Aquatic Ecology **36:** 355–369, 2002.
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Factors regulating autotrophy and heterotrophy in the main channel and an embayment of a large river impoundment

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Accepted 17 August 2001

Key words: bacteria, DOC, nutrient limitation, phytoplankton

Abstract

We characterized seasonal patterns of phytoplankton and bacterial biomass, production and nutrient limitation along a lateral transect within a large river impoundment. We hypothesized that the balance between autotrophy and heterotrophy was related to depth gradients and differences in water residence time (WRT) between the main channel and an embayment. Heterotrophy predominated in the main channel with bacterial production exceeding phytoplankton production by a factor of 3.3. In the embayment, autotrophy and heterotrophy were more closely balanced (ratios of bacterial to phytoplankton production ca. 0.8). Phytoplankton and bacterial biomass were positively correlated with WRT. However, WRT accounted for less than 50% of variation and its predictive power was comparable to models based on nutrient or DOC concentrations. Bacterial production was correlated with phytoplankton biomass and production suggesting that algal-derived C may be an important substrate for bacterial growth even in systems dominated by allochthonous inputs. Our experimental data suggest that nutrient limitation may be important particularly in embayments where biomass was somewhat higher and substrate concentrations were lower. Nutrient limitation in the main channel was rare whereas N and P amendments consistently stimulated phytoplankton growth rates in the embayment. Bacterial cell densities did not respond to nitrogen or phosphorus additions in either the main channel or embayment.

Introduction

Ecologists have long been interested in the balance and coupling between autotrophic and heterotrophic processes because of their central importance to organic matter cycling in ecosystems (Lindemann, 1942; Odum, 1969). The traditional view of a trophic pyramid (i.e., a large 'base' of autotrophic production supporting consumers) has given way to an appreciation that heterotrophy may exceed autotrophy when external carbon subsidies supplement internal (autochthonous) primary production (del Giorgio & Peters, 1993, 1994; del Giorgio & Gasol, 1995). Spatial and temporal variability in the balance between autotrophy and heterotrophy has important implications for material and energy cycling within food webs (Polis et al., 1996). Waterbodies dominated by autotrophic activities are net sources of organic carbon, net sinks of inorganic C, N and P and have an herbivore-based trophic structure. A predominance of heterotrophic activity drives a net consumption of organic carbon, net mineralization of C, N and P and a detritivore-based food web.

The worldwide increase in water retention structures during the last half century has made the study of impoundments especially important (Dynesius & Nilsson, 1994; Vorosmarty et al., 1997), but much less research has been conducted on autotrophic- heterotrophic coupling in these systems. Impoundments display attributes of both lakes and rivers depending upon the rate of discharge from the dam. Typically, they experience shorter water residence times and higher allochthonous inputs of nutrients, organic carbon and suspended particles than lakes. However,

they are less reliant on allochthonous sources of organic matter than free-flowing rivers and can support high phytoplankton production, especially near the dam and during periods of reduced discharge (Kimmel et al., 1990). During periods of elevated discharge, the suspended particulate load carried in flowing waters reduces light penetration and constrains primary production (Alpine & Cloern, 1992; Cole et al., 1992; Dokulil, 1994).

Allochthonous carbon inputs, coupled with constraints imposed on primary production, should favor a predominance of heterotrophic activity in rivers and impoundments. Findlay et al. (1991) showed that bacterial production in the Hudson River exceeded phytoplankton production by 7-fold. By comparison, bacterial production in lentic and marine systems averages only about 30% of phytoplankton production (Cole et al., 1988) and ratios of phytoplankton photosynthesis to bacterial respiration are near unity (del Giorgio & Peters, 1993, 1994; del Giorgio & Gasol, 1995). Bacterial and phytoplankton production are correlated across lentic and marine systems suggesting that bacteria depend on algal-derived carbon or that both share a common limiting substrate (Robarts & Wicks, 1990; Le et al., 1994; Ochs et al., 1995). In heterotrophic systems, weak coupling between phytoplankton and bacterial production is expected if bacteria depend on allochthonous C inputs.

Water residence time (WRT) and mixing depth may play an important role in regulating the balance between phytoplankton and bacterial production in river impoundments. Seasonal and localized low-flow conditions may permit phytoplankton blooms such that rates of primary production equal or exceed bacterial production. Spatial variability in WRT arises from longitudinal gradients in channel geomorphology and from lateral variation in flow velocities. Embayments are typically shallow and have longer WRT compared to the main channel. Shallow depths result in higher ambient light levels within the water column particularly in impoundments where advective forces preclude thermal stratification. The combined effects of greater light availability and reduced advective losses result in horizontal gradients in phytoplankton abundance (Marzolf et al., 1991; Spaink et al., 1998) that favor a predominance of autotrophy within embayments. Nutrient depletion will result in resource limitation within embayments when algal nutrient demands exceed rates of supply. In the main channel, greater depths result in lower average irradiance and favor a predominance of heterotrophy. Low algal production also acts to maintain high per capita resource availability and may preclude nutrient limitation.

As a part of a larger study on organic matter transport, deposition and transformation in a large river impoundment, we characterized seasonal and spatial variability in phytoplankton and bacterial biomass, production and nutrient limitation. A time series of samples was obtained along a lateral transect that included the main channel and an embayment. Data were used to test two hypotheses: (1) heterotrophy predominated in the main channel whereas autotrophy and heterotrophy were more closely balanced in the embayment, and (2) WRT constrained biomass and production in the main channel while substrate limitation (nutrients, labile organic C) was restricted to the embayment. Seasonal and spatial differences in the taxonomic structure of phytoplankton assemblages were also analyzed to detect community-level responses to changing nutrient and WRT conditions.

Materials and methods

Study area

Kentucky Lake was formed in 1944 and is the last in a series of 8 impoundments created from the Tennessee River by the Tennessee Valley Authority. The lake is 290 km in length, has a surface area of 648 km^2, a mean depth of 5.4 m and a maximum depth of 21 m (in the old river channel; Sickel, 1989). The lake's watershed is 104 117 km^2 in area and is comprised of 68% forested, 26% agricultural, and 4.5% urban lands (MARC 1990). Annual discharge from the dam is 63 km^3 and the average water retention time of the lake is 16.7 days (TVA, 1980).

Five sampling sites were chosen along a lateral transect that extended across the main stem of the lake and into an embayment. The embayment is located approximately 32 km above Kentucky Dam. It has an area of 1.5 km^2 and an average depth of 3.6 m. Estimates of water turnover time in the embayment based upon embayment volume and stream inflow (Ledbetter Creek) average 100 days (Johnson, 1992). Two stations were within the embayment, two stations were in the main channel and one was at the mouth of the embayment. Lake depth ranged from 2 m at the most upstream station to 8 m at the mouth of the embayment and 16 m in the main channel. The average depth for the main channel (cross section) is 9 m. Samples were collected monthly from May to November (excluding

October) in 1997. No significant differences in chemical or biological parameters were found between the two stations within the embayment or between the two stations within the main channel. Therefore, a single averaged value is presented to compare embayment and main channel data.

Temperature, light and dissolved nutrients

Temperature was measured at 1-m intervals (surface to bottom) using a YSI Model 3800 Water Quality logging system. Light (Photosynthetic Active Radiation) profiles were obtained with a LiCor LI-185b Submarine Photometer equipped with a spherical quantum sensor. Attenuation coefficients for downwelling irradiance (Kd) were calculated from linear regressions of natural logarithms of downwelling irradiance against depth (Kirk, 1994). Water samples were collected just below the surface and 1-m above the bottom with a Van Dorn water sampler. Dissolved organic carbon (DOC) was measured on an automated total carbon analyzer (Shimadzu Model TOC-5050A) after sparging for four minutes to remove inorganic carbon. Nitrate concentrations were measured using the automated cadmium reduction method (APHA, 1992). Soluble reactive phosphorus (SRP) concentrations were determined using the ascorbic acid method (APHA, 1992). Nitrate and SRP analyses were conducted on a Lachat QuikChem 8000 Flow Injection Analyzer.

Phytoplankton

Water samples for chlorophyll, primary production and phytoplankton enumeration were taken at 3 depths between the surface and the 1% light level. Samples for chlorophyll analyses were filtered through 1.2 μm Whatman GF/C, macerated in 5 ml of 90% acetone and allowed to extract for 12 hours at 4 °C. Extracts were analyzed for chlorophyll *a* and pheophytin *a* on a Hitachi Model 100-40 spectrophotometer with a 1 cm pathlength and 2 nm bandwidth. Optical densities were measured at 664 nm and 750 nm, and at 750 nm and 665 nm after acidification to correct for pheophytin *a* (Wetzel & Likens, 1991).

Primary production was measured using the isotope technique of Vollenweider (1969). Radiocarbon (0.54 μCi of $[^{14}C]$-$NaHCO_3$) was added to three 60-ml BOD bottles (two light bottles and one dark bottle) which were incubated at each of the three depths for 2 h at mid-day. Samples were filtered through 0.45 μm Gelman GN-6 filters and radioactivity was measured with a Beckman LS -5000CE liquid scintillation counter. Production data were used to derive photosynthesis-irradiance (P-I) models based on the tangential equation of Jassby & Platt (1976). Equations were derived for monthly data pooled across sites. These models accounted for 71% to 96% of the variation in biomass-specific production. The average estimate of light utilization efficiency (α) for all sites and dates was 0.549 ± 0.108 mg C mg chla^{-1} h^{-1} μmole quanta^{-1} m^{-2}. The maximum photosynthetic rate (P^b_{max}) averaged for all sites and dates was 1.74 ± 0.22 mg C mg chla^{-1} h^{-1}. These estimates are comparable to values reported previously for Kentucky Lake (Marzolf et al., 1991; Spencer et al., 1998).

Samples for phytoplankton enumeration were preserved with 2.25-ml of M3 fixative (APHA, 1992) and stored in the dark at room temperature until analysis. Subsamples were filtered through 0.45 mm Millipore membrane filters, cleared in glutaraldehyde and mounted with EUPARAL. Identification and enumeration of phytoplankton was made with an Olympus BH-2 microscope at 500× and 1250×, under Nomarski differential interference contrast. Cell measurements were made on 15–20 randomly selected cells of predominant species. Volumes of the cells were estimated by comparing cells to simple geometric shapes. The mean cell volumes for the common species were multiplied by population density to derive an estimate of species biovolume. Biovolume was converted to biomass assuming a specific gravity of 1. Algal carbon was estimated from biomass using taxon-specific conversion factors (Olrik et al., 1996).

Bacteria

Water samples were taken just below the surface and 1 m from the bottom for estimation of bacterial production and cell densities. Production was measured by the ^{3}H-thymidine (^{3}H-TdR) method with chloroform-phenol extraction (Wicks & Robarts, 1987; Bell, 1993). Three to four replicate samples (10 ml) were placed in 20 ml glass scintillation vials for each site and depth. 50 μl of 20 nm ^{3}H-TdR (16.8 μCi) was added and the vials were incubated *in situ* (1 m below the surface) in a plexiglass chamber. Incubations occurred away from direct sunlight and the length of incubation was temperature dependent (20–60 min depending on season). Incubation was ended with the addition of 37% formaldehyde. 5N NaOH (525 μl) was added to each sample and samples

remained at room temperature for 1 h. Trichloroacetic acid (TCA, 100%) was added and samples were placed on ice before filtration. Samples were filtered onto nitrocellulose filters (0.45 μm Schleicher & Schuell) at low pressure (<100 mm Hg). Vials were rinsed with 2 ml ice-cold 5% TCA and this was added to the filtrate. The sides of the filter funnel were rinsed three times with 5% TCA to ensure all of the sample was washed onto the filter. Filters were rinsed with chloroform-phenol (50% [w/v]), and ice-cold 80% ethanol before being placed into 20 ml plastic scintillation vials. Ethyl acetate (1 ml) was added to each vial to dissolve the filters, and the solution was left for 30 min before 10 ml of scintillation cocktail (Scintiverse E) was added.

An isotopic dilution assay was performed in November 1997 to determine if background levels of thymidine affected the results of the experiments. Unlabeled thymidine was added to composite samples (three replicates) from the main channel (stations 4 and 5) and the embayment (stations 1 and 2) as 2 nm, 5 nm and 10 nm. Radiolabelled thymidine was added (20 nm) to each replicate sample. Background thymidine did not significantly dilute the amount of radiolabelled thymidine introduced into the samples.

Samples for bacterial enumeration were preserved with 250 μl of 37% formaldehyde and stored at 4 °C until analysis. Two to four replicate samples were collected for each station and depth (or treatment for growth rate experiments). Enumeration followed the procedure of Porter & Feig (1980). Subsamples (1 ml) were taken from each vial and inoculated with DAPI solution (0.5 μg ml^{-1}). After 5–10 min, subsamples were filtered onto 0.2 μm Millipore GTBP filters and immediately examined under a microscope. Bacteria were enumerated using a Zeiss Axioplan microscope equipped with a HB050 Mercury Lamp (Exciter filter: G365, Beam Splitter: FT395, Barrier filter: LP420). Enumerations were made at 1000× under oil immersion. Twenty randomly selected grids were counted per slide and two to three replicate slides were made for each sample.

For calculation of bacterial carbon, an average cell biovolume of 0.1 μm^3 was used based on measurements of cell size and previously published values (Scavia & Laird, 1987; Chrzanowski & Hubbard, 1988; Riemann et al., 1990; Findlay et al., 1991; Morris & Lewis, 1992; Hudson et al., 1992; Ochs et al., 1995). The carbon per cell was estimated using calculations from Norland (1993). Biomass was calculated by multiplying carbon content (180 fg C μm^{-3}) by the average biovolume and abundance of bacteria per sample. Bacterial biomass was used to convert thymidine incorporation estimates to carbon production using the following equation (Bell 1993):

$$\mu\text{g C L}^{-1}\text{ h}^{-1} = (\text{moles TdR L}^{-1}\text{ h}^{-1})\,(\text{cells mole}^{-1})\,(\text{carbon cell}^{-1})$$

where an empirical value of 2×10^{18} cells mole^{-1} was used based on Moriarty (1986).

Nutrient enrichment experiments

Nutrient addition experiments were conducted on three dates (May, July, August) at each of three sites (embayment, mouth of the embayment and main channel). Experimental design and analysis were patterned after Bukaveckas & Shaw (1998) and Vrede et al. (1999). Translucent polyethylene containers (10 l) were used for the experiments. Water was pumped from approximately 1 m below the surface into a 125 l mixing container before being transferred into the cubitainers. Water was passed through a 150 μm zooplankton net to eliminate large zooplankton. The experimental design consisted of 12 enclosures: 3 replicates each of controls, phosphorus addition (+P), nitrogen addition (+N), and a combination of nitrogen and phosphorus (+PN). Inorganic nitrogen was added as $NaNO_3$ (400 μg l^{-1}) and phosphorus was added as NaH_2PO_4 (10 μg l^{-1}). The cubitainers were incubated for 48 hours at 1 m depth. Chlorophyll concentrations and bacterial cell densities were determined at the start and end of each experiment to quantify growth responses. Phytoplankton responses were expressed as the percent increase in Chl *a* compared to enclosures with no nutrients added:

$$\text{Nutrient response} = (\text{Chl}_{\text{nutrients}} - \text{Chl}_{\text{control}})/\text{Chl}_{\text{control}},$$

where $\text{Chl}_{\text{nutrients}}$ represents the mean Chl *a* concentration after incubation among the three replicates of the particular nutrient addition treatment and $\text{Chl}_{\text{control}}$ is the mean Chl *a* concentration after incubation among replications where no nutrients were added. Ratios of growth rates (ln-transformed chlorophyll and bacterial cell densities) under ambient and nutrient-saturated conditions were also used to quantify the severity of nutrient limitation (Sterner, 1994). Significant treatment effects were determined using one-way analysis of variance (ANOVA) and Student–Newman–Keuls comparisons of treatment means. Statistical significance was determined at the $p < 0.05$ level.

In addition to the *in situ* enclosure experiments, a laboratory dilution assay was performed on one date (August, 1997) following the method of Painchaud et al. (1996). Composite samples (surface and bottom) were collected at each of three sites (embayment, mouth and channel). Two treatments were made from each composite sample: one culture consisted of untreated water and one consisted of untreated water and filtered water (0.2 μm Millipore GTBP) in a 1:4 ratio. Three replicates were prepared for each treatment and site. Cultures were kept in autoclaved-sterilized plastic bottles in the dark at room temperature for 36–40 hours. Subsamples (10 ml) were removed at 12-h intervals for enumeration. Growth rate was determined by natural log-transformation of the count data using calculations described in Painchaud et al. (1996).

Statistical analysis

Measurements of biomass and production were analyzed statistically using a two-way analysis of variance in which month and location (embayment vs. main channel) were tested as explanatory variables. Variability in these data was also related to several environmental parameters through linear regression. Water retention time, water temperature, and DIN and SRP concentrations were evaluated as predictors of phytoplankton and bacterial biomass and production. For bacteria, correlations with DOC, chlorophyll *a*, phytoplankton biomass and production were also tested. All statistical analyses were conducted using SIGMASTAT (Version 2.0, 1992–1995).

A multivariate procedure (canonical correspondence analysis) was used to analyze seasonal and spatial differences in phytoplankton community composition in relation to selected environmental variables. Canonical correspondence analysis (CCA) is a weighted average method that relates to a unimodal response model in which the abundance of any species has a limited value range for each environmental variable (Ter Braak, 1988). Environmental parameters included water retention time, temperature, light attenuation, chlorophyll, conductivity, DIN, SRP and dissolved SiO_2 concentration. The variables of DIN, SRP, water retention, light and temperature were log-transformed because of non-normal distribution. Site scores were estimated from the linear combination of the environmental parameters that form the ordination axes. Relative carbon biomass of 70 dominant organisms were used for this analysis.

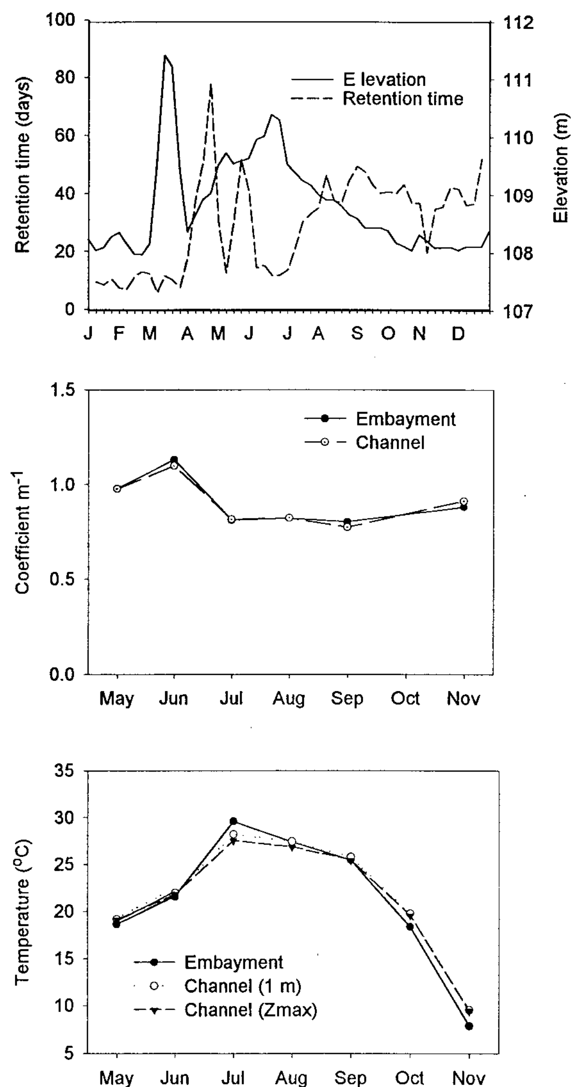

Figure 1. (Upper) Water retention time and surface elevation of Kentucky Lake during 1997 (weekly averages). Data provided by Hancock Biological Station, the Tennessee Valley Authority and U.S. Geological Survey. (Middle) Average monthly PAR attenuation coefficients for Ledbetter embayment and the main channel of Kentucky Lake during May-November, 1997. (Lower) Water temperatures 1 m from the surface of Ledbetter embayment and at 1 m from the surface and bottom of the main channel in Kentucky Lake during May-November, 1997.

Results

Lake physical-chemical conditions

Pronounced seasonal variability in water retention time and lake surface elevation was observed during the period of study (Figure 1). High rainfall in June resulted in short water retention (<20 days)

and high pool elevation (>110 m). Late summer (July–November) was characterized by longer water retention (30–50 days) and lower pool elevation (ca. 108 m). Despite variation in WRT, PAR attenuation coefficients (Kd) showed little seasonal variation (range = 0.8 to 1.1 m^{-1}) and were similar in both the embayment and main channel (Figure 1). Attenuation coefficients corresponded to photic depths ($z_1\%$) of 4–5 m. Photic depths exceeded the average depth of the embayment (3.6 m) but included only half of the water column in the main channel (average depth = 9 m). Water temperatures ranged from 7 to 30 °C during the period of study and showed little variability among sites or with depth (Figure 1). As no thermal (or chemical) stratification was observed, we present chemistry data as averages for the entire water column.

Nutrient concentrations (N, P and Si) were higher in the main channel than in the embayment. Nitrate concentrations ranged from 50 to 300 $\mu g\ l^{-1}$ in the main channel but did not exceed 150 $\mu g\ l^{-1}$ in the embayment (Figure 2). Throughout July–September, nitrate concentrations were near detection limits (<5 $\mu g\ l^{-1}$) in the embayment but did not drop below 50 $\mu g\ l^{-1}$ in the main channel. Ammonium concentrations ranged from 30 to 80 $\mu g\ l^{-1}$ in the main channel and from 20 to 40 $\mu g\ l^{-1}$ in the embayment. Phosphorus (SRP) concentrations in the embayment ranged from <5 to 20 $\mu g\ l^{-1}$. In the main channel, low SRP concentrations in mid-summer (ca. 10 $\mu g\ l^{-1}$) were preceded and followed by higher concentrations (30–50 $\mu g\ l^{-1}$) during June and November. Dissolved SiO2 concentrations increased gradually from 2–3 mg l^{-1} in May to 8–9 mg l^{-1} in November (data not shown). Dissolved SiO_2 was 1–2 mg l^{-1} higher in the main channel as compared to the embayment. DOC concentrations showed pronounced seasonal variability but little spatial variability (Figure 2). DOC increased from 3 mg l^{-1} in June to 10 mg l^{-1} in July–August before decreasing to early summer values.

Biomass and production

Bacterial biomass was always less than phytoplankton biomass in both the embayment and main channel (Figure 3). On average, bacterial biomass was 30% (embayment) and 38% (main channel) of phytoplankton biomass. Lowest values (7–24%) occurred in June–July during peak phytoplankton biomass and highest values (65–82%) were associated with low phytoplankton biomass in September. For both phytoplankton and bacteria, volumetric estimates of biomass were generally higher in the embayment but these differences were small in comparison to the 2-fold difference in depth. As a result, areal estimates of biomass were similar among the embayment and channel sites. Algal biomass in the main channel was positively correlated with the average WRT during the preceding 10 days ($r^2 = 0.32$; $p < 0.001$). Bacterial biomass was significantly ($p < 0.001$) correlated with N-DIN ($r^2 = 0.46$), water retention time ($r^2 = 0.44$), and DOC ($r^2 = 0.45$).

Despite large differences in biomass, areal rates of autotrophic and heterotrophic production were similar. Averaged for the period of study, bacterial production in the main channel exceeded phytoplankton production by a factor of 3.3. This estimate was biased by a single large value (10-fold difference in November) and does not typify summer conditions when bacterial production exceeded phytoplankton production by a factor of 1.4 to 2.2. Autotrophic and heterotrophic production were more closely balanced in the embayment with bacterial production averaging 85% of phytoplankton production. Largest differences were in July and September when bacterial production was about half of phytoplankton production. Bacterial production was highest in June, and decreased through the sampling period. Bacterial production was most strongly correlated with phytoplankton biomass ($r^2 = 0.57$; $p < 0.001$) and phytoplankton production ($r^2 = 0.33$; $p = 0.009$).

Growth limitation assays

Phytoplankton responses to nutrient additions differed seasonally and among sites (Table 1). In May, a significant response to nutrient addition was detected only in the embayment (P stimulation) and ratios of growth rates at ambient to nutrient-saturated levels ($r_{amb} : r_{sat}$) were high (> 80%). During July, 2 of 3 experiments showed nutrient effects (excluding main channel) and ratios of $r_{amb} : r_{sat}$ had decreased to 50–80%. By August, nutrient limitation was evident at all three sites and growth rates at ambient nutrient levels were <25% of nutrient-saturated rates. Among the July–August experiments, responses to N addition were greater than for P addition although in all cases highest chlorophyll concentrations were observed in enclosures receiving both P and N.

Bacterial cell densities showed no response to additions of nitrogen and phosphorus during experiments conducted at three sites in July and August

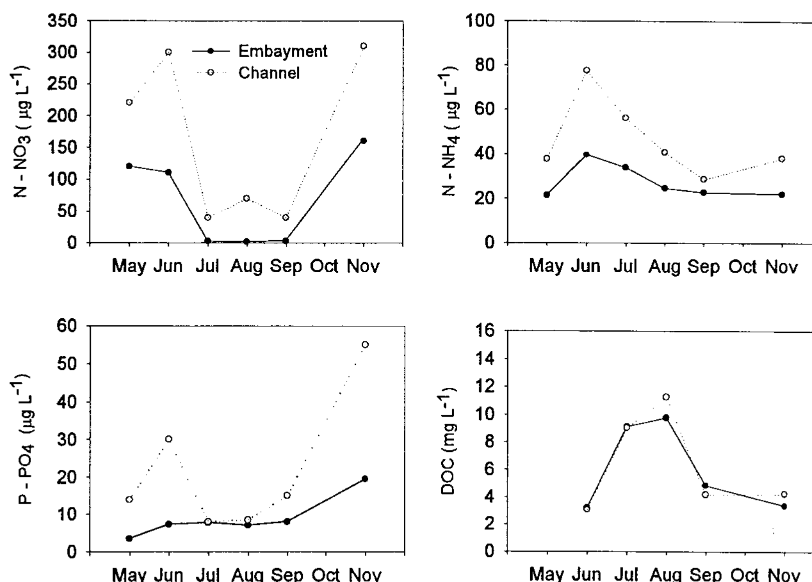

Figure 2. Concentrations of N-NO3, N-NH4, P-PO4 and DOC in Ledbetter embayment and the main channel of Kentucky Lake during May–November, 1997 (average for water column).

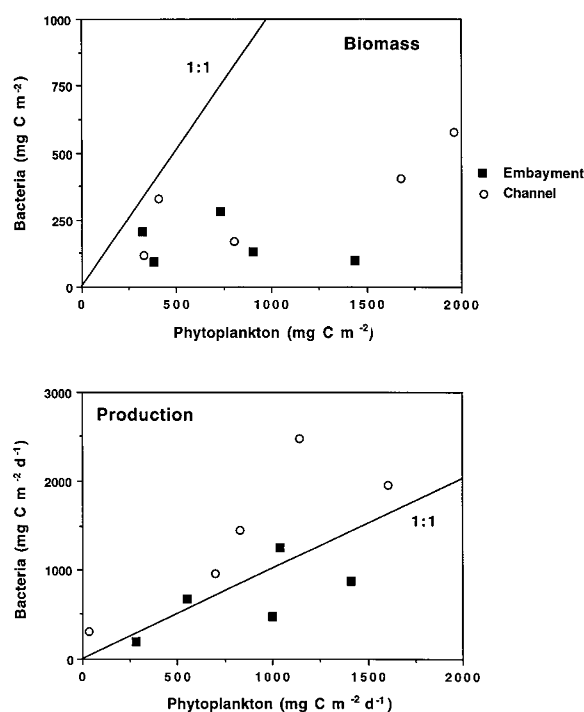

Figure 3. Phytoplankton and bacterial biomass (top panel) and production (bottom panel) in Ledbetter embayment and the main channel of Kentucky Lake during May-November, 1997. All data are expressed as areal values.

(Figure 4). Bacterial densities in nutrient-enriched enclosures were not significantly different from densities in control enclosures ($p = 0.33$). As a result, estimated growth rates at ambient nutrient concentrations were within 80–100% of nutrient-saturated growth rates. When per capita substrate availability was altered through dilution of cell densities (experiment conducted in August), pronounced differences in bacterial responses were observed among the embayment, embayment mouth and main channel (Figure 5). In the main channel, bacterial growth rates in undiluted cultures were comparable to those observed in diluted cultures suggesting that increases in per capita substrate availability had no effect on bacterial growth. In the embayment, undiluted cultures showed little growth whereas densities in diluted cultures increased fourfold suggesting that growth rates were substrate limited. Intermediate results were obtained at the mouth of the embayment where modest growth was observed in undiluted cultures and higher growth rates in diluted cultures.

Phytoplankton community composition

CCA axes 1 and 2 accounted for 56% of the variance in phytoplankton community structure among samples collected monthly at three sites (embayment, mouth of the embayment, main channel). Samples collected during the same month were grouped closely in ordination space whereas samples collected at a given

Table 1. Chlorophyll a concentrations in experimental enclosures (mean for 3 replicates ± standard deviation). Data shown are initial (Control-0) and final (Control-48, +N, +P, +NP) concentrations during the 48 h incubation. The severity of nutrient limitation is expressed as a ratio of ambient and nutrient-saturated growth rates (r_{amb}:r_{sat}). Stations are denoted as Emb (embayment), Mou (mouth of embayment) and Chan (main channel). Significant pair-wise differences were assessed among Control (48), +N, +P and +NP enclosures by a Student–Newman–Keuls t-test at $p < 0.05$

Station	Month	Chlorophyll (μg L^{-1})					Significant response	$r_{amb} : r_{sat}$
		Control (0)	Control (48)	+N	+P	+NP		
Emb	May	34.1 ± 10.8	76.4 ± 18.3	58.8 ± 8.3	99.3 ± 5.6	144.2 ± 2.5	P/NP	0.80
Mou		27.0 ± 4.6	110.9 ± 29.4	74.4 ± 10.4	122.7 ± 68.6	98.0 ± 30.9	–	0.99
Chan		21.8 ± 3.5	69.3 ± 20.4	81.1 ± 25.3	83.5 ± 13.9	83.7 ± 10.9	–	0.94
Emb	July	17.7 ± 2.9	36.7 ± 4.0	49.2 ± 7.8	57.0 ± 4.1	66.8 ± 6.4	N/P/NP	0.76
Mou		31.0 ± 3.7	37.9 ± 6.0	60.7 ± 0.7	32.8 ± 2.5	71.9 ± 2.3	N/NP	0.52
Chan		14.5 ± 2.8	43.2 ± 15.1	53.0 ± 6.7	56.4 ± 9.3	67.9 ± 12.3	–	0.80
Emb	Aug	20.6 ± 2.4	22.7 ± 0.4	40.9 ± 6.6	21.4 ± 1.3	50.1 ± 6.3	N/NP	0.21
Mou		31.4 ± 4.5	27.8 ± 0.5	48.4 ± 3.5	25.8 ± 0.8	57.1 ± 10.7	N/NP	0.01
Chan		35.6 ± 2.8	24.0 ± 3.1	54.1 ± 0.9	27.1 ± 5.0	63.0 ± 5.3	N/NP	0.01

site (through time) were widely separated in ordination space (Figure 6). Seasonal succession reflected shifts between diatom/flagellate-dominated communities during early- and late-summer and cyanobacteria-dominated communities in mid-summer (Figure 6). May and November communities were dominated by centric diatoms (*Cyclotella meneghiniana, Melosira ambigua*) and flagellates (*Chlamydomonas* spp., *Cryptomonas erosa, Peridinium cinctum*). Mid-summer months were dominated by *Oscillatoria limnetica, Anabaena wisconsinense*, and *Pseudoanabaena galeata*. The environmental variables that best explained variation in species composition were, for Axis 1, temperature and nitrogen (0.76 and −0.51, respectively) and, for Axis 2, SiO2 (−0.88).

Discussion

Our estimates of autotrophic production are based on short-term ^{14}C uptake, a method that may not account for loss of photosynthate through respiration (Carignan et al., 2000). Algal respiration has been shown to be an important sink for C in rivers, estuaries and other turbid systems where phytoplankton spend much of the day in darkness (Alpine & Cloern, 1988; Lewis, 1988; Cole et al., 1992). In Kentucky Lake, algal respiration may be particularly important in the main channel where only half of the water column is within the photic zone. Estimates of algal respiration vary by 10-fold (5–50% of P^b_{max}; Raven & Beardall, 1981) although values in the range of 5–15% of P^b_{max} are thought to approximate respiration by riverine phytoplankton (Cole et al., 1992; Howarth et al., 1996; Caraco et al., 1997). At 5% of P^b_{max}, we estimate that respiration was 34% (main channel) and 22% (embayment) of phytoplankton production. With correction for estimated phytoplankton respiration, ratios of bacterial to phytoplankton production increase from 0.9 to 1.1 (embayment) and from 1.6 to 2.4 (channel). Therefore, our overall finding that embayment conditions favor a closer balance between autotrophy and heterotrophy is not substantially effected. These data emphasize the importance of mechanisms regulating the critical depth ($z_1\%$:z_{mean}) in determining the balance between autotrophy and heterotrophy in advective environments and non-stratified lakes (Huisman et al., 1999).

Findlay et al. (1991) reported higher ratios of bacterial to primary production (7- fold) than we measured in the main channel of Kentucky Lake. The two waterbodies are similar with respect to their length, depth, water residence time and nutrient status. However, the Hudson River is twice as turbid (based on Kd) and areal phytoplankton production is half that observed in Kentucky Lake. Kentucky Lake is the last in a series of 8 impoundments on the main stem of the Tennessee River and it is likely that a substantial fraction of the rivers suspended sediment load is deposited in upstream basins. As a result, transparency is relatively high and changes in discharge have little effect on attenuation. Greater transparency may allow higher net phytoplankton production in comparison to free-flowing rivers and account for lower ratios

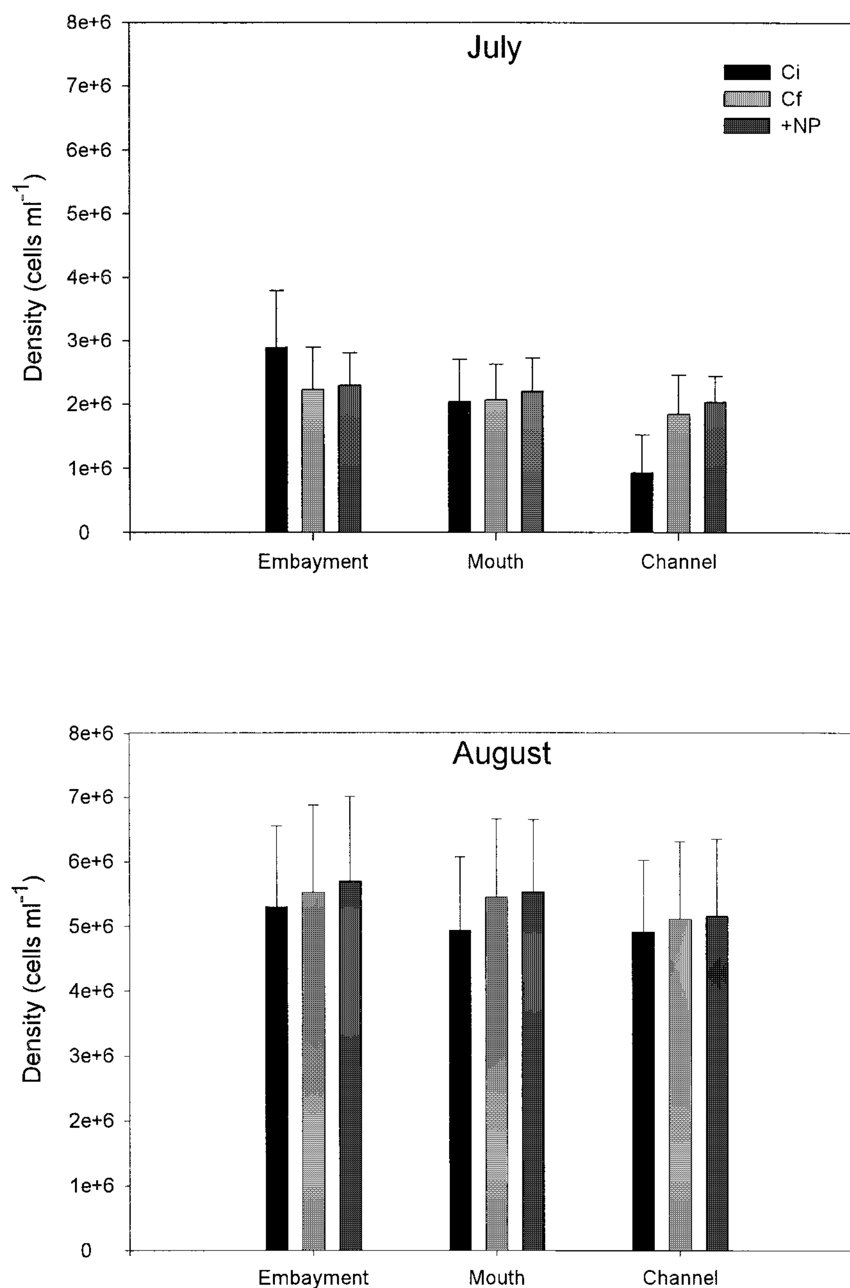

Figure 4. Changes in bacterial cell densities in response to nutrient enrichment during July (top panel) and August (lower panel) experiments conducted at three sites within Kentucky Lake. 'Ci' denotes control enclosures at 0 h, 'Cf' denotes control enclosures after 48 h, '+NP' dentoes nutrient-enriched enclosures after 48 h. Data shown are means and standard errors for 3 replicate enclosures.

of bacterial to phytoplankton production. Our growing season averages are likely to be conservative with respect to annualized conditions because ratios were greatest during the warmwater months. By November, phytoplankton production in the main channel had declined 50-fold from its peak in July whereas bacterial production declined only 8-fold (peak in June). As a result, bacterial production exceeded phytoplankton production by 10-fold.

While Kentucky Lake may be broadly categorized as a riverine environment based on its hydrology and geomorphology, the mechanisms that regulate au-

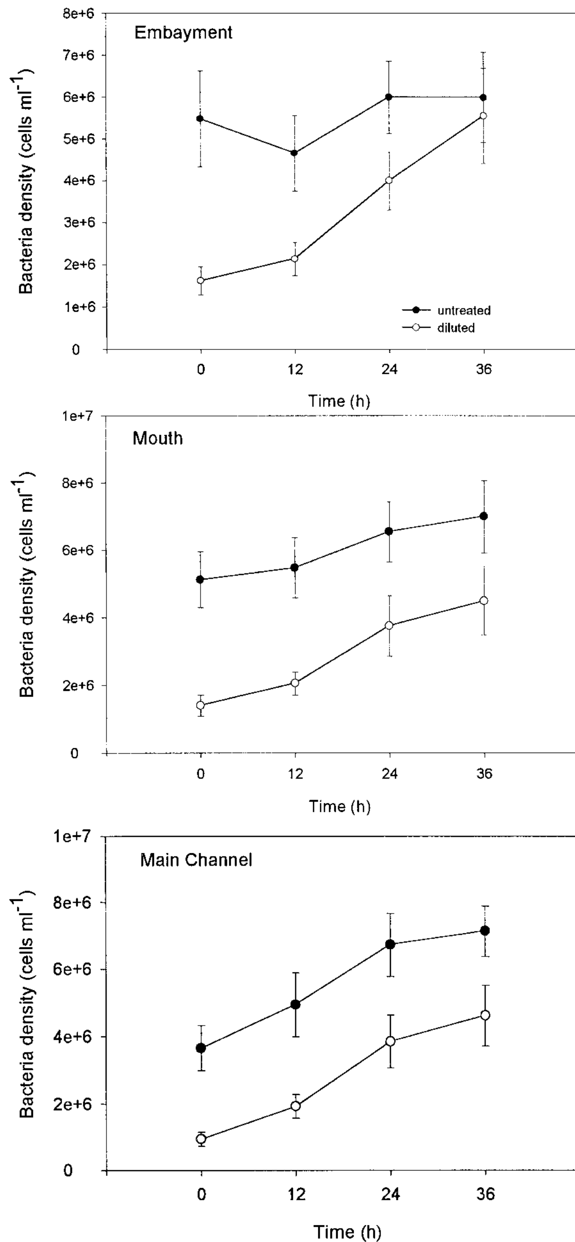

Figure 5. Changes in bacterial cell densities in diluted and undiluted cultures from the embayment (top panel), embayment mouth (middle panel), and main channel (bottom panel) of Kentucky Lake. Experiment was conducted in August 1997. Data shown are means and standard errors for 3 replicate cultures.

totrophic and heterotrophic activity may differ from those operating in free-flowing rivers. A number of studies have suggested that plankton production in both rivers and impoundments is constrained by advective losses. Søballe & Kimmel (1987) analyzed data from over 600 waterbodies in the United States and found that algal abundance per unit of phosphorus increased as a function of water residence time. Correlations between plankton biomass and WRT have also been reported from a number of site-specific studies (Pace et al., 1992; Thorp et al., 1994; Basu & Pick, 1996). Our study period spanned a range of WRT conditions (10–50 d; mean = 33 d) that was representative of annual conditions (range = 5–50 d; mean = 28 d). Phytoplankton and bacterial biomass were positively correlated with WRT. However, WRT accounted for less than 50% of variation and its predictive power was comparable to models based on nutrient or DOC concentrations. Volumetric estimates of phytoplankton and bacterial abundance were generally higher in the embayment compared to the main channel where WRT was presumably shorter but differences were small and in some cases not statistically significant. Thus, our data do not provide compelling evidence that WRT is the primary determinant of phytoplankton and bacterial activity in Kentucky Lake. In rivers, elevated discharge derives from source areas (lower-order streams and groundwater) where plankton abundance is likely to be low (Garnier et al., 1995). Increases in discharge cause reductions in plankton densities (within a fixed reach of the river) when downstream losses exceed the sum of upstream inputs and *in situ* growth rates. In Kentucky Lake, discharge is dominated by inputs from a series of impoundments upstream (accounting for 85% of lake outflow). Thus, changes in discharge may act to increase or decrease plankton abundance depending on abundances in upstream impoundments.

Our experimental data suggest that nutrient limitation may be important particularly in embayments where biomass was somewhat higher and substrate concentrations were lower. Statistically significant responses to nutrient addition were detected on all three dates in the embayment but only on one date (August) in the main channel. Nutrient limitation in the main channel was rare despite artificially high light levels during *in situ* incubations. The 1 m incubation depth exposed phytoplankton from the main channel to 2.8-fold higher daily PAR than those experienced by phytoplankton circulating through the average depth of the main channel (9 m). In the embayment, light levels in-

side the enclosures were similar (within 10%) to those experienced by phytoplankton circulating through the mean depth of the embayment (calculated as per Gosselain et al., 1994). Nutrient additions consistently stimulated growth rates of phytoplankton collected from the embayment and by August growth rates were less than 20% of nutrient-saturated growth rates.

Results from bioassay experiments were in agreement with chemistry data showing consistently lower nutrient concentrations in the embayment and declines in nutrients during late summer. The rapid decline in summer nitrogen levels to near detection limits is a pattern that has been observed in previous years (Hancock Biological Station, unpubl. data). Nitrogen concentrations were often below the half-saturation constants reported for a variety of algal taxa (20–200 μg l^{-1}; Sterner & Grover, 1998). The fall and rise of dissolved inorganic N corresponded to the onset and decline of cyanobacterial dominance suggesting that atmospheric N fixation may be important in supporting new production. Phytoplankton responses to N and the combined N+P addition were greater than for P addition alone. The occurrence of nutrient limitation in Kentucky Lake is consistent with the few studies that have directly measured nutrient limitation in impoundments (Sterner, 1994; Knowlton & Jones, 1996; Grover et al., 1999). Upstream and in-lake retention of N by phytoplankton uptake and microbial denitrification may account for the low nitrate concentrations in Kentucky Lake. Downstream gradients of decreasing NO_3 have been observed in other regulated rivers (Kohler, 1994; Lair et al., 1999; Bukaveckas et al., in press) but are not generally characteristic of natural lake-chain systems (Soranno et al., 1999).

The processes regulating bacterial biomass and productivity are much less understood. Some studies have shown bacteria to be regulated by organic carbon availability (e.g., Riemann & Søndergaard, 1986), while others have shown that nitrogen (Kirchman, 1990) or phosphorus (Brett et al., 1999) can act as limiting factors. Nutrient limitation was not evident for bacterial communities in Kentucky Lake. Bacterial cell densities showed no response to additions of N or P despite low ambient nutrient levels during July and August. As we excluded metazoan but not protozoan grazers from our *in situ* enclosures, we cannot discount the possibility that higher bacterial growth rates were masked by increased losses to small grazers. When per capita substrate availability was increased through cell dilution, we observed positive growth responses in the embayment but not in the main channel. These results were based on a single dilution assay performed in August but suggest that substrate limitation (most likely labile C) may occasionally be important. Higher bacterial abundance in the embayment coupled with longer water residence time may have resulted in depletion of labile C. Seasonal patterns in DOC concentration and bacterial abundance also suggest that C limitation may be important. Bacterial biomass peaked in August when nutrient concentrations were lowest but DOC concentrations were high. A 2 m rise in lake surface elevation during May–June preceded a substantial increase in lake DOC concentrations (from 3 to 10 mg l^{-1}). Inundation of nearshore areas and upstream inputs may contribute to higher lake DOC concentrations. On an annual basis, bacterial communities may shift from weak substrate limitation during summer to temperature limitation throughout the rest of the year (Felip et al., 1996). In Kentucky Lake, bacterial biomass and production reached their lowest levels in November when temperatures were below 15 °C.

The predominance of heterotrophic metabolism in Kentucky Lake is consistent with predictions of the River Continuum Concept (Vannote et al., 1980). However, it is important not to underestimate the importance of autotrophy in these systems. Bacterial production was correlated with phytoplankton biomass and production suggesting that algal-derived C may be an important substrate for bacterial growth. These data and other studies (Morris & Lewis, 1992; Foreman et al., 1998) suggest that bacterial production in rivers and impoundments may be dependent on autochthonous sources of labile organic carbon despite large inputs of allochthonous organic matter. In rivers, downstream declines in DOC quality have been inferred from changes in molecular weight and bacterial growth responses (Leff & Meyer, 1991; Sabater et al., 1993; Cotner & Gardner, 1993). Autochthonous production within downstream impoundments such as Kentucky Lake may provide labile C that fuels bacterial remineralization of recalcitrant C from upstream and floodplain sources (Wetzel, 1992).

Data from this study generally supported our stated hypotheses. Heterotrophic processes were found to predominate C cycling in the main channel of Kentucky Lake. The 3–4 fold excess of bacterial production over phytoplankton production emphasizes the importance of allochthonous inputs in this and other riverine ecosystems (Benner et al., 1995; Howarth et al., 1996). Heterotrophic activity is supported by upstream sources, lateral inputs (following periods of

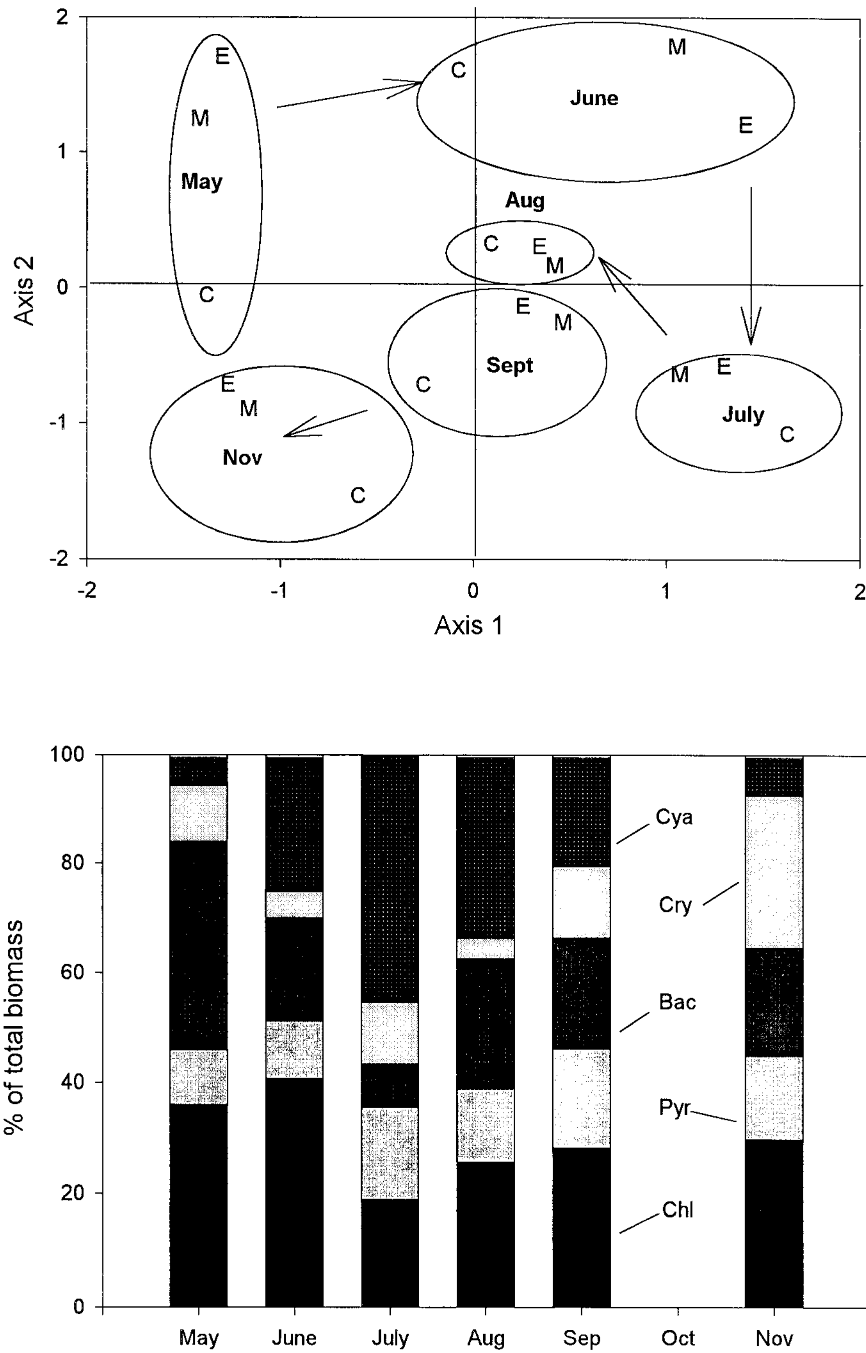

Figure 6. (Upper Panel) Bi-plot of CCAscores for phytoplankton samples collected in the embayment (E), mouth of the embayment (M) and main channel (C) of Kentucky Lake during May–November, 1997. Axes 1 and 2 represnt 56% of the variation in phytoplankton community composition. (Lower Panel) Proportion of total phytoplankton biomass represented by species of Chlorophyta (Chl), Pyrrophyta (Pyr), Bacillariophyta (Bac), Chrysophyta (Cry), and Cyanophyta (Cya). Data shown are averages for samples collected in the embayment, mouth of the embayment and main channel of Kentucky Lake.

shoreline inundation) and autochthonous production although existing data do not allow us to partition these sources. The predominance of heteretrophy suggests that Kentucky Lake is a net source of CO_2 which is consistent with measurements of CO2 supersaturation in this (G. Kipphut, pers. comm.) and other lakes (Cole et al., 1994; del Giorgio et al., 1997; Cai et al., 1999). Differences in biomass and production between the main channel and embayment were small. These data, combined with the fact that embayments constitute a small proportion of lake volume, do not lend support to the hypothesis that production within the embayment plays an important role in supporting plankton communities in the main channel (Reynolds, 1994; Reynolds & Descy, 1996; Spaink et al., 1998). Similarities in phytoplankton species composition between the embayment and main channel suggest that growth conditions favored the same dominants despite differences in mixing depth, WRT and nutrient concentrations. Seasonal rather than spatial variability in these and other environmental parameters was the primary determinant of species composition as well as biomass and production.

Light limitation and, on an annual cycle, temperature, may be the most important factors determining the balance between autotrophy and heterotrophy. Low water temperature and short WRT favor a predominance of heterotrophy while at higher temperatures, the ratio of autotrophy to heterotrophy increases. Higher water temperatures allow for secondary limitation by substrates (N for phytoplankton and labile C for bacteria) particularly in embayments where biomass is somewhat higher and substrate concentrations are lower. A general paradigm may be considered in which free- flowing rivers are characterized as resource-saturated (with respect to mineral nutrients and organic C) and the combined effects of low temperature and light availability favor a predominance of heterotrophy. Longer WRT and greater light availability characteristic of many natural lakes favors a closer balance between autotrophy and heterotrophy and resource-limited conditions. Impoundments occupy an intermediate position and shift from resource-saturated (advection regulated) conditions at low temperature to resource-limited (substrate regulated) conditions at high temperature and low flow.

In summary, our investigation of phytoplankton and bacterioplankton in a mid-latitude impoundment focused on lateral variation in water residence, light availability and nutrients and their utility in explaining differences in production. Caparisons among main channel and embayment sites revealed that the former were dominated by heterotrophic processes. In the embayment, heterotrophy was closely balanced by autotrophy and the incidence of substrate limitation was more frequent. We observed that temporal variation in water residence time was not a primary determinant of seasonal variability in phytoplankton or bacterial production and hypothesize that this may be a general attribute of impoundments whose source waters are upstream impoundments.

Acknowledgements

We are grateful to the staff at Hancock Biological Station, particularly Gary Rice for assistance with field work and Karla Johnston for conducting nutrient analyses. This research was supported by a grant from the DOE/ EPSCoR program. This paper is a contribution to the University of Louisville's Center for Watershed Research and Murray State University's Center for Reservoir Research.

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