ABSTRACT

Spatial and Temporal Patterns of Planktonic and Community Metabolism along the Riverine-Lacustrine Gradient in Texas Reservoirs

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In this study I quantified planktonic and community metabolism of the upper mixed zone along the riverine-lacustrine gradient in four Texas reservoirs from May 2005 to March 2006. Planktonic metabolism was estimated using the laboratory incubation methodology. The diel change of subsurface dissolved oxygen *in-situ* was used to determine community metabolism. In direct contrast to the predictions of the traditional reservoir zonation model, planktonic P:R ratio in the lacustrine zone was significantly less than one, while planktonic P:R ratios exceeded one in both the riverine and transition zones. Community P:R ratios were less than one in all three zones during the study, indicating net community heterotrophy at all locations. On average the plankton was responsible for 82% of total community production but only 33% of total community respiration. The factors controlling planktonic and community P and R were consistent with previous studies.

Spatial and Temporal Patterns of Planktonic and Community Metabolism along the Riverine-Lacustrine Gradient in Texas Reservoirs

by

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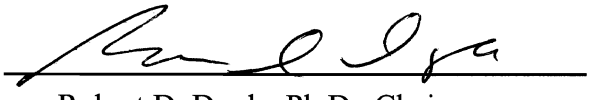
A Thesis
Approved by the Department of Biology

Robert D. Doyle, Ph.D., Chairperson

Submitted to the Graduate Faculty of
Baylor University in Partial Fulfillment of the
Requirements for the Degree
of

Master of Science

Approved by the Thesis Committee



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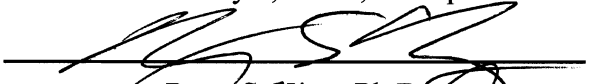

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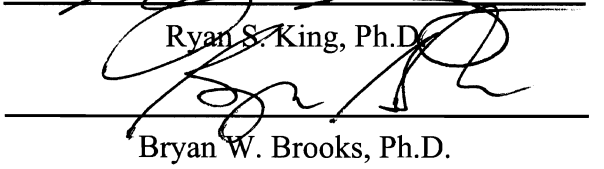

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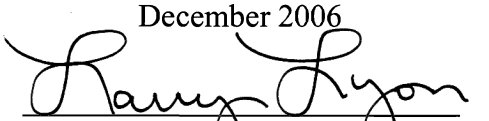
Accepted by the Graduate School
December 2006



J. Larry Lyon, Ph.D., Dean

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ACKNOWLEDGMENTS

I would like to take this opportunity to thank the people who have made this work possible. Foremost, I thank my mentor, Dr. Robert Doyle, for his incredibly patient guidance, without which this wouldn't have been possible. I thank Dr. King and Dr. Brooks for being on my defense committee and reviewing my thesis. Finally, my thanks go to the Department of Biology and Baylor University for giving me the opportunity of study and research here. A portion of this thesis was supported by grants from the United States Environmental Protection Agency through the Texas Commission on Environmental Quality to Bryan W. Brooks and Robert. D. Doyle.

Dedication

To

my family and friends

for

their continual love and inspiration

CHAPTER ONE

Introduction

1.1 Ecological Importance of P:R Ratios

The balance between daily primary production and community respiration has long been studied because of its central importance to organic matter and energy cycling in ecosystems (Lindeman, 1942; Odum, 1969). Primary production and community respiration are the major metabolic pathways where organic matter is produced and destroyed (Cole *et al.*, 2000). Primary production fixes inorganic carbon from the atmosphere and provides organic matter to the biosphere while community respiration recycles organic carbon back to inorganic carbon. Ecosystem metabolism provides a measure of the overall activity of an ecosystem and determines the efficiency of resource processing (Lopez-Archilla *et al.*, 2004).

The daily ratio of the primary production to the total community respiration is often used to quantitatively classify communities according to their predominantly heterotrophic or autotrophic characteristics (Odum, 1956). Heterotrophic communities have higher daily community respiration than daily primary production (P:R <1) whereas autotrophic communities have primary production higher than respiration (P:R >1). The balance of the daily production and the respiration differentiates between allochthonous lakes, which import most organic matter from outside of its boundaries,

and autochthonous lakes, which provide most organic matter from internal source (del Georgio and Peters, 1994; Cole *et al.*, 2000). Although the traditional term autotrophy has been used for ecosystems with P:R greater than 1, P:R greater than 0.5 might be a more sensible dividing line on the sources of carbon. P:R ratios larger than 0.5 indicate that over half of the respired energy is attributable to autochthonous primary production, while P:R ratios less than 0.5 mean that most respired energy comes from external sources (Allan, 1995).

1.2 Planktonic Metabolism vs. Community Metabolism

Ecologists have long been interested in the P:R ratios of aquatic ecosystems (Lindeman, 1942; Odum, 1956; Odum, 1957; Teal, 1957; Fontaine and Ewel, 1981; Duarte and Agusti, 1998). For example, daily P:R ratios of many lakes and streams with different conditions have been published (Table 1). In Table 1, ratios less than one indicate allochthonous inputs of organic matter are needed to balance respiration demands; ratios larger than one illustrate that the plankton is a net source of organic matter and oxygen, as well as a sink for CO_2 and inorganic nutrients (Cole *et al.*, 2000; Carignan *et al.*, 2000; Hanson *et al.*, 2003).

Many researchers have focused on planktonic P:R ratios because the primary production in most large impoundments is mainly from phytoplankton (Kimmel *et al.*, 1990). From a trophic-dynamic viewpoint, phytoplankton is usually the major producer in reservoirs and provides the energy obtained by photosynthesis for synthesizing complex organic

substances (Lindeman, 1942). Phytoplankton generates about 70% of the world's atmospheric oxygen supply (Reynolds, 1984). Production of plankton forms the base for most aquatic food chains.

Table 1. Gross primary production (GPP, g C $m^{-2}day^{-1}$), respiration (R, g C $m^{-2}day^{-1}$), and P:R ratios from various studies

Source	Study area	Area type	Sampling period	Methods	GPP	R	P:R
Fontaine and Ewel, 1981	Little Lake Conway, Florida	Part of a multilo-bed lake	Annual	Dial oxygen change Light and dark bottles	3.16	3.27	0.97
Lopez-Archilla *et al.*, 2004	Santa Olalla, Spain	Lake	Annual (2 years)	Diel oxygen change	2.96	3.20	0.92
Odum, 1957	Silver Springs, FL	Small stream	Winter	Diel oxygen change	3 ~ 13.13	1.05 ~ 1.88	2.9 ~ 7.0
Carignan *et al.*, 2000	12 oligotrophic lakes in Canadian Shield	Lake	May to October	Light and dark bottles	0.07 ~ 0.72	0.05 ~ 0.96	Medi-an 1.7
Del Giorgio and Peters, 1994	20 lakes in Southern Quebec	Lake	May to August	^{14}C method and dark bottles	0.07 ~ 1.5	0.27 ~ 1.17	< 1.0
Cole *et al.*, 2000	4 lakes in Wisconsin	Lake	Annual	Diel oxygen change	0.3 ~ 1.97	0.73 ~ 2.4	< 1.0
Wilcock *et al.*, 1998	23 lowland streams, New Zealand	Streams	Summer	Diel oxygen change	0.2 ~ 10.95	0.59 ~ 14.1	<1.0

However, phytoplankton is not the only producer of the whole community production. The primary producers that contribute to the community primary

production in reservoirs come from one of the four categories: planktonic algae (phytoplankton), planktonic phototrophic bacteria, attached algae (periphyton), and macrophytes (Kimmel *et al.*, 1990). Community respiration in aquatic ecosystems is influenced by primary producers, bacteria, zooplankton, benthos, aquatic invertebrates, fish, and other organisms. The balance between community production and respiration provides an overview for the resource processing in the whole aquatic ecosystems (Lopez-Archilla *et al.*, 2004).

1.3 Reservoir Zones

Reservoirs are created by human activities for specific purposes, including flood control, water storage, generation of electrical energy, and recreation (Wetzel, 2001). Reservoirs are usually described as intermediates between rivers and natural lakes with respect to their unique morphometry and hydrology (Kimmel & Groeger, 1984, Kimmel *et al.*, 1990). According to Thornton *et al.* (1981)'s heuristic model of reservoir zonation, three distinct zones, the riverine zone, the transition zone, and the lacustrine zone, occur along a longitudinal gradient (Figure 1). Subsequently, distinct physical, chemical and biological patterns develop longitudinally from the riverine zone to the lacustrine zone (Wetzel, 2001). Based on previous descriptions of reservoir zones, characteristics of each zone are discussed below separately (Thornton *et al.*, 1981; Kimmel *et al*. 1990; Cole and Hannan, 1990; Wetzel, 2001).

1.3.1 Riverine Zone

The riverine zone is usually relatively narrow and shallow because of the river geomorphology. It is characterized by higher flow, shorter water residence time, and higher levels of suspended solids and available nutrients. Water in the riverine zone is usually well mixed and aerobic (Wetzel, 2001). High particulate turbidity commonly reduces light penetration and limits primary production in this zone (Kirk, 1985). In addition, decomposing allochthonous material often places high demands on dissolved oxygen in the riverine zone where the depth is shallow.

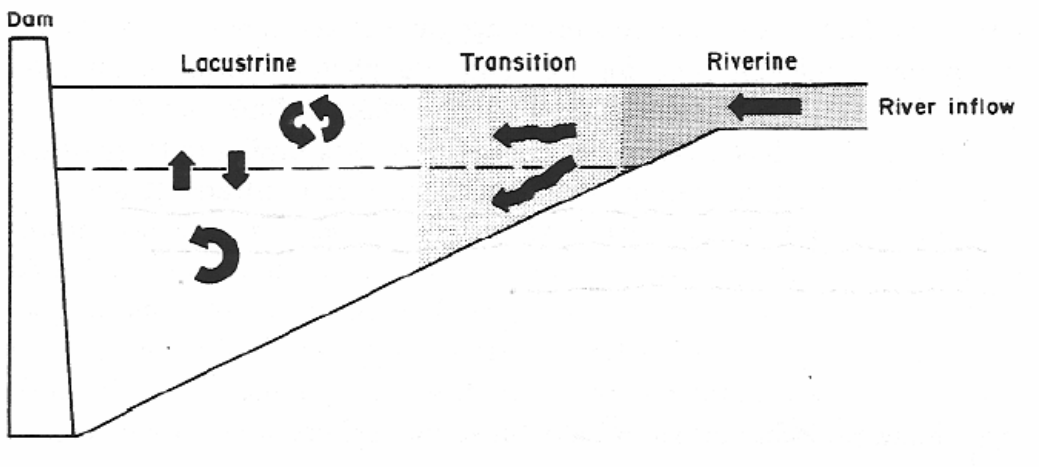

Figure 1. Zones along the longitudinal gradient in reservoirs. (from Thornton, 1990)

1.3.2 Transition Zone

The transition zone is the most dynamic zone of the reservoir (Kennedy et al., 1985). Transition zone depths are intermediate in the three zones. Here, water velocities decrease because energy is dispersed over larger areas in the transition zone (Wetzel, 2001). As a result, the transition zone becomes a zone of sedimentation.

Water retention times correspondingly increase due to the decreased flow velocity. Decreased turbidity results in enhanced depth of light penetration and increased rates of photosynthetic productivity by phytoplankton. A shift occurs to an increasing percentage of total organic matter loading from phytoplankton and rooted vascular plants (Kennedy *et al.*, 1985).

1.3.3 Lacustrine Zone

The characteristics of the lacustrine zone become more similar to natural lake ecosystems (Wetzel, 2001): the retention time is the longest, the dissolved nutrients and abiogenic turbidity are low, higher transparency and a deeper photic layer. This portion of the reservoir is often stratified thermally. The lacustrine zone has many properties of natural lakes in regard to planktonic production, limitation by nutrients, sedimentation of organic matter, and decomposition in the hypolimnion (Wetzel, 2001).

1.4 Predicted Changes of Metabolism along the Riverine-Lacustrine Gradient

Kimmel *et al.* (1990) considered factors influencing the changes of P:R ratios from the riverine zone to the lacustrine zone due to the distinct characteristics of reservoir zones. Their speculation regarding expected P:R ratios is described as follows.

As previously introduced, the riverine zone is characterized by higher levels of available nutrients, suspended solids, and light extinction. In riverine zones, areal primary productivity is often light-limited, and depth of the mixed layer usually exceeds that of the photic layer. Therefore, areal primary production in the riverine zone is

relatively low. However, phytoplankton biomass and productivity per unit volume of the photic zone can be high. Furthermore, heterotrophic bacterial production, which consumes dissolved oxygen and contributes to respiration, is relatively high in riverine zones because of high allochthonous input of organic carbon. All of these factors lead to the presumption or expectation that the ratio of primary production to respiration (P:R) in this zone is generally less than one.

In transition zones, the rates of photosynthetic production by phytoplankton increase as a result of the enhanced depth of light penetration. Because both light and nutrients are rich for algal photosynthesis, the transition zone can be the most fertile region in the reservoir. In the transition zone, bacterial production remains high while primary production increases dramatically, which causes P:R to approximate one.

The lacustrine zone usually has higher water transparency and a deeper photic layer. However, it also has lower concentrations of dissolved nutrients and suspended particles. In addition, the volumetric phytoplankton productivity of the photic zone is reduced. Moreover, because the allochthonous organic matter decreases along the riverine zone to the lacustrine zone, heterotrophic bacterial production tends to decrease. The heterotrophic bacterial production is minimized in the lacustrine zone, which will dramatically reduce respiration. Therefore, P:R ratios in the lacustrine zone are generally expected to be higher than one.

1.5 Contribution of Planktonic Metabolism to Community Metabolism

The relative contributions of the primary producer groups to the total photosynthetic production of organic matter in reservoirs are undetermined (Kimmel *et al.*, 1990). However, the contributions of these primary producer groups along the riverine-lacustrine gradient are likely differ due to their different physical, chemical and biotic characteristics.

In the riverine zone, rooted macrophyte and submersed timber support periphyton growth and colonization (Kimmel *et al.*, 1990). The benthos in the riverine zone may strongly influence the community metabolism because of the shallow depth and low water column volume to sediment surface area ratio. Thus, planktonic metabolism in the riverine zone is generally one of several groups that may contribute significantly to total community metabolism.

As for the transition zone, since its physical, chemical and biotic characteristics are intermediate in the three reservoir zones, the contribution of planktonic metabolism to community metabolism in transition zones is likely to be between the riverine zone and the lacustrine zone.

In the lacustrine zone, the development of attached algal and rooted macrophytes is restricted by the large water-level fluctuations and the deep depth (Kimmel *et al.*, 1990). Thus the contribution of the planktonic producers to the total primary production is maximized (Ryder, 1978; Kimmel and Groeger, 1984). In addition, benthic communities may have a reduced influence on metabolism due to increased depths and

high volume to sediment surface ratios. Therefore, planktonic metabolism is expected to account for the majority of total community metabolism.

1.6 Methods for Calculating the Community and Planktonic Metabolism

1.6.1 Open Water Methods

Open water methods obtain changes of O_2 or CO_2 by assaying sequential water samples in *in-situ*. Open water methods always measure the total community metabolism in the whole ecosystem.

1.6.1.1 Diel Oxygen Change Method Odum (1956) suggested a method to estimate photosynthetic production and respiration using a mass-balance model in conjunction with diurnal oxygen measurements (APHA, 1998). Chapra (1997) presented a graphical expression of Odum's idea, the delta method, to estimate reaeration, production and respiration.

Cole *et al.* (2000) described the method to calculate production and respiration from diel O_2 curves. In darkness, the decreased change in oxygen concentration came from community respiration (R) and exchange with the atmosphere (D). In daylight, oxygen concentration changed due to R, D, and GPP. Net ecosystem production (NEP) is the difference between GPP and R. By assuming that community respiration is unaffected by light, gross daytime production can be estimated by adding R, measured in the dark, to the net daytime production.

1.6.1.2 Pros/Cons Open water methods are based on direct observations hence they can reflect the community metabolism in natural ecosystems (Chapra, 1997). The direct observations of net rates can be used in a readily integrated form. Thus, the assessment of the daily production and respiration in water column communities may improve accuracy and applicability of the primary production estimates. Furthermore these methods are relatively inexpensive and can be applied to very shallow systems.

One of the drawbacks of these methods is that the oxygen exchange with the atmosphere is difficult to quantify. In addition, the open water methods can not be used to calculate daytime respiration (Szyper *et al.*, 1992). Thus, gross primary production has to be estimated with these methods by assuming that daytime respiration is equal to nighttime respiration (Cole *et al.*, 2000). However, the respiration in daytime may not be the same as that during night (Cole *et al.*, 2000).

1.6.2 Container Methods

Some of the drawbacks of open method open water methods can be overcome by isolating the plankton community in a container. The containers may then be incubated in the lab or *in-situ* and metabolic processes were estimated through change of O_2 or/and ^{14}C (Lind, 1985; Fee, 1973; APHA, 1998). The container methods always estimate planktonic metabolism.

1.6.2.1 O_2 vs. ^{14}C The light and dark bottle method (Lind, 1985) for measuring gross primary production and respiration is often used in aquatic studies.

This method can be used to compare the oxygen changes that occur in plankton communities contained in clear bottles with those occurring in dark bottles. The difference between bottle incubations and diurnal changes should reflect the difference between the planktonic- and non-planktonic components of oxygen production and consumption in the ecosystem.

Also, ^{14}C can be used in the light and dark bottle method to measure production. After incubation, the plankton are collected on a membrane filter and assayed for radioactivity. The quantity of carbon fixed is proportional to the fraction of radioactive carbon assimilated (APHA, 1998). However, the respiration in the light bottles can not be measured using the ^{14}C method.

1.6.2.2 Lab Incubation vs. In-situ Incubation Water samples can be incubated *in-situ* or returned to the lab. It is important for the incubation temperature to matche that of the field due to the temperature's influence on the metabolic process.

Lab incubation has several advantages. Firstly, it can be applied to quantify the metabolic changes in lab without the limitation of light and weather in *in-situ*. Furthermore, when studying large lakes and simultaneous measurements at distant stations are needed, the lab incubation methods are appropriate (Wetzel and Likens, 2000).

Historically, most incubations have been conducted *in-situ* (Fee, 1973; Lind, 1985; Wetzel and Likens, 2000). In this case, the sealed glass bottles are incubated in

different depths through the water column. The main advantage of these methods is that water samples are in natural temperature and light conditions. The problem for *in-situ* incubation is that, based on Fee (1973)'s technique, the *in-situ* methods for measuring phytoplankton production are not adequate when the water body is large because the stations processed each day are too small to provide a comprehensive view of the whole water body.

1.6.2.3 Calculation of Planktonic Metabolism *Fee method*---Calculations of daily areal production can be performed using the method of Fee (1973, 1998), which utilize a computer program available at http://www.umanitoba.ca/institutes/fisheries/PSpgms.html. Fee reported that there are three relationships that must be known. They are: (1) solar PAR (Photosynthetically Available Radiation) as a function of time (I_0 *(t)*, top curve in Figure 2); (2) photosynthesis as a function of PAR (Photosynthesis vs. I, middle curve in Figure 2), and (3) percent of solar PAR as a function of depth (*Iz*, bottom left curve). The depth profile of PAR is calculated by multiplying I_0 by the percent of surface PAR that reaches each depth (*Iz*), where I_0 is the incident surface light and *Iz* is the PAR in z depth. Photosynthesis as a function of depth is then calculated from the photosynthesis and PAR curve. The instantaneous areal rate of photosynthesis is obtained by integrating the P_z curve from the surface down to the depth of the euphotic zone (Zeu). The whole procedure is repeated at successive time intervals in order to obtain a set of instanceous depth integrals over the entire day.

Areal gross productivity can be calculated using daily PAR data. The input variables include light extinction, *Chlorophyll a*, P^Bmax, and alpha^B (where alpha^B is the slope of the Photosynthesis per unit *Chlorophyll a vs. I* curve; P^Bmax is the maximum production in high light intensities per unit *Chlorophyll a*). Fee's computer program can linearly interpolate these variables for days between sampling dates and calculate the daily areal gross production and respiration.

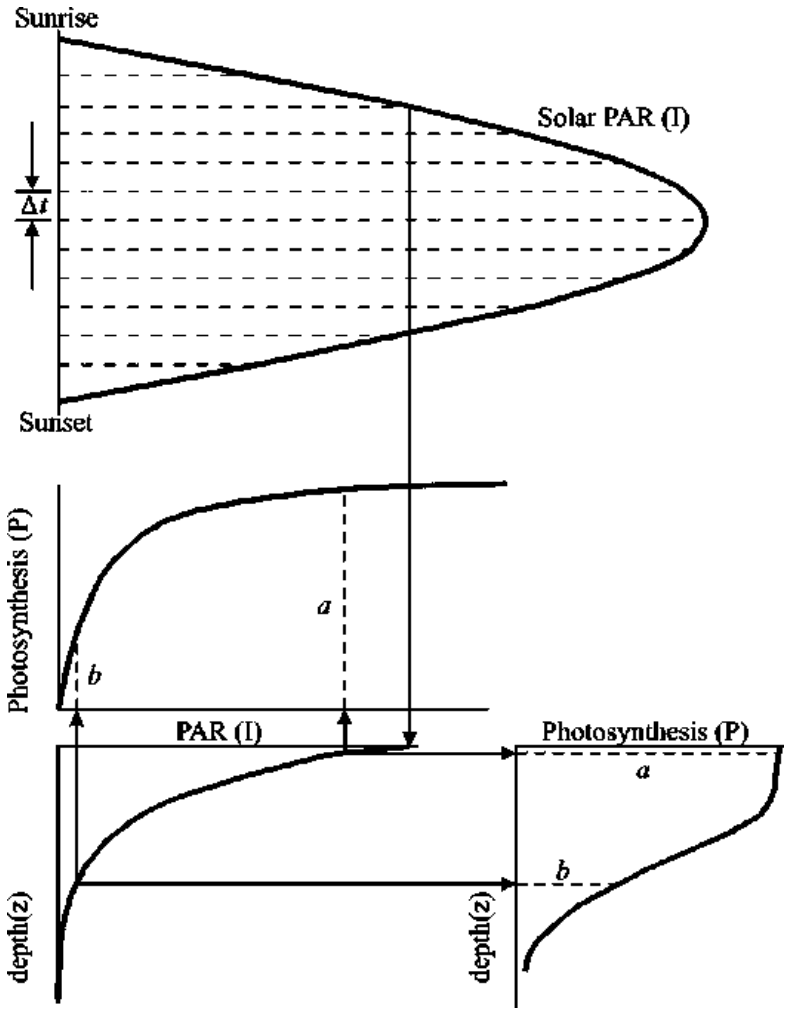

Figure 2. The procedure used to estimate *in-situ* photosynthesis (Fee, 1998)

Walsby method---Following Fee's method, Walsby (1997) described the use of standard spreadsheets to calculate the daily integral of photosynthesis based on measurements of phytoplankton concentration and light attenuation made at narrow depth intervals, and measurements of surface irradiance made at frequent time intervals throughout the day. The web site, where Walsby's spreadsheets can be found, is available at http://www.bio.bris.ac.uk/research/walsby/integral.htm. Walsby also discussed corrections for reflectance at the wind-roughened water surface, changes in *Chlorophyll* between depths, and the effects of temperature on photosynthesis. The input variables include light extinction, *Chlorophyll a*, P^Bmax, alpha^B, beta (coefficient of photo inhibition at high light intensity), respiration, temperature, and irradiance under water surface. The daily integral of photosynthesis can be calculated by numerical analysis based on the photosynthesis-irradiance curve and field light data under water.

1.6.2.4 Pros/Cons Container methods can separate the water sample from outside ecosystems. These methods can be used to clarify the change of production and respiration in each container without the oxygen diffusion with the atmosphere during the experiment.

The drawbacks include that container methods are not as convenient as those open water methods. In addition, container methods are more expensive. These methods are seldom used in flowing waters because the majority of the community is benthic and heterogeneous. It is also questionable to make measurement without the normal

turbulence when production is a function of current flow (Odum, 1956). The absence of turbulence influences the amount of nutrients, light, and CO_2, which could consequently influence the primary production inside the containers. Last, the container methods have some calculation issues, which can make the calculation of the daily production and respiration more complicated.

1.7 Focus of Current Research

The main objective of this study is to determine:

1. The spatial variability of planktonic and community metabolism among the three reservoir zones.

2. The temporal variability of planktonic and community metabolism among different sampling seasons.

3. The predictor variables that best explain the variation in planktonic and community metabolism.

4. The contribution of planktonic metabolism to community metabolism.

This study tests the following hypotheses:

1. Ho: Planktonic metabolism remains the same in three reservoir zones.

2. Ho: Community metabolism remains the same in three reservoir zones.

3. Ho: Planktonic metabolism does not vary seasonally.

4. Ho: Community metabolism does not vary seasonally.

5. Ho: The contribution of planktonic metabolism to community metabolism remains the same at the three reservoir zones.

6. Ho: The contribution of planktonic metabolism to community metabolism does not vary seasonally.

7. Ho: The change of P:R ratio along the riverine-lacustrine gradient is supported by the traditional pattern, which includes that the ratio is less than one in the riverine zone, around one in the transition zone and greater then one in the lacustrine zone

CHAPTER TWO

Materials and Methods

2.1 Study Area

Four reservoirs in Texas were sampled in this study. These reservoirs represent a certain range of characteristics in Texas reservoirs (Table 2).

Table 2. Descriptive information and trophic status of the four reservoirs. SA= surface area; zm=mean depth; WA=watershed area; Chla=*Chlorophyll a*; TP= total phosphorus.

Reservoir	SA (km^2)	zm (m)	WA (km^2)	Trophic State*	Mean Chla (mg/m^3)	Mean TP (mg/m^3)
Lake Aquilla	13.3	4.9	660	Mesotrophic	4.72	65.90
Lake Conroe	84.9	6.2	1153	Eutrophic	15.89	36.94
Lake Lewisville	94.2	6.1	4299	Eutrophic	8.13	70.29
Cedar Creek	138.8	5.5	2589	Eutrophic	26.66	69.31

*-- TNRCC, April 2002, Texas Water Quality Inventory, 2000, SFR-50/00

Lake Aquilla is located in Hill County, near Hillsboro, Texas. It impounds Aquilla Creek. Cedar Creek Reservoir, which is accumulated from Cedar Creek, is located in the Trinity River Basin. It is about 10 miles west of Athens, Texas. Lake Conroe starts at Conroe Dam in Montgomery County and is located north of downtown Houston. Lake Lewisville, which locates near Lewisville and north of

Dallas, impounds the Elm Fork Trinity River in Denton County, Texas. The reservoirs are shown in Fig. 3.

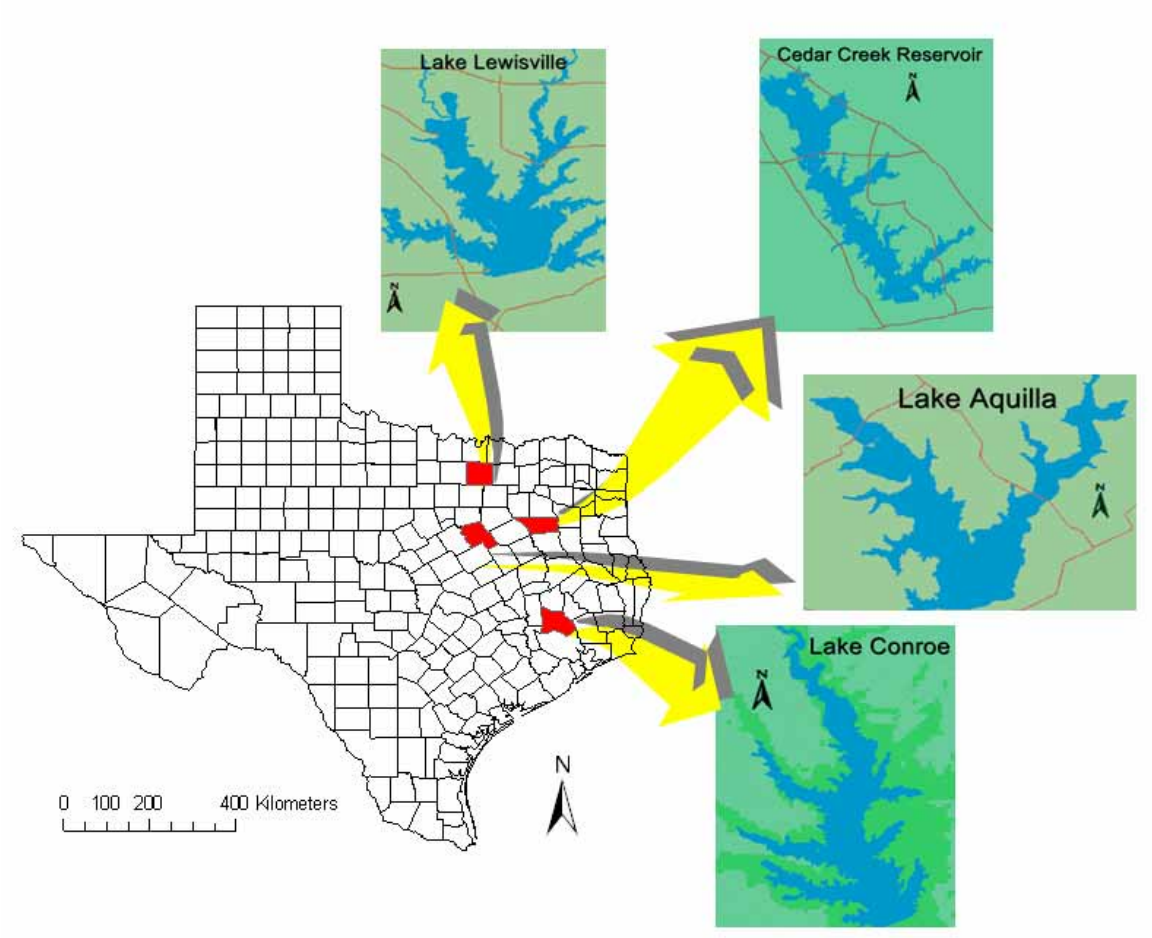

Figure 3. The maps of the four reservoirs and their locations in Texas.

2.2 Sample Collection

For each reservoir, four stations along two different coves through the riverine-lacustrine gradient were sampled while a ninth station at the dam was used as a lacustrine station. Of the four stations along each cove, the two upstream stations were considered to be in the riverine zone and the other two were in the transition zone. The

sampling locations were selected based on the conceptual approach for characterizing reservoir zones. Each of the four reservoirs was sampled three times from May, 2005 to March, 2006 in order to collect the data in different seasons including spring, summer and winter.

I used a Trimble GPS GeoExplorer® series to obtain the coordinates of each station. Water samples from nine stations in each reservoir were collected just below the water surface at 0.3m.

2.3 Field Data Collection

24-hour dissolved oxygen (DO) data were measured continuously using YSI 600 XLM® multiparameter datasondes configured with the YSI 650 MDS® multiparameter display system at surface depth (approximately 0.3m below water surface) in each station. In addition, the temperature, pH, turbidity, *Chlorophyll a*, salinity and conductivity under water surface in each sampling station were also measured by YSI600 XLM® multiparameter datasondes. The secchi depth was collected by secchi disk to estimate the visibility of the water in each station.

Light (Photosynthetic Active Radiation) profiles were obtained by a LiCor light meter equipped with a spherical quantum sensor. The light extinction data were gathered beginning at the water surface and at 1m or 0.5m intervals down to the approximate depth of the euphotic zone (1% of the incident light, Horne and Goldman, 1994). Based on the

light data collected, the vertical extinction coefficient, *n"*, was computed as described by Lind (1985).

HOBO temperature sensors (Onset, HOBO® Water Temp Pro) were used to collect continuous temperature data at different depths in each station. Sensors were distributed 1m intervals throughout the water column and recorded data of 5-minute intervals. The mixing depth was determined from the profile of depth and temperature in the early morning (0600AM). I considered the water column to be stratified at the depth when water temperature changed by 1°C/m or more. This depth of stratification was considered the mixing depth (Zmix).

Vertical profiles of temperature and dissolved oxygen were also collected at each station sometime during the deployment period. These profiles were used to determine if vertical DO stratifications was occurring during the day.

2.4 Laboratory Data Collection

Water samples were collected below the water surface at 0.3m in the field. The samples were stored in coolers and transported to the laboratory for further laboratory data collection.

2.4.1 Turbidity

Turbidity was measured by a HACH 2100N Turbidimeter. The turbidimeter was calibrated using StablCal® calibration set with sealed vial standards. There are four standards used in calibration in sequence. They were <0.1 NTU, 20.00 NTU, 200.0

NTU, and 1000 NTU. Each vial standards was shaken and wiped thoroughly before calibrating the turbidimeter. In addition, before measuring the turbidity of samples, the samples were also shaken. Turbidity measured in this study was total turbidity including algal turbidity and non-algal turbidity. Algal turbidity in water is caused by plankton and other small organisms (Wetzel and Likens, 2000) and may be related to *Chlorophyll a*. But I didn't separate the total turbidity into algal and non-algal turbidity in this study.

2.4.2 Chlorophyll a

Samples for *Chlorophyll a* analyses were filtered through GF/F glass fiber filter (47mm) and frozen no longer than 28 days. Frozen filters were then ground in 14ml of 90% acetone and allowed to extract for 4~10 hours at 4°C. Then the acetone extract was separated from the residue by centrifugation in a clinical centrifuge. Extracts were analyzed for *Chlorophyll a* on a Beckman Model DU650 spectrophotometer with 1cm pathlength and 2nm bandwidth. Optical densities were measured at 750nm, 665nm, 645nm and 630nm. The extract was acidified with 0.1N Hydrochloric acid at 750nm and 665nm to correct for pheophytin-a (Wetzel and Likens, 2000).

2.4.3 Light and Dark Bottle Method in the Lab Incubation

When the water samples arrived in the laboratory, a mixture of gases containing CO_2 in atmospheric concentrations (~350 ppm CO_2), six percent O_2 and the balance of N_2 was bubbled through them to lower the oxygen level of the sample. The purpose of this

step was to prevent photorespiration in the algae caused by high oxygen concentrations from leading to the underestimated true net photosynthesis. The saturation of oxygen in dark bottles was adjusted to about 70% while that in light bottles was adjusted to around 30%. In this way, the possibility that photorespiration affected the measurement of production was very small.

The light and dark bottle method in the lab incubation (Fee, 1973) was used in this experiment. This method compares the oxygen changes that occur in plankton communities contained in clear bottles with those occurring in dark bottles during a 9 to 12 hour period. In light bottles, oxygen is evolved during photosynthesis and consumed by plankton respiration. In dark bottles, only respiration occurs.

The 300ml Biochemical Oxygen Demand (BOD) bottles were filled with the water samples and placed in an incubator at the same temperature as that in the lake for 9~12 hours. Prior to incubation, for each bottle, initial oxygen concentration was measured using the YSI oxygen meter (Model 5000) with a YSI self-stirring BOD probe (MODEL 5010). After the 9 to 12 hour incubation, the final oxygen concentration in each BOD bottle was measured. For each bottle, the oxygen change was calculated as the difference between the initial and final concentrations and was normalized to plankton biomass using the *Chlorophyll a*.

Photosynthesis was determined as the change in oxygen concentration of samples incubated in BOD bottles under various light levels. Incubation was conducted under three different light intensities ranging from dark (0 uE.m^{-2}.s^{-1}), low-light (40-80

*u*E.m^{-2}.s^{-1}) to high-light (400-600 *u*E.m^{-2}.s^{-1}). The high light levels were sufficient to saturate photosynthesis. Triple samples for each station were incubated at each of the three light levels in the incubator with the lake temperature.

Planktonic respiration was measured as the decrease oxygen concentration in dark bottles. The net production was measured as the increase in oxygen concentration in clear bottles under high and low light levels. The gross production is the sum of net production and respiration. The maximum production (P^Bmax) was the gross production calculated from the clear bottles only under the high light intensities. Alpha^B was calculated as the slope of the observed production rates between the dark and low light incubations.

2.4.4 Calculation of Planktonic Metabolism

With these parameters above, the potential daily gross primary production and respiration were calculated using the Walsby (1997) method. Walsby used the standard spreadsheets to integrate the phytoplankton photosynthesis through time and depth. The input variables include light extinction, *Chlorophyll a*, P^Bmax, alpha^B, beta (coefficient of photoinhibition in high light intensities), respiration, temperature, and irradiance under water surface. I assumed that beta was equal to zero. Light data for this was obtained from the Texas solar radiation database in UT-Austin solar energy laboratory. The web link is http://rredc.nrel.gov/solar/new_data/confrrm/au/. The light data I chose represented the light levels of a cloudless day at that time of year. Therefore, the

estimated planktonic production values should be considered the potential production under full sunlight conditions. Actual planktonic production in cloudy days should be lower. Volumetric gross production was calculated by dividing areal gross production by the mixing depth (Zmix).

2.4.5 Calculation of Community Metabolism

In this study, the calculation of community production and respiration followed the continuous diel oxygen method by Cole *et al*. (2000). The changes in subsurface dissolved oxygen concentration were used to estimate net and gross aquatic community productivities by constructing diurnal oxygen curves.

The gross aquatic volumetric community production and respiration were estimated by subsurface (0.3m) dissolved oxygen data collected with YSI multiparameter datasondes for each 15-min interval over 24-h period as described by Cole *et al.* (2000). The respiration at night was determined by the oxygen change during the dark period and corrected for the diffusion of oxygen between the water and the atmosphere. I assumed the respiration during the daytime was the average respiration rate during the night. The daily gross primary production, which is zero during night, was estimated by the daytime parameters, including the oxygen change, respiration and the oxygen diffusion with atmosphere.

Areal community rates for the surface mixed layer were computed from the subsurface volumetric rates by multiplying by the appropriate depth. Volumetric

community respiration rates were multiplied by the total mixing depth determined from the 0600AM HOBO temperature profiles. Most shallow stations (<5m) showed no vertical temperature stratification. Areal community production rates were multiplied by the stations mixing depth unless the YSI temperature and DO profiles collected later in the day showed evidence of a shallower daily stratification depth. At 22 stations I found that the DO profile during the day was not homogeneous down to the 6AM mixing depth. Instead, short-term heating of the surface layer confined daytime DO increases to a shallower depth. In these cases I multiplied the subsurface volumetric rates by the apparent mixing depth to compute daytime community production.

The diffusive exchange with the atmosphere (D) can be either positive or negative. In systems, *k* is generally modeled as a function of wind speed (MacIntyre et al. 1995). The net community production and the nighttime respiration (R_{night}) can be obtained directly from the oxygen data. Therefore, the daily community GPP and R can be calculated by assuming that the daytime respiration equals that at night. In this study, *k* was calculated according to the equations by Cole and Caraco (1998) based on the wind speed and temperature in each sampling station. The wind speed data were taken from the TCEQ website. Further information about wind can be found at http://www.tceq.state.tx.us/cgi-bin /compliance/monops/daily_summary.

2.4.6 Morphology Data

Morphometric parameters were generalized from the field coordinates overlaid on the existing lake maps and GIS information. The coordinates were collected by Trimble GPS in sampling stations at lakes. Morphometric data contained upstream distance, upstream perimeter, upstream area, transect width, shoreline density (Dsl, Osgood, 2005) and shoreline development index (SDI, Hutchinson, 1957). Upstream distance (km) was the distance from each sampling station to the conservation pool elevation. Similarly, upstream perimeter (km) and area (km^2) were calculated for each station and represented the perimeter and surface area of the impounded reservoir upstream of the sampling transect. SDI indicates the regularity of the shoreline and increases above 1.0 for the shape of the water body deviated from that of a perfect circle (Lind, 1985). Dsl ($m\ ha^{-1}$) is computed as the ratio between shoreline length (m) and impounded area (ha) and provides the index of shoreline-associated impacts normalized to lake surface area (Osgood, 2005). Dsl increases when surface area decreases for lakes of similar shape or when lake shapes become less circular.

2.5 Data Analysis

The classification and regression tree (CART) analysis was introduced to obtain the best predictors of daily planktonic and community production as well as their respiration. The software used for CART in this study was S-Plus. RPART library in S-Plus 2000 (Insightful Corp., Seattle, WA, USA) was used to conduct CART analyses.

CART is a nonparametric method, which is ideally suited for exploring and modeling complex ecological data (De'Ath and Fabricius, 2000; McCune and Brace, 2002). CART explains the variation of a single response variable by repeatedly splitting the data into more homogeneous groups, using one or more predictor variables (King *et al*., 2005; De'Ath and Fabricius, 2000). Predictor variables can be categorical, ordinal and numerical while response variables can be either categorical (classification tree) or numerical (regression tree). In this study, the regression trees were used because the response variables were numerical.

CART model is expected to generate a tree which can explain the most variation (r^2) in the response variable. A splitting procedure is repeated until the tree is overlarge, which is then pruned back according to cross-validation of the model. In this study, the tree was pruned under the 1SE rule which is to choose the best tree by taking the smallest tree within one standard error above the minimum relative error (De' Ath and Fabricius, 2000).

In this study, the explanatory variables used in CART model included physical, chemical, biological and morphological data. The predictor variables included lakes identifications, seasons, stations, cove, presence/ absence of wastewater inflow, mixing depths, Zmix:Zeu, light extinction, water temperature, *Chlorophyll a*, NO_2^--NO_3^-, NH_3-N, PO_4^-, TN, TP, upstream distance, transect width and SDI.

Control parameters required before the CART analysis includes: the minimum number of observations in terminal groups, the minimum number of observations in a

terminal node and the number of cross-validations to be done. According to the sampling, the minimum numbers of observations in terminal groups and nodes were 4 and 8, respectively. Cross-validation was used in CART models to determine the most appropriate size of the tree. 10-fold cross-validation was conducted in this study.

Physical, chemical and metabolic data were log-transformed for statistical analysis to fit the assumptions of normal distribution and equal variance among seasons and stations. For morphometric data, one-way parametric ANOVA was used to test if there is a significantly difference among zones. For chemical and metabolic data, two-way parametric ANOVA (zone and season) was utilized to compare the differences among zones and seasons. Three-way ANOVA (lake, zone and season) was used to evaluate the lake effect. I evaluated three key factors (*Chlorophyll a*, light extinction and Zmix:Zeu) impacting instantaneous rates of metabolism for a significant lake effect. In cases where the interactions between the main effects were not significant, the main effects were evaluated separately. The significant parametric ANOVA was followed by a Fisher's Least Significant Difference (LSD) multiple range test, which can determine which means were different from each other (α=0.05). Nonparametric ANOVA was conducted if the log-transformed data did not meet the normal distribution and equal variance assumptions. In cases where the interactions between the main effects were not significant, a LSD multiple range test on ranked data at α=0.05 was performed to determine which means were different from each other. In this study, STATGRAPHICS Plus (Version 5) was used to conduct ANOVA analysis.

In addition, a t-test was employed to examine whether the P:R ratios were different from one. Planktonic and community P:R ratios were investigated in different zones. In each zone, planktonic and community P:R ratios were compared with one. The t-test was also conducted in STATGRAPHICS Plus (Version 5).

CHAPTER THREE

Results

3.1 Lake Impact on Key Factors Controlling Metabolism

Key factors which influence instantaneous rates of aquatic metabolism were evaluated among lakes, reservoir zones and seasons. Three-way ANOVA found the interactions among lakes, zones and seasons were not significant for any of key factors. The key factors were significantly different among distinct reservoir zones (Table 3). However, key factors did not vary significantly among lakes or among seasons. Because lake impact on each key factor was not significant, I did not consider among lake variations for any of the remaining analyses.

Table 3. Significance of key factors from three-way ANOVA throughout this study.

Key factor	Lake	Zone	Season
Chlorophyll a	0.119	0.022	0.446
n"	0.641	<0.001	0.901
Zmix:Zeu	0.522	<0.001	0.333

3.2 Morphometric, Physical and Chemical Parameters

Morphometric variables along the riverine-lacustrine gradient are summarized in Table 4. The mean SDI in these lakes ranged from 1.85 to 12.32 and Dsl from 24.6 to 1655 m ha^{-1}. The mean SDI was significantly different among three zones (one-way

Table 4. Morphometric parameters along the riverine-lacustrine gradient in the four reservoirs. Mean±SE (n), superscripts showed the homogeneous grouping according to LSD test after one-way ANOVA. Means with same grouping letter are not significantly different at α=0.05.

Parameter	Riverine Zone	Transition Zone	Lacustrine Zone	p-value (Zones)
SDI	$3.1\pm0.3(14)^{A}$	$3.5\pm0.3(16)^{B}$	$8.4\pm0.6(4)^{C}$	<0.001
Dsl (m ha^{-1})	$492.0\pm93.6(14)^{A}$	$140.1\pm87.5(16)^{B}$	$37.4\pm175.0(4)^{C}$	<0.001
Upstream Area (km^2)	$466.2\pm708.0(16)^{A}$	$2651.4\pm708.0(16)^{B}$	$2175.3\pm1416.0(4)^{B}$	<0.001
Upstream Distance (km)	$1.2\pm0.6(16)^{A}$	$2.8\pm0.6(16)^{B}$	$14.2\pm1.2(4)^{C}$	<0.001
Upstream Perimeter(km)	$5.4\pm15.1(14)^{A}$	$16.2\pm14.2(16)^{B}$	$285.1\pm28.3(4)^{C}$	<0.001
Transect Width (m)	$412.9\pm225.0(16)^{A}$	$919.4\pm225.0(16)^{B}$	$2909.5\pm450.0(4)^{C}$	<0.001
Depth (m)	$2.1\pm0.3(16)^{A}$	$3.4\pm0.3(16)^{B}$	$14.7\pm0.5(4)^{C}$	<0.001

parametric ANOVA, $p<0.5$). A multiple range test (LSD, α=0.05) showed the highest mean SDI was found in the lacustrine zone and the lowest in the riverine zone. The significant increase in SDI along the gradient showed that the reservoir progressively became more irregular as one moves from the upstream to the downstream. The highest Dsl was found in the riverine zone and the lowest in the lacustrine zone ($p<0.05$; α=0.05) indicating that the influence of the shoreline should become progressively smaller. As I expected, upstream distance, perimeter, area and transect width along the riverine-lacustrine gradient changed significantly in the downstream direction. For each of these parameters, the highest value occurred in the lacustrine zone and the lowest in

the riverine zone, except the upstream area which was lower in the riverine zone than in the other zones ($p<0.05$; $\alpha=0.05$).

Physical, biological and chemical parameters were also evaluated along the riverine-lacustrine gradient (Table 5). Two-way ANOVA always found the interaction between seasons and zones was not significant for any of the variables. Therefore, I investigated the impact of reservoir zones and sampling seasons on each parameter.

Table 5. Spatial patterns of physical, chemical and biological parameters in the four reservoirs using two-way ANOVA. See Table 4 for details.

Parameter	Riverine Zone	Transition Zone	Lacustrine Zone	p-value (Zones)
Temperature (°C)	24.5±0.4(38)	24.4±0.3(47)	24.4±0.7(12)	0.980
Zmix: Zeu	1.1±0.1(38)^{A}	1.6±0.1(47)^{B}	2.9±0.2(12)^{C}	<0.001
n"	2.8±0.3(38)^{A}	2.8±0.3(47)^{A}	1.2±0.6 (12)^{B}	<0.001
Turbidity (NTU)	35.6±10.4(38)^{A}	24.7±8.8(46)^{A}	5.9±17.2(12)^{B}	0.002
Secchi (m)	0.5±0.04(38)^{A}	0.5±0.03(47)^{A}	1.0±0.06(12)^{B}	<0.001
Chlorophyll a (mg m^{-3})	35.9±3.7(38)^{A}	35.0±3.2(46)^{A}	19.0±6.2(12)^{B}	0.015
PO_4 (µg/L)	116.3±46.6(38)	43.3±39.6(46)	5.2±77.4(12)	0.274
NO_3-N (µg/L)	830.8±326.8(38)	459.5±277.7(46)	285.9±542.7(12)	0.780
NH_3-N (µg/L)	63.8±16.7(38)	28.8±14.2(46)	58.6±27.7(12)	0.789
TP (µg/L)	213.1±58.0(37)^{A}	135.0±47.2(46)^{A}	42.3±92.3(12)^{B}	0.038
TN (µg/L)	2345.3±534.1(38)	1667.5±460.1(45)	1092.9±886.8(12)	0.307

Surprisingly, only temperature and TN were found to be significantly different among the three seasons. The range of temperature was from 9.20 to 34.43°C with a grand mean of 25.40°C. Temperature (°C) was significantly different among seasons with the highest value in summer (31.6±0.5), the lowest in winter (14.0±0.5) and intermediate in the spring (27.8±0.5) ($p<0.001$, $\alpha=0.05$). In addition, TN was significantly lower in the winter than in other seasons.

As expected, most physical and biological parameters varied significantly among the reservoir zones, suggesting each zone to be unique. Turbidity was significantly lower in the lacustrine zone ($p<0.05$; $\alpha=0.05$) but was not significantly different between the riverine and transition zone. As expected, the spatial pattern of light extinction coefficient and secchi depth was related to turbidity. The light extinction of lacustrine zones was significantly lower than that of other zones ($p<0.001$, $\alpha=0.05$, Table 4) while secchi depth showed the opposite pattern. Zmix:Zeu increased significantly from the riverine zone to the lacustrine zone. The pattern of Zmix:Zeu indicated that the proportion of the water column below the eutrophic depth (1% incident light) increased in the downstream direction. However, temperature was not significantly different among zones ($p=0.980$).

The grand mean *Chlorophyll a* concentration across all lakes, zones and seasons was 34.1mg.m^{-3} and the range was from 1.7 to 118.4mg.m^{-3}. The *Chlorophyll a* in the lacustrine zones was significantly lower than that in the other two zones ($p=0.015$, $\alpha=0.05$). *Chlorophyll a* did not vary significantly among seasons ($p=0.413$).

Most nutrient parameters were highly variable and did not show consistent or significant differences among reservoir zones. Only TP in the lacustrine zone was significantly lower than that in the other zones ($p=0.038$, $\alpha=0.05$).

3.3 Photosynthetic Parameters for Laboratory Incubation

Photosynthetic parameters including P^Bmax, R and alpha^B were calculated from the laboratory incubation and used to estimate planktonic production and respiration. Two-way ANOVA showed that the interaction between seasons and zones was not significant for any of the photosynthetic parameters ($p>0.05$).

Table 6. Photosynthetic parameters in different reservoir zones and seasons. See Table 4 for details. The unit of P^Bmax and R is mgO_2 mg $chla^{-1}$ hr^{-1}. The unit of Alpha^B is mgO_2 mg $chla^{-1}Ein^{-1}m^{-2}$.

Parameter	Riverine Zone	Transition Zone	Lacustrine Zone	p-value(Zones)
P^Bmax	19.5±2.0(38)	17.5±1.8(46)	18.1±3.5(12)	0.875
R	5.3±0.8(38)	2.8±0.7(46)	3.0±1.5(12)	0.188
Alpha^B	26.9±2.4(38)	25.7±2.2(46)	30.4±4.2(12)	0.303
Parameter	May-June	July-August	January-March	p-value(Seasons)
P^Bmax	14.6±1.4(36)^A	29.5±1.4(35)^B	8.2±1.6(5.9)^C	<0.001
R	3.8±0.8(36)^A	5.7±0.8(35)^A	1.2±1.0(25)^B	<0.001
Alpha^B	23.8±2.1(36)^A	36.0±2.1(35)^B	18.1±2.5(25)^C	<0.001

P^Bmax ranged from 2.5 to 59.8 mgO_2 mg $chla^{-1}$ hr^{-1}. The range of planktonic respiration in BOD bottles was 0.4 to 40.1 mgO_2 mg $chla^{-1}$ hr^{-1}. P^Bmax, R, and Alpha^B were not significantly different among zones, but all of them varied significantly among

seasons (Table 6). P^Bmax and $Alpha^B$ had the highest, lowest and intermediate values in the summer, winter and spring respectively. R was significantly lower in the winter than in other seasons.

3.4 Planktonic Production, Respiration and P:R Ratios

3.4.1 Spatial and Seasonal Variation of Planktonic P, R, and P:R Ratios

Table 7 shows the mean planktonic production, respiration and P:R ratios in three zones of the four lakes sampled from May, 2005 to March, 2006. Both areal and

Table 7. Spatial and temporal patterns of planktonic areal and volumetric production, respiration and P:R ratios in the four reservoirs using two-way ANOVA. Pln=Planktonic, AP=Areal production ($gO_2\ m^{-2}\ d^{-1}$), AR=Areal respiration ($gO_2\ m^{-2}\ d^{-1}$), VP=Volumetric production ($gO_2\ m^{-3}\ d^{-1}$), VR=Volumetric respiration ($gO_2\ m^{-3}\ d^{-1}$). See Table 4 for details.

	Spatial Patterns			
P & R	Riverine Zone	Transition Zone	Lacustrine Zone	p-value (Zones)
Pln AP	8.4±1.8(38)	8.6±1.6(46)	7.9±3.2(12)	0.292
Pln AR	$6.6\pm1.2(38)^A$	$7.0\pm1.1(46)^A$	$12.3\pm2.1(12)^B$	<0.001
Pln VP	$4.1\pm0.9(38)^A$	$3.8\pm0.9(46)^A$	$0.87\pm1.7(12)^B$	<0.001
Pln VR	$2.9\pm0.3(38)^A$	$2.2\pm0.3(46)^A$	$1.3\pm0.5(12)^B$	<0.001
Pln P:R	$1.4\pm0.2(38)^A$	$1.4\pm0.1(46)^A$	$0.7\pm0.3(12)^B$	0.009
	Seasonal Patterns			
P & R	May-June	July-August	January-March	p-value (Seasons)
Pln AP	$11.0\pm1.7(36)^A$	$9.9\pm1.8(35)^A$	$2.6\pm2.1(25)^B$	<0.001
Pln AR	$7.7\pm1.1(36)^A$	$10.7\pm1.1(35)^A$	$2.7\pm1.4(25)^B$	<0.001
Pln VP	$4.5\pm0.9(36)^A$	$4.4\pm1.0(35)^A$	$1.1\pm1.1(25)^B$	<0.001
Pln VR	$2.6\pm0.3(36)^A$	$3.3\pm0.3(35)^A$	$0.8\pm0.3(25)^B$	<0.001
Pln P:R	1.27±0.16(36)	1.28±0.16(35)	1.51±0.19(25)	0.430

volumetric results were evaluated for seasonal and spatial differences. There was no interaction between seasons and zones for any of the parameters ($p>0.05$).

Gross planktonic areal production was not significantly different among three zones ($p=0.292$, Table 7). However, temporal variability was found when comparing the three study periods ($p<0.001$, $\alpha=0.05$). Mean planktonic areal production was higher in the spring and summer while it was lower in the winter.

Planktonic areal respiration was significantly higher in the lacustrine zone than that in the other two zones ($p<0.001$, $\alpha=0.05$). Planktonic areal respiration had significantly lower values in the winter and higher values in the spring and summer ($p<0.001$, $\alpha=0.05$), which was the same temporal pattern as that observed in planktonic areal production.

Mean planktonic volumetric production and respiration were both lower in the lacustrine zone than in the other zones ($p<0.001$, $\alpha=0.05$, Table 7). In addition, they were also significantly different among seasons with the higher mean value in the spring and summer ($p<0.001$, $\alpha=0.05$).

Planktonic P:R ratios of all zones during the sampling periods had the mean of 1.33 and ranged from 0.22 to 6.42. Planktonic P:R ratio in the lacustrine zone was lower than those in other two zones ($p=0.009$, $\alpha=0.05$). However, planktonic P:R ratios did not vary significantly among seasons ($p=0.430$).

Planktonic P:R ratios in each zone were also compared to the traditional concept which predicts P:R <1 in the riverine zone, P:R around one in the transition zone, and

P:R>1 in the lacustrine zone (Kimmel *et al.* 1990). My finding showed almost the exact opposite pattern. I found P:R ratio to be significantly greater than one in riverine and transition zones (t-test, p=0.001; p=0.006) and significantly less than one in the lacustrine zone (t-test, p-value=0.013).

3.4.2 CART Results of Planktonic Areal Production, Respiration and P:R ratios

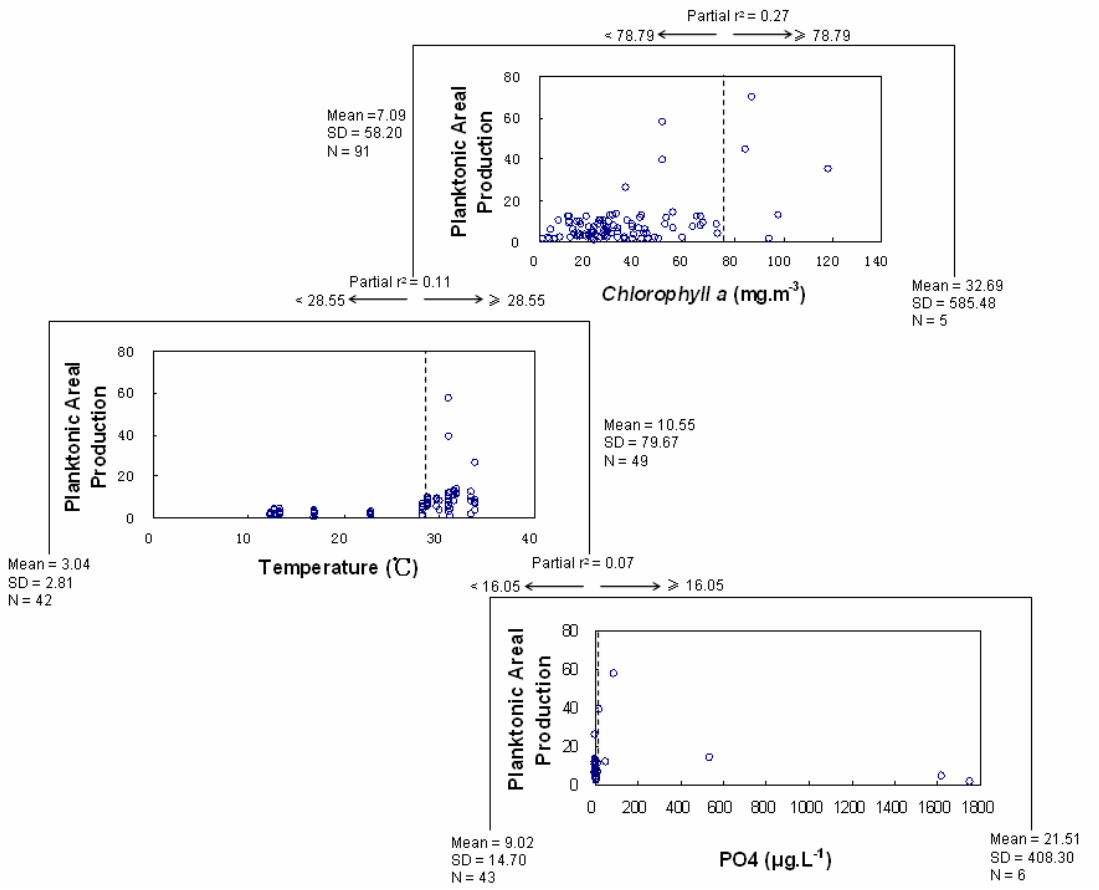

Figure 4. Results from CART analysis of gross planktonic areal production. Scatterplots reveal the response of planktonic production at each level of the tree. The vertical dotted line in each plot shows the threshold values which are illustrated to the left and right of each split. The predictor in x-axis of each scatterplot best explains variation of planktonic production. Mean, standard deviation (SD) and number of stations (N) summarized the data to the left and right in every split. Variance (r^2) explained by predictors is shown above the threshold values.

The variation in gross planktonic areal production for all stations throughout the study was best explained by *Chlorophyll a*, temperature and PO_4 (Fig.4). Gross planktonic areal productions were higher at stations with *Chlorophyll a* ≥78.79 mg m^{-3} (r^2=27%). At stations with lower *Chlorophyll a*, gross planktonic areal production was much lower at temperature <28.55°C (r^2=11%). However, the variation in 49 stations with temperature ≥28.55°C was further split by PO_4 (r^2=7%), as stations with PO_4 ≥16.05ug/L had higher production than that of the stations with PO_4 <16.05ug/L. The complete tree explained a total of 45% of the variation in gross planktonic areal production.

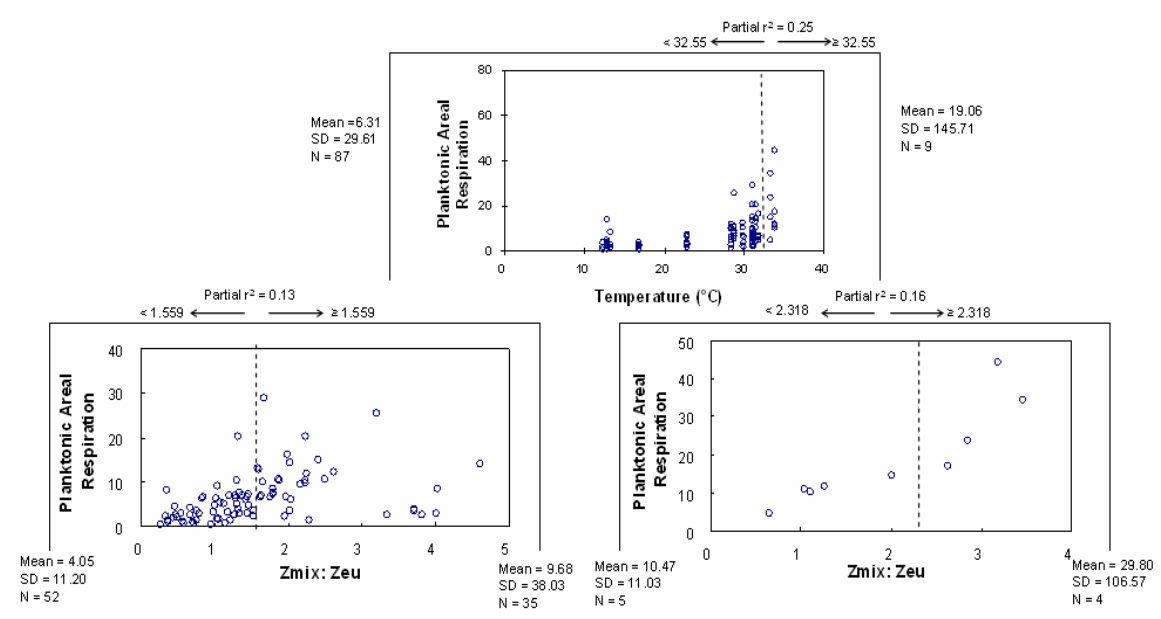

Figure 5. Results from CART analysis of planktonic areal respiration. See Fig. 4 for details.

The variation in planktonic areal respiration for all stations in this study was best explained by temperature and Zmix:Zeu (r^2=54%, Fig.5). Planktonic areal respiration

was much higher during warm periods (≥32.55°C, r^2=25%). However, planktonic areal respiration were also dependent on Zmix:Zeu when temperature was high (r^2=16%). During warmer periods, stations with Zmix:Zeu ≥2.318 had a mean areal respiration of 29.80 g O_2 m^{-2} d^{-1} compared to 10.47 g O_2 m^{-2} d^{-1} at stations with Zmix:Zeu <2.318. When the temperature was below 32.55°C, 13% of the variation in the 87 stations was explained by Zmix:Zeu. Planktonic respiration was higher at stations with Zmix:Zeu ≥1.559, with a mean of 9.68 g O_2 m^{-2} d^{-1} at 35 stations.

The CART analysis results of planktonic P:R ratios indicated that mixing depth was the primary factor that correlated with the planktonic P:R ratios (Fig 6, r^2=30%). Planktonic P:R ratios were highest at stations with mixing depth, lower than 1.21m. Variation in the 80 observations with depth ≥1.21m could not be further split because cross-validation and 1-SE rule indicated the number of split should be one.

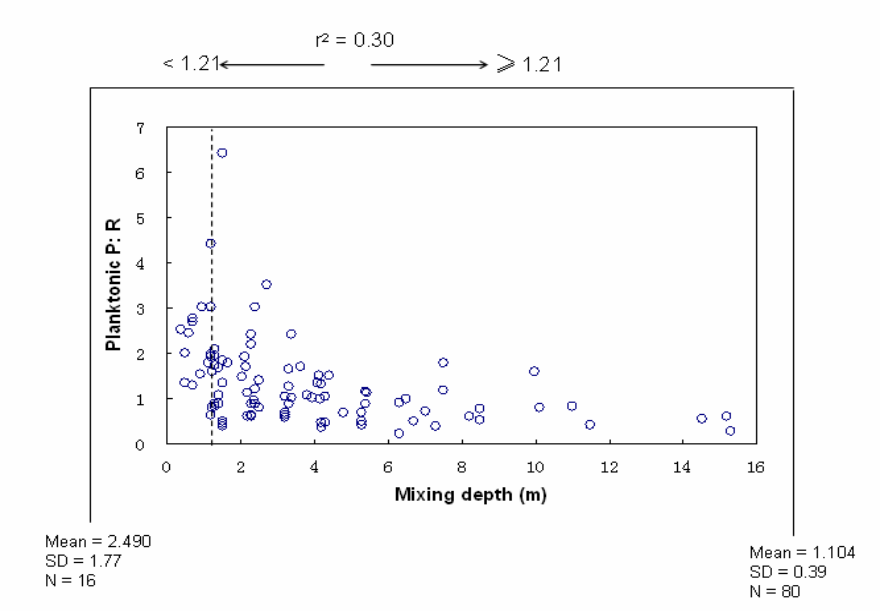

Figure 6. Results from CART analysis of planktonic P:R ratios. See Fig. 4 for details.

3.5 Community Production, Respiration and P:R Ratios

3.5.1 Spatial and Seasonal Variation of Community P, R, and P:R Ratios

Community metabolism data are not available for the winter period. Therefore, the seasonal analysis for the data only compared the data of the spring (May-June) to that of the mid summer (July-August).

Table 8. Spatial and temporal patterns of community areal and volumetric production, respiration and P:R ratios in the four reservoirs using two-way ANOVA. Com=Community, AP and AR stand for areal production and areal respiration ($gO_2\ m^{-2}\ d^{-1}$); VP and VR are volumetric production and volumetric respiration ($gO_2\ m^{-3}\ d^{-1}$); see Table 4 for details. At the $p<0.06$ level, Com VR is significantly different among zones.

	Spatial Patterns			
P & R	Riverine Zone	Transition Zone	Lacustrine Zone	p-value (Zones)
Com AP	$16.7\pm2.1(26)^{A}$	$14.2\pm2.0(30)^{A}$	$36.0\pm4.2(7)^{B}$	0.001
Com AR	$22.0\pm4.1(26)^{A}$	$22.1\pm3.8(30)^{A}$	$64.2\pm7.8(7)^{B}$	0.001
Com VP	$8.0\pm0.8(26)^{A}$	$5.1\pm0.7(30)^{B}$	$4.3\pm1.5(7)^{B}$	0.016
Com VR	$9.7\pm0.9(26)^{A}$	$6.6\pm0.8(30)^{B}$	$7.5\pm1.7(7)^{AB}$	0.053
Com P:R	$0.87\pm0.06(26)$	$0.79\pm0.05(30)$	$0.65\pm0.11(7)$	0.254
	Seasonal Patterns			
P & R	May-June	July-August	p-value (Seasons)	
Com AP	$20.9\pm2.5(30)$	$23.7\pm2.3(33)$	0.848	
Com AR	$24.3\pm4.5(30)$	$28.9\pm4.3(33)$	0.323	
Com VP	$5.6\pm0.9(30)$	$5.9\pm0.8(33)$	0.789	
Com VR	$7.6\pm0.9(30)$	$8.3\pm0.8(33)$	0.167	
Com P:R	$0.83\pm0.07(30)$	$0.71\pm0.06(33)$	0.148	

From the estimates of gross community production and respiration, mean areal and volumetric values in each zone were computed (Table 8). Results of community

metabolism were compared among zones and seasons, respectively. ANOVA analysis showed the interaction between seasons and zones was not significant. The spatial and seasonal differences are discussed as follows.

The mean community areal production and respiration was 17.75g O_2 m^{-2} d^{-1} and 26.74 g O_2 m^{-2} d^{-1}, respectively. Both community areal production and respiration were significantly higher in the lacustrine zone than those in the other zones ($p=0.001$, $\alpha=0.05$). However, neither of them was significantly different between the two sampling seasons ($p>0.05$).

Community volumetric production was significantly different among zones. Community volumetric respiration was not significantly different at $p=0.05$ but showed significant differences among zones at a $p<0.06$ level of confidence (Table 8). The community volumetric production and respiration were higher in the riverine zone where high plankton biomass occurs in very shallow area with the lowest Zmix:Zeu.

Community P:R ratios did not show significant spatial or temporal patterns. Moreover, community P:R ratios in each zone during the study were compared against the traditional concept that P:R should be <1 in the riverine zone, around 1 in the transition zone, and >1 in the lacustrine zone (Kimmel *et al.* 1990). I found that community P:R ratio was significantly less than 1 for all zones (t-test, $p<0.05$).

3.5.2 CART Results of Community Areal Production, Respiration and P:R ratios.

The variation of gross community areal production for all stations throughout the study was best explained by SDI (Fig.7, r^2=33%). The cross-validation and 1-SE rule of CART analysis permitted only one variable to be retained in the model. The mean community areal production was highest when SDI was greater than 7.669, which occurred at 4 stations. However, when SDI was lower than 7.669, production was much lower, with a mean of around 16 g O_2 m^{-2} d^{-1}.

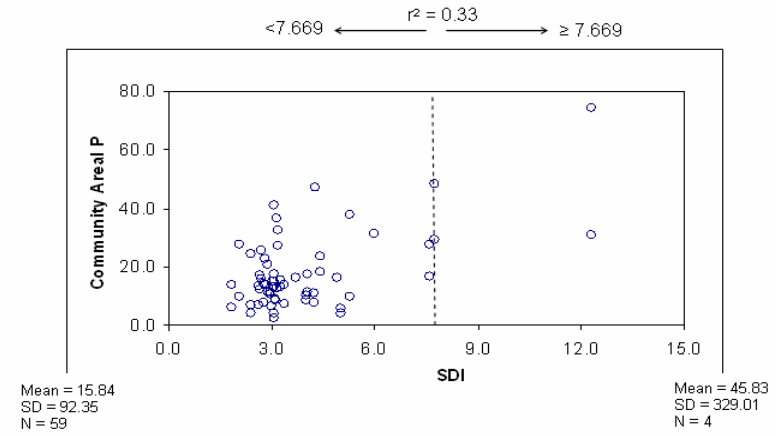

Figure 7. CART results of gross community areal production. See Fig. 4 for details.

For community areal respiration, Zmix:Zeu, temperature and SDI were the factors that best explained the observed variability (Fig.8, r^2=59%). Stations with the highest respiration were typically associated with Zmix:Zeu ≥2.235. This split explained 43% of the total variation. When Zmix:Zeu was larger than 2.235, stations with temperature ≥31.25°C tended to have the highest respiration (r^2=9%). The tree was split a second

time by Zmix:Zeu when Zmix:Zeu was below 2.235. The stations with Zmix:Zeu < 1.519 had a mean of nearly 15 g O_2 m^{-2} d^{-1}. In the stations with Zmix:Zeu ≥ 1.519, SDI accounted for an additional 2% of the variation. Although the relationship was weak in this final split (r^2=2%), the cross-validation and 1-SE rule suggested that SDI should be retained in the model.

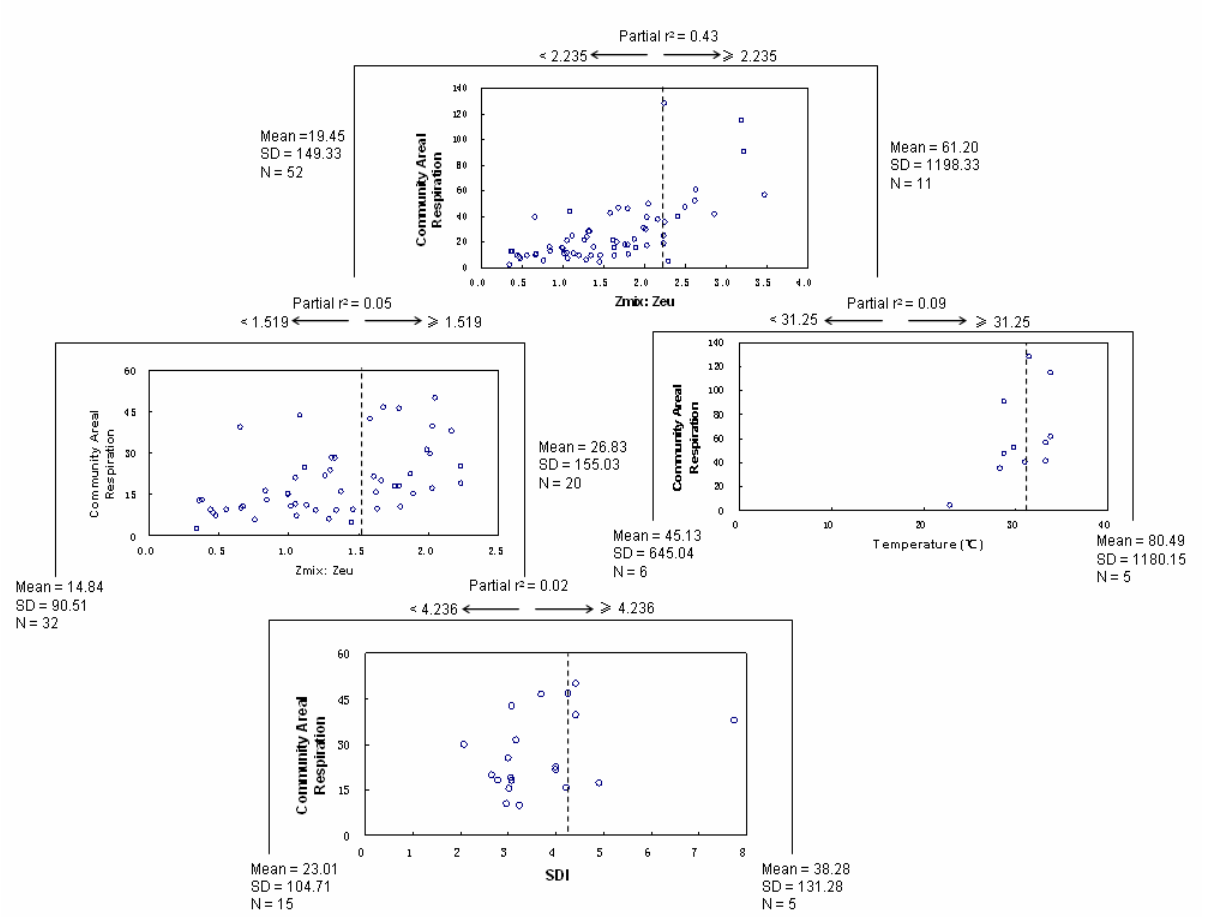

Figure 8. CART results of community areal respiration. See Fig. 4 for details.

A CART analysis model for community P:R was also attempted. However, the cross-validation indicated that with the increased number of splits, the x-error increased.

The explanatory variables may be too many while the variance in community P:R ratio is not large enough to suggest CART modeling.

3.6 Contribution of Planktonic Metabolism to Community Metabolism

The proportional contribution of planktonic metabolism to total community metabolism was evaluated from mean volumetric production and respiration of the upper mixed layer of the water column. The slope in the plot of planktonic volumetric production vs. community volumetric production (Fig. 9, $y=0.82x$, $r^2=0.30$) was around 0.82, which indicated that the planktonic production on average contributed to 82% of total community production. In Fig 9, I found several obvious outliers. The two highest outliers of planktonic volumetric production were both from Lake Lewisville in different sampling periods. These highest values came from the same station, which was in Pecan Creek and received waste water treatment plant inflow, in Lake Lewisville transition zone where the *Chlorophyll a* and nutrients were both abundant (*Chlorophyll a* >50 mg m^{-3}). The three outliers of community volumetric production (Fig. 9), which were higher community production values with lower planktonic production values, all occurred in shallow riverine zones. Two of these were located in the upstream area of Lake Conroe where *Hydrilla verticillata*, a rooted aquatic plant, was abundant. The high biomass of *Hydrilla verticillata* at these two stations likely contributed to the high community production values observed. The relationship became much stronger (y=

0.79x, R^2=0.63) when I removed the outliers of planktonic and community volumetric production. The slope was largely unchanged at 0.79.

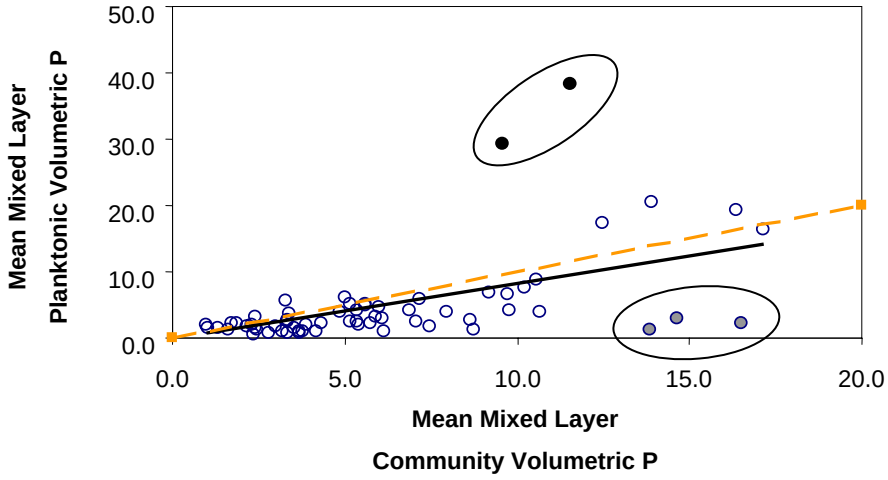

Figure 9. The relationship between gross community volumetric production (g O_2 m^{-3} d^{-1}) and planktonic production (g O_2 m^{-3} d^{-1}) for all sampling stations in the four reservoirs throughout the study. Solid line depicts the fitted least-squares regression equation for all stations. The dashed line is the 1: 1 line. The black and grey dots in two circles stand for the outliers in planktonic and community P, respectively.

The slope between planktonic respiration and community respiration (Fig. 10, y=0.332x, r^2=0.13) indicated that planktonic respiration only contributed a small part (around 33%) to the community respiration with a range from <10% to 100% of community respiration explained by planktonic respiration. Nevertheless, the low r^2 of the relationship indicated there was a high degree of variability. Moreover, nearly all the volumetric planktonic respiration data were below the 1:1 line, indicating that community volumetric respiration almost always exceeded planktonic volumetric respiration.

The ratio of planktonic production to community production was calculated and analyzed with two-way ANOVA (season x zone) in order to further explore how

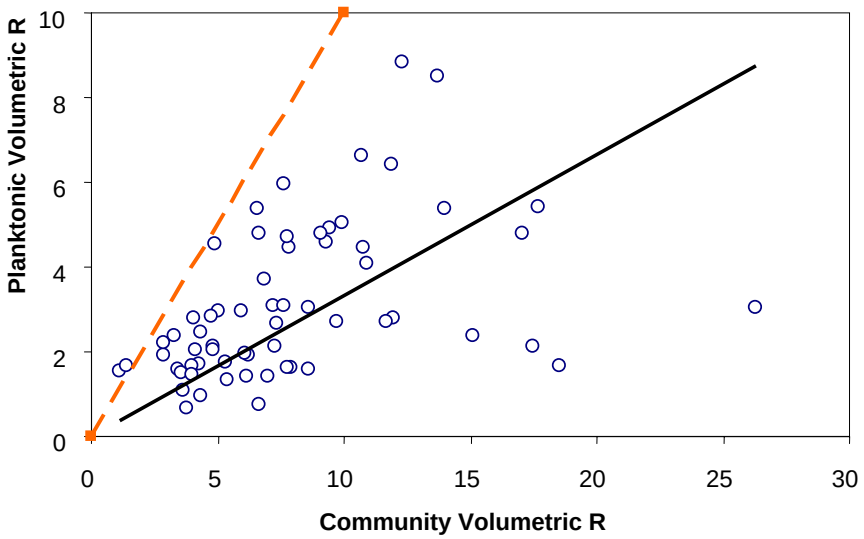

Figure 10. The relationship between the community volumetric respiration (g O_2 m^{-3} d^{-1}) and planktonic respiration (g O_2 m^{-3} d^{-1}) for all sampling stations in the four reservoirs throughout the study. Solid line depicts the fitted least-squares regression equation. The dashed line is the 1: 1 line.

the proportional contribution of planktonic production to total community production changed among zones and between seasons. Similarly, the ratio of planktonic respiration to community respiration was calculated and analyzed. The interaction between seasons and zones was not significant ($p>0.05$). The results illustrated that planktonic production contributed less to community production in the lacustrine zone than in the other zones (Table 9, $p=0.027$, $\alpha=0.05$). The contribution of planktonic respiration to community respiration was higher in the transition zone and lower in the lacustrine zone (Table 9, $p=0.039$, $\alpha=0.05$). However, the contribution of both

planktonic production and respiration to total community production and respiration did not vary significantly between the two sampling seasons ($p>0.05$).

Table 9. The contribution of planktonic metabolism to community metabolism. See Table 4 for details. The ratios are same when calculating based on areal and volumetric values because the same mixing depth is used in areal production and respiration to get volumetric values.

Contribution	Riverine Zone	Transition Zone	Lacustrine Zone	p-value (Zones)
Pln P: Com P	$0.73 \pm 0.1(26)^{A}$	$0.88 \pm 0.1(30)^{A}$	$0.33 \pm 0.2(7)^{B}$	0.027
Pln R: Com R	$0.46 \pm 0.05(26)^{AB}$	$0.49 \pm 0.04(30)^{A}$	$0.25 \pm 0.09(7)^{B}$	0.039
Contribution	May-June	July-August		p-value (Seasons)
Pln P: Com P	$0.60 \pm 0.1(30)$	$0.70 \pm 0.1(33)$		0.359
Pln R: Com R	$0.38 \pm 0.05(30)$	$0.42 \pm 0.05(33)$		0.322

CHAPTER FOUR

Discussion

4.1 Spatial Patterns of Morphometric, Physical, and Chemical data

Many studies describe the expected morphometric, physical and chemical features of each reservoir zone (Kimmel *et al.*, 1990; Cole & Hannan, 1990; Thornton *et al.*, 1990). However, in many cases, these descriptions are based on relatively little actual data. Furthermore, I found few studies that specifically tested the predictions of this model (Fleituch et al., 2001; Bernot et al. 2004).

Morphometric data in this study supported the previous descriptions along the riverine to the lacustrine gradient. Many morphometric parameters including SDI, Dsl, upstream area, distance, perimeter, transect width and depth showed distinct changes along the riverine-lacustrine gradient in agreement with Thornton's heuristic model.

Physical patterns were also in general agreement with prediction of previous work (Kimmel *et al.*, 1990; Cole & Hannan, 1990; Thornton *et al.*, 1990). As expected by the zonation model, the secchi depth was significantly higher in the lacustrine zone while turbidity and light extinction in the lacustrine zone were significantly lower. However, I consistently found no difference between the riverine and transition zones for most of these parameters.

Most chemical data did not vary significantly among reservoir zones and their variability was very high. Only TP was significantly lower in the lacustrine zone as predicted by the zonation model. Although trends of mean nutrient concentrations decreased in the downstream direction and therefore may lend or provide some support for the predicted patterns, there were no significant differences except for TP.

Kimmel *et al.* (1990) postulated that mean *Chlorophyll a* should be relatively low in the riverine zone, increase significantly in the transition zone and fall again in the lacustrine zone. However, my data do not support this prediction. According to my data, the mean *Chlorophyll a* in the lacustrine zone was significantly lower than those in the other two zones. Kimmel *et al*. (1990) suggested that the low *Chlorophyll a* in the riverine zone would be maintained due to high turbidity in this zone. However, my data were collected under relatively low-flow conditions and I found no significant differences in turbidity and light extinction coefficient between the riverine and transition zones.

Thus, in general, morphometric and physical data generated in this study supported the zonation model. But *Chlorophyll a* and most nutrient parameters showed a different pattern from the expected one.

4.2 Factors Correlated with Planktonic and Community Metabolism

4.2.1 Factors Correlated with Planktonic P, R, and P:R Ratios

The key factors controlling planktonic and community P, R and P:R ratios identified by my CART analysis are in general agreement with the literature.

Chlorophyll a was one of the major predictors correlating with gross areal planktonic production. Gross areal planktonic productions had the highest values at stations with *Chlorophyll a* ≥78.79 mg m^{-3}. *Chlorophyll a* has been used as the fundamental index of phytoplankton abundance (Kalff, 2002). It is likely that high planktonic production occurs where phytoplankton is more abundant. The result was consistent with del Giorgio and Peters (1994) who found that the rates of phytoplankton production were positively correlated with *Chlorophyll a* concentration. However, at stations with lower *Chlorophyll a*, gross planktonic areal production was associated with water temperature and PO_4 concentration. The temperature from CART results separated the winter sampling period, which implied a seasonal pattern of planktonic production. Furthermore, PO_4 concentration was also related to planktonic production, which may indicate the nutrient influence on phytoplankton production (Goldman, 1968; Likens, 1972; Schindler, 1978; Kimmel *et al.* 1990). Therefore, my results strengthen the biomass and nutrient's impact on planktonic production.

Water temperature and Zmix:Zeu best explained the variation of planktonic areal respiration during the study. Similar to planktonic production, the highest planktonic respiration was found at stations with higher temperatures. This is likely due to temperature's important role in the health of plankton (Dodds, 2002). Moreover, variations were further explained by Zmix:Zeu, which is a factor that relates to the light climate. A circulating phytoplankton cell is photosynthesizing for less time when Zmix:Zeu ratio is larger (Lind *et al.*, 1992). My results indicated that high planktonic

respiration was associated with the larger Zmix:Zeu ratios. In general, primary factors influencing the planktonic respiration imply the temporal and spatial patterns.

Mixing depth was the primary factor that correlated with the planktonic P:R ratios. Mean planktonic P:R ratios were higher when the mixing depth was lower than 1.21m. Those shallow stations were mostly in riverine zones. Depth has been previous shown to influence different aspects of lake metabolism: respiration and production rates are inversely related to mean depth respectively (Welch *et al.* 1976; Fee, 1979; Mathias and Barica 1980; del Giorgio and Peters, 1994). These inverse relationships between respiration or production and mean depth reflect the increased contribution in shallow lakes of highly productive zones, with high rates of nutrient resuspension and organic C supply (Mathias and Barica 1980). My data suggest that P:R ratios are primarily predicted by mixing depth, which has distinct characteristics in nutrients concentration, light extinction and biomass.

4.2.2 Factors Correlated with Community P and R

Variation in gross community areal production was best explained by SDI. In my results, the mean gross community areal production was greater with larger SDI ratios. For lakes with the same surface area, as SDI increased, more irregularity is indicated (Osgood, 2005). Though 33% of the variation in community areal production was explained by SDI, only four stations with larger SDI, which were all in the lacustrine, were split by CART.

Stations with higher respiration rates were typically associated with higher Zmix:Zeu as expected. With higher Zmix:Zeu ratio, the highest respiration occurred when water temperature was warmer. Although community respiration was not significantly different between the spring and summer, I believe that there are likely seasonal changes for the year-round data. Unfortunately, I do not have the winter data for community metabolism. In addition, greater SDI had higher community respiration when Zmix:Zeu was in the range from 1.5 to 2, though the relationship was weak in this split (r^2=2%).

4.3 Spatial and Temporal Patterns of Planktonic and Community Metabolism

4.3.1 Spatial Patterns of Planktonic and Community Metabolism

Photosynthetic parameters including P^Bmax, R and Alpha^B were found to be in the range as reported from other photosynthetic studies (Melcher, 1994; Millard *et al.*, 1996; Carignan *et al.*, 2000) and similar to the results for Lake Texoma in Texas reported by Baugher (2001). Planktonic areal and volumetric production and respiration were also consistent with previous results (del Giorgio and Peters, 1994; Carignan *et al.*, 2000). However, compared with the range revealed from community metabolism studies (Fontaine and Ewel, 1981; Wilcock et al., 1998; Cole *et al.*, 2000; Hanson *et al.*, 2003), community areal production and respiration in the lacustrine zone were roughly 50% higher than the results from previous studies. It is likely that the reservoirs in this study were more eutrophic than many of those previous studies.

The spatial patterns of planktonic areal production in my study conflict with patterns predicted by the traditional zonation model (Kimmel *et al.* 1990). The zonation model proposes that planktonic areal production is often light-limited in the riverine zone and nutrient-limited in the lacustrine zone while the transition zone is often the most fertile region of the reservoir. Nevertheless, my planktonic areal production data illustrated that there was not a significant difference among the three zones. Although *Chlorophyll a* was lower in the lacustrine zone, the increased water clarity apparently allowed the plankton to compensate the production. So that planktonic areal rate did not vary significantly among reservoir zones. However, the spatial pattern of planktonic volumetric production do follow Kimmel *et al.* (1990)'s description that the planktonic volumetric production is high in the riverine zone and is reduced in the lacustrine zone.

Planktonic areal and volumetric respiration in the riverine zone and the transition zone were not significantly different. However, planktonic respiration in the lacustrine zone was significantly different from those in the riverine and transition zones. Planktonic volumetric respiration in the lacustrine zone was about 50% lower than in the riverine and transition zones even though much deeper water column in this zone resulted in significantly higher areal respiration rates.

Fontaine and Ewel (1981) revealed that gross community areal production and respiration were significantly higher in deep stations and lower in shallow areas. In addition, they showed gross community volumetric production and respiration were

greatest at the shallow stations. My results supported their finding because I found the exactly same spatial patterns of community metabolism.

Kimmel *et al.* (1990) suggested that P:R <1 in the riverine zone, P:R around one in the transition zone, and P:R >1 in the lacustrine zone. However, my results do not support the traditional concept (Table 10). In my study, planktonic P:R ratios were larger than one in the riverine and transition zone whereas they were less than one in the lacustrine zone.

Table 10. Predicted and observed value of P:R ratios in reservoir zones. p-values from t-test are shown for each reservoir zone.

Comparison	Riverine Zone	Transition Zone	Lacustrine Zone
Thornton model	P:R <1	P:R =1	P:R >1
Current study (Planktonic)	P:R >1 (p=0.001)	P:R >1 (p=0.006)	P:R <1 (p=0.013)
Current study (Community)	P:R <1 (p=0.008)	P:R <1 (p<0.001)	P:R <1 (p=0.001)

In contrast to the predictions of the zonation model, planktonic P:R ratios were less than one in the lacustrine zone. However, this finding is not entirely unexpected. Several studies have suggested that respiration exceeds photosynthesis in the epilimnion of oligotrophic lakes, estuaries, and ocean (Sorokin, 1971; del Giorgio and Peters, 1993, 1994; del Giorgio et al., 1997; Duarte and Agusti, 1998). Based on a review of the literature on planktonic production and respiration, del Giorgio and Peters (1993) found

that planktonic P:R ratios are general below one in oligotrophic and mesotrophic lakes and are greater than one in eutrophic lakes. I see a similar *relative* pattern with P:R >1 in the more eutrophic riverine and transition zones which have higher *Chlorophyll a* biomass and high rates of planktonic volumetric production. In the lacustrine zone, with lower *Chlorophyll a* and planktonic production, I found P:R <1.

Another fact that could influence the planktonic P:R ratio is water color. Previous research suggested that the impact of allochthonous carbon on lacustrine planktonic metabolism is greater in colored lakes (Salonen and Hammar, 1986). Thus, planktonic metabolism may be also related to the water color, which was unfortunately not included in my study.

The community P:R ratios were less than 1 for all zones in these reservoirs. In the lacustrine zone, community areal and volumetric respiration was approximately twice as large as community production, indicating that community respiration was satisfied by both autochthonous planktonic production and imported production (McKenna, 2003). In riverine and transition zones, community areal and volumetric respiration was also lower than the community production. Thus, the aquatic ecosystem in these reservoirs was heterotrophic and allochthonous organic matter was required to support a portion of the aquatic respiration (Hanson *et al.*, 2003). My results are in agreement with some previous results that found community P:R ratios less than one (Wilcock *et al.*, 1998; Cole *et al.*, 2000; McKenna, 2003). Other researchers work showed that community P:R ratio can be greater than one or around one in various conditions with vegetated

stream and eutrophic lakes (Odum, 1957; Hanson *et al.*, 2003; Fontaine and Ewel, 1981; Lopez-Archilla *et al.*, 2004).

4.3.2 Temporal Patterns of Planktonic and Community Metabolism.

Temporal patterns were generally found in my data and identified by both CART model and ANOVA analysis. Planktonic production and respiration were both significantly different among the three sampling seasons. The higher values occurred in the spring and summer while the lower occurred in the winter. Moreover, results from CART analysis supported the temporal patterns. Based on the CART analysis for areal planktonic production and respiration, I found that water temperature was one of the primary factors that explained the variation in production and respiration. The temporal patterns of planktonic metabolism in my results were consistent with other studies which likewise found strong seasonal patterns (Servais *et al.*, 1984; Uehlinger, 2006).

Community production and respiration, both areal and volumetric values, were not significantly different between the two sampling seasons for which community data are available. However, CART model for areal community respiration showed that temperature was an important correlate. This may be due to the experiment limit. There is no winter data available for seasonal comparison and the difference in temperature before May and July were relatively low. Therefore, the temporal patterns for community metabolism are perhaps not apparent in my data set.

Previous studies suggest that light and temperature are major factors controlling the metabolism of aquatic ecosystem (Fisher *et al.*, 1982; Uehlinger, 2006). Both light and temperature are subject to strong seasonal variation, especially at mid and high latitudes (Servais *et al.*, 1984; Uehlinger, 1993; Uehlinger, 2006). Light is generally considered to be the predominant factor over the short term and is the ultimate energy source for primary producers. Temperature regulates the metabolic processes as supported from my results (Uehlinger, 2006).

4.4 Contribution of Planktonic Metabolism to Community Metabolism

There is no reason to expect planktonic and community metabolism to be the same because they measure different components of lake metabolism using different methods (Hanson *et al.* 2003). Data collected during my study supported this idea. First, my results indicated that planktonic production contributed about 82% to total community production. However, planktonic respiration only contributed around 33% to total community respiration. This is not consistent with Fontaine and Ewel's (1981) results. They found that the planktonic production was responsible for 44% of the gross production while 54% of the community respiration was due to the plankton.

My results suggest that planktonic producers are the primary producer groups for the total autochthonous community production in reservoirs. However, according to Fontaine and Ewel's study (1981), submersed macrophytes and associated epiphytes contributed to the remaining half of community production. Nevertheless, Texas

reservoirs may not provide sufficient underwater light to support high levels of macrophytes as seen in their study.

The contribution of planktonic production to community production was much lower in the lacustrine zone than those in the other zones. This conflicts with Kimmel *et al.* (1990)'s opinion, who believed that contribution of the planktonic producers to the total primary production is maximized in the lacustrine zone.

Moreover, the high levels of community respiration relative to the planktonic respiration in my results suggest that allochthonous sources of organic matter subsidize community respiration (del Giorgio and Peters, 1994). Numerous studies have shown that the riverine zone contributes significant amount of organic carbon from the watershed to reservoirs and the littoral sediments are an important site for system respiration in lakes (Cole *et al.*, 2000; Vadeboncoeur *et al.*, 1996). In addition, bacterial communities in water column consume dissolved oxygen and should contribute to respiration. Bacterial heterotrophy in aquatic ecosystems plays an important role in the overall carbon cycle (Lind, 2002).

4.5 Summary and Recommendations

This study focused on the spatial and temporal variability of planktonic and community metabolism along the riverine-lacustrine gradient. The primary factors that best explained the variability of planktonic and community metabolism were explored.

This study also investigated the contribution of planktonic metabolism to total community metabolism.

The hypotheses were summarized and discussed as follows.

1. Ho: Planktonic metabolism remains the same among the three reservoir zones. Planktonic areal production remained the same among the three reservoir zones. However, planktonic areal respiration was significantly higher in the lacustrine zone. Planktonic volumetric production and respiration were significantly lower in the lacustrine. Moreover, planktonic P:R ratios were also significantly lower in the lacustrine zone.

2. Ho: Community metabolism remains the same among the three reservoir zones. For community areal production and respiration, the values in the lacustrine were significantly higher. However, community volumetric production and respiration were significantly higher in the riverine zone. Only community P:R ratios remained the same among the three reservoir zones.

3. Ho: Planktonic metabolism does not vary seasonally. For both areal and volumetric values, the planktonic production and respiration were lower in the winter. However, planktonic P:R ratios did not vary seasonally.

4. Ho: Community metabolism does not vary seasonally. This hypothesis can not be rejected. Community production and respiration were not significantly different between seasons. Community P:R ratios did not vary seasonally either. However, only two season data were available for community metabolism.

5. Ho: The contribution of planktonic metabolism to community metabolism remains the same at the three reservoir zones. This hypothesis was rejected. The contributions of planktonic production and respiration to community production and respiration were lower in the lacustrine zone.

6. Ho: The contribution of planktonic metabolism to community metabolism does not vary seasonally. This hypothesis can not be rejected. The contributions of planktonic production and respiration to community production and respiration did not vary seasonally. However, there was no winter data for community metabolism.

7. Ho: The change of P:R ratio along the riverine-lacustrine gradient is supported by the traditional pattern, which includes that the ratio is less than one in the riverine zone, around one in the transition zone and greater then one in the lacustrine zone. I rejected this hypothesis. Planktonic P:R ratios were greater than one in the riverine and transition zone while lower than one in the lacustrine zone. Community P:R ratios were lower than one in all three zones.

There were some other important findings other than the results of the hypotheses. The variability of planktonic areal production was explained by *Chlorophyll a*, temperature and PO_4. The primary predictors for planktonic areal respiration were temperature and Zmix:Zeu. The planktonic P:R ratios were best explained by mixing depth. Moreover, Zmix:Zeu was the only predictor for community areal production. Factors controlling community areal respiration included Zmix:Zeu, temperature and SDI.

However, the low r^2 from these factors implied that there were important factors which were not measured.

On average planktonic production contributed around 80% to total community gross production. On the other hand, planktonic respiration only accounted for about 33% of total community respiration.

Unfortunately, community data in the winter were not available. CART results of community respiration implied temperature was one factor that explained the variability of respiration. Thus, the community metabolism data for the whole year would be helpful to reveal the seasonal patterns of community metabolism. In addition, further studies based on samples from a greater number of stations representative of the lacustrine zones would provide valuable data for extrapolation to the whole lacustrine zone of metabolism estimations. Furthermore, the distance of sample stations was so far away between the transition zone and the lacustrine zone. Several intermediate stations may help to find out the spatial patterns along the riverine-lacustrine gradient. At last, future studies based on dissolved carbon (DOC), which was not measured in this study, would be useful to evaluate the influence of DOC on lake metabolisms.

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