}, alpha, and respiration were determined by measuring changes in dissolved oxygen (DO) in light–dark bottle incubations (Fee 1973). Dissolved oxygen concentrations were measured with a YSI 5000 benchtop dissolved oxygen meter with a 5010 BOD probe. Three subsamples were incubated under light-saturating (PAR = 375–425 μmol s^{-1} m^{-2}) artificial lighting; three under low light (PAR = 30–80 μϖ mol s^{-1} m^{-2}); and three in darkness (foil wrapped). Incubations lasted 6–12 h and were maintained at ambient reservoir temperature. Respiration (mg O_2 m^{-3} h^{-1}) was calculated as the decrease in DO in dark bottles and was assumed to be constant in dark and light. The light-saturated rate of gross production (P_{MAX}, mg O_2 m^{-3} h^{-1}) was estimated as the average net production in the high-light bottles plus the respiration rate computed from the dark bottles. Alpha was computed as the slope of the line of apparent net production under low-light conditions (0–80 μmol s^{-1} m^{-2}, $n = 6$). Oxygen data were converted to carbon equivalents (mg C m^{-3} h^{-1}) by multiplying by 0.375 (mass ratio of C to O_2) and assuming a photosynthetic quotient of 1.0 (Wetzel and Likens 2000).

Potential areal daily gross primary production and respiration of the surface mixed layer were calculated using the Walsby (1997) method. Gross production was integrated over time (sunlight hours) and depth down to the photic depth (Z_{EU}) or mixing depth (Z_{MIX}) if less than Z_{EU}. The input variables included light extinction, chlorophyll *a*, P_{max}, alpha, beta (coefficient of photoinhibition), respiration, temperature, irradiance and depth of the surface mixed layer (Z_{MIX}). Beta was assumed to be zero because of the turbid nature of the water in the reservoirs sampled. Light energy data collected at 5 min intervals for a cloudless day around the time of the study were obtained from the Texas Solar Radiation Database (University of Texas, Austin, Texas, USA). Light energy data were converted to PAR based on the empirical conversion factors determined by Fisher et al. (1982). Therefore, the estimated planktonic production values should be considered the potential daily production under full sunlight conditions. Respiration was assumed to be constant over time and depth down to Z_{MIX}. Average volumetric planktonic production and respiration in the surface mixed layer were determined by dividing the areal rates by Z_{MIX} at each site. Eight observations were omitted due to minimal DO changes in the light–dark bottles coupled with very low chlorophyll levels.

We evaluated differences in log-transformed production and respiration rates among zones using three-factor analyses of variance (ANOVA) followed by Tukey–Kramer least squares multiple comparison test ($\alpha = 0.05$, JMP ver. 7.0, Cary, North Carolina, USA).

The three factors were zone, reservoir, and sampling year. To evaluate effects of trophic state, we performed simple linear regressions of log-transformed production and respiration rates on log-transformed chlorophyll *a* concentrations for data from each reservoir zone across all reservoirs sampled. Differences among slopes from each zone were evaluated with a modified Student's *t* test (Zar 1996).

Net carbon flux was estimated by subtracting areal planktonic production rates from corresponding respiration rates and taking the average for each of the three zones within each reservoir ($n = 24$). Open-water surface area of each reservoir was determined by digitizing the main water body of each reservoir's GIS shape file, i.e. without its arms. The difference between the whole reservoir surface area and the open-water area was assigned to inflow or mid-reservoir zones based on the percentages of inflow and mid-reservoir area calculated for the two sampled arms in each reservoir. The average carbon flux of the inflow, mid-reservoir, and open-water zones in each reservoir was then multiplied by the corresponding surface area. These products were summed to obtain the net areal carbon flux for each reservoir.

We computed the ratio of the actual mixing depth (Z_{MIX}) to the theoretical euphotic depth based on light attenuation (Z_{EU}) as a scaling factor to understand the light climate of the phytoplankton. In cases where the ratio is larger than 1.0, plankton spend part of the day circulating in darkness beneath the euphotic zone where photosynthetic production is impossible, but respiration continues. The larger the ratio, the greater the potential for areal production to be light limited. In cases where the calculated ratio is ≤ 1.0, there is light penetration throughout the surface mixed zone (often to the physical bottom of the water column). The smaller the ratio, the more light is available to cells in the entire surface mixed layer and the higher the average light of the mixed layer.

Results

Physical and chemical factors

Reservoir water levels were near conservation pool in 2005 but in 2006 all of the reservoirs except Texana were 3–4 m below conservation pool. Texana experienced a large storm event that resulted in high inflows and a significant increase in water levels the week prior to being sampled. Ambient summer water temperatures at the eight reservoirs ranged from 24 to 36°C, with a mean temperature of 30°C. Morphological characteristics exhibited a pronounced longitudinal gradient from shallow, narrow morphometry in inflow zones to wider, deeper features in open-water zones (Table 1). Mixing depth (Z_{MIX}) also exhibited a strong gradient; however, measures of photic depth (Z_{EU}) in the inflow zone were not statistically different from those in the mid-reservoir zone (Tukey–Kramer $\alpha = 0.05$). Turbidities and chlorophyll *a* concentrations were extremely variable, but significantly lower in the open-water zones than in the mid-reservoir zones, with intermediate values in the inflow zones.

There were important trophic differences among the eight reservoirs. Also, trophic indicators such as secchi depth, total phosphorus, N:P ratios, and chlorophyll concentrations were not always consistent within the same reservoir (Table 2). Cedar Creek, Lewisville, Conroe, and Aquilla were eutrophic according to mean chlorophyll *a* and total phosphorus concentrations, whereas Buchanan was mesotrophic, and Canyon and Stillhouse Hollow were relatively oligotrophic. Among the eight reservoirs, Texana was unusual because phosphorus levels were high while chlorophyll *a* and planktonic productivity rates were low. In addition to the high flow conditions, Texana was heavily colonized by macrophytes including water hyacinth (*Eichornia crassipes*) and generally had colored water associated with high levels of dissolved organic carbon, which can suppress phytoplankton production (del Giorgio and Peters 1994).

Planktonic metabolism

Volumetric production rates at the 85 reservoir sites ranged from 0.04 to 11 g C m^{-3} day^{-1}. The maximum rate occurred in the Lewisville-B arm, whose water quantity and quality is characterized by an effluent-dominated stream receiving discharge from a 53,000 m^3 day^{-1} wastewater treatment plant (Brooks et al. 2006). Other high values (1.6–6.5 g C m^{-3} day^{-1}) occurred in Cedar Creek-A arm, which receives 17,000 m^3 day^{-1} of treated wastewater. These effluent-dominated streams had high nutrient levels (e.g. 2 mg l^{-1} dissolved phosphorus), low N:P ratios, and

Table 1 Geometric means and 95% confidence interval (CI) of physical and chemical characteristics of 85 reservoir sampling sites

Characteristic	Inflow ($n = 43$)		Mid-reservoir ($n = 48$)		Open-water ($n = 29$)	
	Geomean	95% CI	Geomean	95% CI	Geomean	95% CI
Morphometry						
Upstream area (km^2)	0.34^{a}	0.19–0.61	1.8^{b}	1.3–2.5	18.3^{c}	10.9–30.7
Shoreline density (m ha^{-1})	322^{a}	140–262	108^{b}	72–105	55^{b}	38–58
Depth (m)	1.9^{a}	1.5–2.3	3.5^{b}	2.8–4.3	9.2^{c}	6.9–12.1
Cross-sectional width (m)	161^{a}	105–247	483^{b}	375–622	1440^{c}	1120
Cross-sectional area (m^2)	267^{a}	176–404	1575^{b}	1180–2100	11150^{c}	7490–16600
Mixing and photic depths						
Z_{MIX}	1.9^{a}	1.5–2.3	3.4^{b}	2.8–4.2	7.1^{c}	5.8–8.7
Z_{EU}	2.0^{a}	1.6–2.3	2.0^{a}	1.6–2.5	3.7^{b}	2.8–4.8
Water chemistry						
Temperature (°C)	30.9^{a}	30.3–31.5	31.0^{a}	30.1–31.0	28.7^{b}	28.1–29.4
Turbidity (NTU)	11^{ab}	8.9–14.5	13^{a}	9.7–17.5	6.5^{b}	3.8–11.3
Soluble reactive P (μg l^{-1})	9.6^{a}	5.5–16.7	8.3^{a}	5.5–12.6	7.7^{a}	4.6–12.7
Total P (μg l^{-1})	79^{a}	55–113	65^{a}	46–90	26^{b}	16–40
Total N (μg l^{-1})	908^{a}	693–1190	835^{a}	674–1030	527^{b}	432–643
Chlorophyll *a* (mg m^{-3})	22^{ab}	17–30	28^{a}	21–37	14^{b}	9.5–22

Only temperature was not logarithmically transformed. Means with the *same lower case letter* were not significantly different (Tukey–Kramer $\alpha = 0.05$)

Table 2 Reservoir age and mean and standard deviation of trophic indicators of sampled reservoirs organized by Secchi depth

Reservoir	Reservoir age (years)	*n*	Secchi (m)	Mean depth[a] (m)	Chlorophyll *a* (mg m^{-3})	Total P (mg m^{-3})	TN:TP (molar)
Canyon	46	11	1.7 ± 1.2	14.3	4 ± 2	15 ± 11	66 ± 49
Stillhouse Hollow	42	10	1.2 ± 1.3	11.2	11 ± 8	21 ± 15	78 ± 103
Buchanan	70	11	0.8 ± 0.5	11.9	27 ± 12	44 ± 47	90 ± 92
Cedar Creek	45	20	0.6 ± 0.4	6.1	56 ± 29	153 ± 162	22 ± 7
Conroe	37	20	0.6 ± 0.1	6.0	42 ± 16	61 ± 21	43 ± 13
Aquilla	27	12	0.5 ± 0.2	4.9	25 ± 14	59 ± 90	42 ± 18
Lewisville	53	18	0.4 ± 0.3	6.6	56 ± 41	414 ± 593	33 ± 20
Texana	31	11	0.4 ± 0.1	5.3	13 ± 3	212 ± 90	8 ± 4

[a] Mean depth is at conservation pool

low suspended solids, which are consistent with other effluent-dominated waterbodies (Brooks et al. 2006).

The median rate of volumetric production in surface mixed layer of the inflow zone was nearly triple the median rate in the open-water zone (Fig. 2a). Volumetric respiration rates were not statistically different among reservoir zones, although rates in open-water zones tended to be lower than in shallower sites. The strong decline in volumetric production coupled with relatively constant respiration resulted in an increasing trend towards heterotrophy in the open-water zone. In contrast, areal phytoplankton production rates varied from 0.15 to 13.2 (median = 2.6) g m^{-2} day^{-1} and were approximately 50% higher in the open-water zone than in the inflow zone (Fig. 2b). Areal respiration rates also increased in the downstream direction.

P:R ratios nearly always declined along the upreservoir to downreservoir gradient regardless of reservoir or sampling year, although they sometimes increased at intermediate sites (Fig. 3). The general trend of decreasing P:R ratios downreservoir was strongly related to the increase in Z_{MIX}/Z_{EU} (Fig. 4,

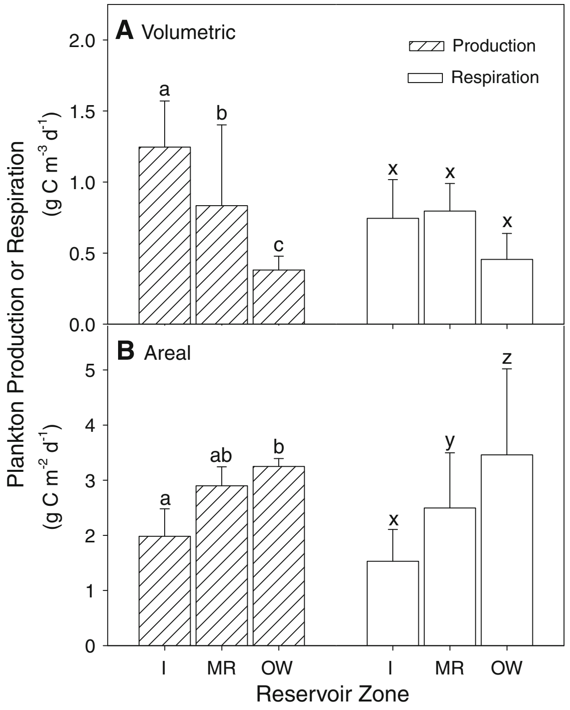

Fig. 2 **a** Medians and standard errors of average volumetric planktonic production (hatched) and respiration (open) in the surface mixed layer by zone. **b** Areal planktonic production (hatched) and respiration (open) by zone. *I* inflow, *MR* mid reservoir, *OW* open water. Zones with the *same lower case letters* were not statistically different based on analyses of means (Tukey–Kramer mean comparison test following significant 3-factor ANOVA, $\alpha = 0.05$, log transformed data). Note the different scales on the *y* axes

$R^2 = 0.57$, $p < 0.0001$). At many of the shallower inflow sites the ratio was < 1.0 indicating the entire surface mixed zone was within the euphotic zone. As the Z_{MIX}/Z_{EU} ratio increased the P:R ratio decreased. When the Z_{MIX}/Z_{EU} ratio was above 2, the P:R ratio was almost always less than 1.0 indicating net heterotrophy over a daily cycle.

Despite temporal variability and variability among reservoirs, P:R ratios were statistically distinct in each zone (Fig. 5). Planktonic P:R ratios at inflow sites (mean = 1.6, median = 1.3) was the only group with a median P:R greater than unity. Mean and median P:R ratios at mid-reservoir sites were slightly lower than unity while at open-water sites the values were well below unity. The mid-reservoir zone was, as hypothesized, the zone where the compensation point occurred (P:R ≈ 1), however our hypothesis that P:R ratios increase at sites further downreservoir was not supported. Rather, our data indicate that P:R ratios are consistently higher at inflow sites and lower at open-water sites.

Relation of production and respiration to chlorophyll

Both production and respiration rates were positively correlated with chlorophyll *a* concentrations (Fig. 6). Production rates at inflow and mid-reservoir sites were more strongly associated with chlorophyll concentrations than rates in the open-water zone. Inflow and mid-reservoir zone regression slopes were not statistically different ($p = 0.127$); however, both of these slopes were steeper than the open-water regression slope ($p = 0.017$). Because slopes of respiration rates did not vary by zone ($p = 0.318$), only one respiration model was developed. At inflow zones, the compensation point occurred at a chlorophyll *a* concentration of 9.5 mg m^{-3}, whereas the mid-reservoir zone compensation point occurred at 35 mg m^{-3}. Intersection of production and respiration lines in the open-water regressions occurred at chlorophyll *a* concentrations less than 1 mg m^{-3}. These results support our second hypothesis that production and respiration rates are positively related to trophic state, with additional evidence that trophic condition exerts a greater influence in inflow and mid-reservoir zones of reservoirs than in open-water zones.

Net carbon flux

Based on 2005 and 2006 summer data, the majority of reservoirs (62%) had inflow zones that were net sinks for planktonic carbon, i.e. production exceeded respiration (Table 3). Exceptions included Canyon and Conroe, whose inflow zones had carbon fluxes near zero; and Texana, which was characterized by low production rates throughout and exhibited a trend opposite those of the remaining seven reservoirs. The average C flux of inflow zones (±SE; $n = 40$) was -0.22 ± 0.12 g C m^{-2} day^{-1}. Negative values indicate carbon sinks. Half of the mid-reservoir zones were net carbon sinks while the other half were sources; nearly all had carbon flux rates that were intermediate between the inflow and open-water zones. The average C flux of the eight mid-reservoir zones was 0.39 ± 0.44 g C m^{-2} day^{-1}. All reservoirs except Aquilla had open-water zones that were carbon sources. Carbon flux in seven open-water zones

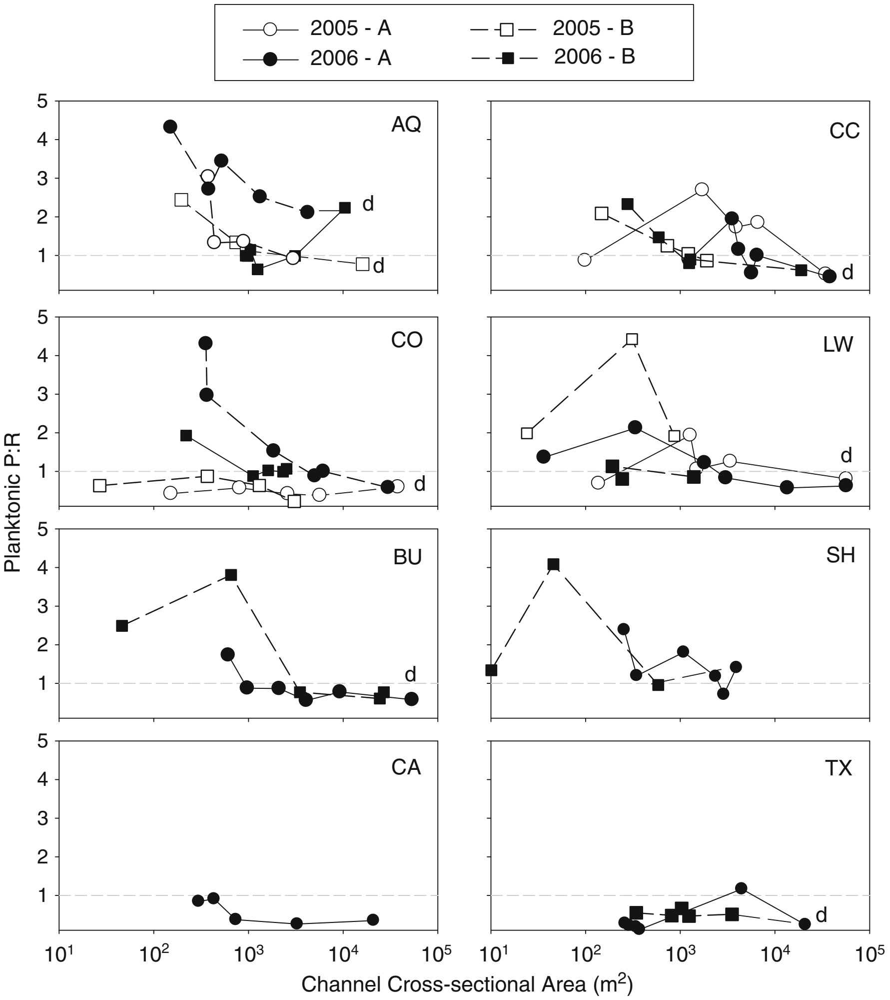

Fig. 3 Planktonic P:R ratios for individual reservoir arms and years plotted against channel cross-sectional area. *AQ* Aquilla, *BU* Buchanan, *CA* Canyon, *CO* Conroe, *CC* Cedar Creek, *LW* Lewisville, *SH* Stillhouse Hollow, *TX* Texana, *d* dam site. Stillhouse dam, Canyon dam, and B-arm samples had insufficient dissolved oxygen change during incubations

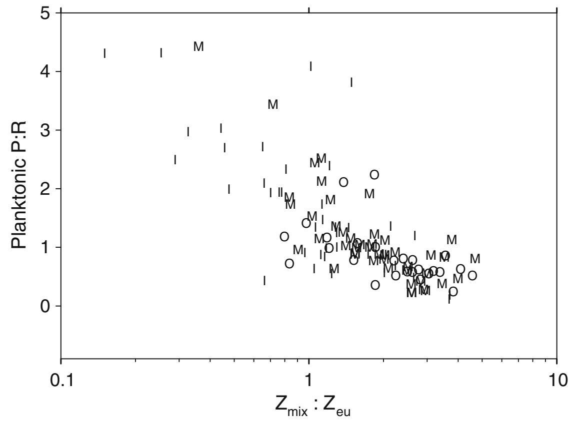

Fig. 4 Planktonic P:R ratios as a function of Z_{MIX}:Z_{EU}. Both axes are logarithmically scaled. Data symbols represent zone of site location: *I* inflow, *M* mid reservoir, *O* open water

ranged from near zero in Stillhouse to a maximum of 3.91 ± 0.67 g C m^{-2} day^{-1} in Cedar Creek, the most eutrophic reservoir. On a whole reservoir basis, carbon fluxes ranged from −0.86 g C m^{-2} day^{-1} in Aquilla to 1.75 g C m^{-2} day^{-1} in Conroe.

Discussion

The hypothesis that P:R ratios increase along an upreservoir to downreservoir gradient was not supported by our results. We found that planktonic production in the inflow zone exceeded respiration in five of the eight reservoirs studied. Production exceeded respiration in the mid-reservoir zone in four of the reservoirs but that was true for only one

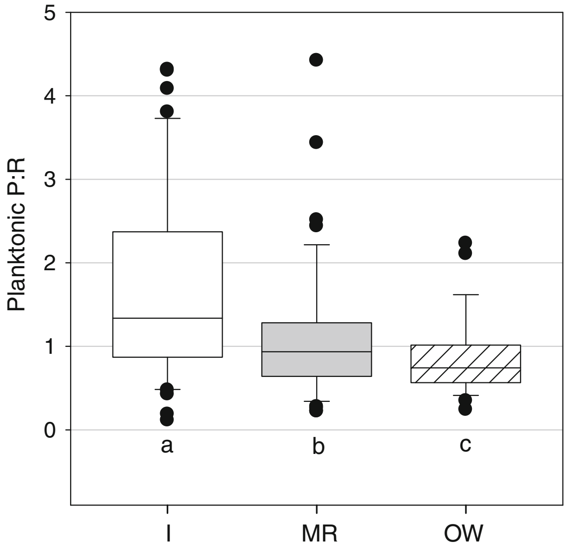

Fig. 5 Median planktonic P:R ratios by zone. *I* inflow, *MR* mid reservoir, *OW* open water. Zones with different *lower case letters* were statistically different based on analyses of means (Tukey–Kramer $\alpha = 0.05$, log transformed data, 3-factor ANOVA)

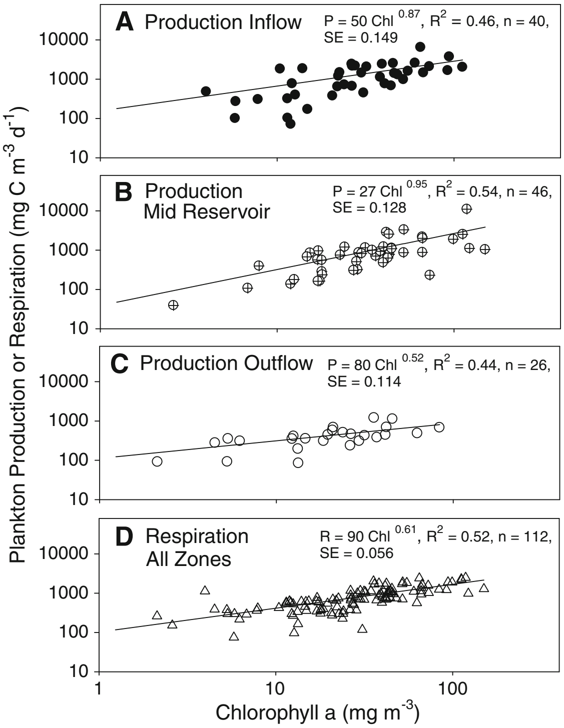

Fig. 6 Planktonic volumetric production and respiration rates as a function of chlorophyll *a* concentrations by zone. Slopes of production rates were significantly different by zone (slope inflow = slope mid-reservoir > slope open-water $\alpha = 0.0167$), however slopes of respiration rates were not different among zones ($p = 0.318$)

reservoir open-water zone. That inflow zones and often mid-reservoir zones act as carbon sinks is somewhat surprising, as streams have generally been regarded as heterotrophic due to large allochthonous inputs of terrestrial organic matter. However, our findings are consistent with recent studies that indicated stream community production rates increased with watershed area, channel width, and nutrient concentrations, but were inversely correlated to canopy cover (Lamberti and Steinman 1997). Therefore as shallow inflowing streams, particularly nutrient rich ones, widen and lose their canopy cover, they can become hot spots of plankton production.

Our summer-only results likely represent maximum production rates and metabolic balances may be different during other seasons. However, Huang (2006) studied four of the reservoirs (Aquilla, Conroe, Lewisville and Cedar Creek) in spring, summer and winter of 2005–2006 and found that whereas production and respiration rates were lower in winter (two-way ANOVA, $p < 0.001$), P:R ratios were not affected by season ($p = 0.430$). Our results also represent periods of low or no flow in most inflow sites, and production rates could be lower during periods of high flow due to increased turbidity induced light limitation and cell wash-out. In the Texas climate, low flow, particularly in summer, is a common hydrologic feature in all but large rivers or effluent dominated streams. Periods of high flow would likely result in the export of greater quantities of dissolved organic carbon, and shorter water residence times which would allow less time for degradation (Tranvik and Jansson 2002). In contrast, volumetric respiration, although influenced by nutrient enrichment, was not significantly correlated to location in these reservoirs. In addition, our comparatively high productivity rates and corresponding autotrophic conditions measured in inflow zones are consistent with results reported by Cotner et al. (2006) who found autotrophy in tropical riverine zones typified by warm, shallow waters. These riverine contributions of autochthonous production can yield labile C sources important to respiration and secondary production at downgradient open-water zones.

Whereas both respiration and production rates were positively related to trophic status, only production was spatially distinct among zones (Fig. 6)

Table 3 Surface area, mean and standard error of flux rate, and net carbon flux by reservoir zone (*I* inflow, *MR* mid reservoir, *OW* open water) and reservoir

Reservoir (surface area) (km^2)	Relative percent area by zone			Mean ± SE areal C flux rate (g C m^{-2} day^{-1})			C flux (Mt C day^{-1})				Whole reservoir C areal flux rate (g C m^{-2} day^{-1})
	I	MR	OW	I	MR	OW	I	MR	OW	Total	
Aquilla (15.9)	42	15	43	−1.03 ± 0.39	−0.72 ± 0.43	−0.74 ± 0.76	−6.9	−1.7	−5.1	−13.6	−0.86
Buchanan (91.4)	19	16	65	−0.76 ± 0.45	1.33 ± 0.47	1.31 ± 0.48	−13.2	19.4	77.8	84.1	0.92
Canyon (38.5)	16	38	46	0.19 ± 0.09	1.12 ± 0.01	1.63	1.2	16.4	28.9	46.4	1.21
Cedar Creek (131)	27	24	49	−1.33 ± 0.46	−0.23 ± 0.4	3.91 ± 0.67	−47.0	−7.2	251	196.7	1.50
Conroe (77.2)	28	21	51	0.29 ± 0.54	2.15 ± 1.04	2.38 ± 1.63	6.3	34.9	93.7	134.8	1.75
Lewisville (88.2)	21	20	59	−0.33 ± 0.51	−1.51 ± 1.12	1.44 ± 0.55	−6.1	−26.7	74.9	42.2	0.48
Stillhouse (26.7)	15	7	78	−0.52 ± 0.26	−0.28 ± 0.32	0.03 ± 0.37	−2.1	−0.5	0.6	−2.0	−0.07
Texana (40.5)	24	18	58	1.72 ± 0.71	1.24 ± 0.29	0.67 ± 0.55	16.7	9.0	15.7	41.5	1.02

Negative C flux indicates a carbon sink. Canyon Lake B arm data was deleted due to minimal oxygen change

and these differences in production rates drove the resulting trends in P:R ratios. Our planktonic production rates were based on optimum summer light regimes, no light inhibition, and seasonally maximum temperatures; thus they represent production potentials, or maxima, rather than annual averages. Actual in situ summer rates of production in the reservoirs are likely somewhat lower due to partial cloud cover on some days, but respiration rates would not likely be affected by that factor. Hence, actual P:R rates are likely lower. Furthermore, many productivity studies present annual averages from high latitude, natural lakes that by comparison have lower temperatures and greater light penetration with depth. Nonetheless, our areal production values were on the upper end of a previously reported range of 0.067–3.975 g C m^{-2} day^{-1} for 70 reservoirs with a range of trophic states (Kimmel et al. 1990). Knoll et al. (2003) examined seasonal production trends in three Ohio reservoirs and found the maximum occurred in late summer in one reservoir but there were only weak seasonal trends in the remaining two reservoirs. Year to year variability in summer maxima may be even greater than seasonal variability.

One physical factor that contributed to higher production rates at inflow and mid-reservoir zone sites was their shallow depth. In a study of over 640 rivers, lakes, and impoundments in the USA, Soballe and Kimmel (1987) found that production rates and chlorophyll *a* concentrations were higher at shallow sites ($r = 0.6$). Even shallow sites with higher inorganic turbidities can exhibit high production rates (Lind et al. 1997). Furthermore, at shallow, upreservoir sites, production rates were more strongly related to trophic state than in open-water portions of the reservoirs. A previous analysis of the 2006 data from these reservoirs demonstrated that phytoplankton production rates were related to nutrient concentrations only at shallow sites (Forbes et al. 2008), suggesting a hierarchical structure in predictor variables at spatial scales (Scott et al. 2008). del Giorgio and Peters (1993) found that mean planktonic production (mg C m^{-3} day^{-1}) was positively correlated with trophic state (as inferred by chlorophyll concentrations, Eq. 1) and that primary production exceeded respiration (Eq. 2) at chlorophyll concentrations greater than 17 mg m^{-3}.

$$\mathrm{P_{lakes}} = 10\mathrm{Chl}^{1.19}\left(r^2 = 0.75,\ n = 163, \mathrm{S_{xy}} = 0.380\right) \tag{1}$$

$$\mathrm{R_{lakes}} = 45\mathrm{Chl}^{0.65}\left(r^2 = 0.91,\ n = 41, \mathrm{S_{xy}} = 0.218\right) \tag{2}$$

In our study, primary production exceeded respiration at chlorophyll *a* concentrations of 9.5 mg m^{-3} in inflow zones and 35 mg m^{-3} in mid-reservoir zones. In contrast, open-water sites were generally heterotrophic regardless of chlorophyll content (Fig. 6) The slope of our respiration regression line (Fig. 6d) is remarkably similar to that for 36 lakes reported by del Giorgio and Peters (1993; Eq. 2) although our intercept is twice as high. This may be in part due to our inability to measure dissolved oxygen changes at sites with chlorophyll *a* values less than 5 mg m^{-3}, while del Giorgio and Peter's data set included chlorophyll concentrations between 0.3 and 1,000 mg m^{-3}. Our higher intercepts may also be a function of latitude and season (summer only). Thus, although others have concluded that respiration is generally high and provides a constant potential for heterotrophic activity regardless of phytoplankton production (Tranvik 1992; Wetzel 1992), we found that respiration rates were related to chlorophyll; however, they did not vary among reservoir zones.

Even when taking the inflow and mid-reservoir zone contributions as carbon sinks into account, the majority of reservoirs in our study were net carbon sources (Table 3). There are several reasons why reservoirs could exhibit even greater heterotrophy than natural lakes. Because reservoirs tend to have larger watersheds and greater hydrologic forcing than natural lakes (Thornton 1990) they may transport and trap more allocthonous and inorganic material than lakes (Harrison et al. 2009). Despite lower relative sediment organic content, global estimates suggest that reservoirs accumulate nearly four times as much organic carbon annually than natural lakes (Dean and Gorham 1998). In addition, river-borne sediment loads have increased approximately 200% in modern times (Falkowski et al. 2000).

Respiration rates in reservoirs may be increased by frequent water column mixing and resuspension of previously settled material. Furthermore, reservoirs may be stratified less often than natural lakes, thus promoting more frequent entrainment of previously settled material into the water column (Filstrup et al. 2009), as observed in midsummer water column turnover at several downreservoir sites during this study.

Finally, autochthonous carbon, including that created in the inflow and mid-reservoir zones, contributes to respiration in open-water zones. High summertime primary productivity in inflow and mid-reservoir zones may increase P:R ratios by CO_2 fixation, but this autochthonous carbon is likely to be decomposed within the same reservoir. Depending on flow and mixing conditions, some portion of this organic carbon would be transported downreservoir to the open-water zone where much of it would decompose or settle (Lind 2002) contributing to lower P:R ratios in the open-water zone and the total reservoir carbon load.

Recent estimates of CO_2 emissions from reservoirs worldwide indicated that they comprise as much as 4–7% of anthropogenically produced CO_2 (St. Louis et al. 2000). However, data on reservoir carbon fluxes are limited, particularly in subtropical and saline systems. The mean carbon flux based of the eight reservoirs in this study was 0.74 (±0.31) g C m^{-2} day^{-1}, and all but two of the reservoirs, Aquilla and Stillhouse, were net heterotrophic. Lake Aquilla was strongly autotrophic in 2006, a low water year, but heterotrophic in 2005, a near-normal water year. Aquilla is shallow, lies in an agricultural watershed, and has experienced sedimentation rates of over 55.5 ha m per year (Amonett and Bednarz, unpub.). Aquilla has a relatively low watershed to impoundment area ratio, a feature that has been associated with significantly greater organic carbon burial rates (Downing et al. 2008). Planktonic metabolism in Stillhouse was essentially at balance in the open-water zone (0.03 ± 0.37 g C m^{-2} day^{-1}), with slightly higher production in the inflow zones, resulting in a whole reservoir flux of −0.07 g C m^{-2} day^{-1}. This oligotrophic reservoir appears to remain more or less at equilibrium with respect to carbon flux. Our eight-reservoir mean carbon flux rate of 0.74 (±0.31) g C m^{-2} day^{-1}, is similar to the mean of 0.96 g C m^{-2} day^{-1} reported by St. Louis et al. (2000) for 22 northern and tropical reservoirs.

The results of this study are based on summer and primarily low-flow conditions and thus may not represent rates during other seasons or periods of varying hydrology. However, it is important to recognize that most estimates of carbon flux are derived from open-water sites and as our calculations show, the inflow and mid-reservoir zones not only account for close to half of the surface area of these reservoirs, they often act as carbon sinks. Clearly, extrapolating open-water measurements of heterotrophy or carbon emissions to the entire reservoir surface area could substantially overestimate carbon flux in reservoirs. Although further study is needed to determine annual rates of production and respiration in subtropical reservoirs, the spatially explicit carbon balances presented in this study should be considered in calculations of global carbon cycling.

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