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# Changes in Primary Production of Pawnee Reservoir as a Result of Reservoir Aging

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**Changes in Primary Production of Pawnee Reservoir as a Result of  
Reservoir Aging**

by

Kristopher A. Fischer

A THESIS

Presented to the Faculty of  
The Graduate College at the University of Nebraska  
In Partial Fulfillment of Requirements  
For the Degree of Master of Science

Major: Natural Resource Sciences

Under the Supervision of Professor Kyle D. Hoagland

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CHANGES IN PRIMARY PRODUCTION OF PAWNEE RESERVOIR AS A  
RESULT OF RESERVOIR AGING

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University of Nebraska, 2000

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The effects of reservoir aging on the annual primary production of a midwestern U.S. reservoir constructed in 1965 (Pawnee Reservoir) were studied by comparing primary productivity from June 1998 through July 1999 to surveys conducted in 1969-70 by Andersen (1971). Sedimentation and associated reservoir aging processes have changed Pawnee Reservoir from a high nutrient, relatively clear water reservoir to a more turbid, light limited, shallower reservoir. During the initial study period, annual primary productivity was  $1,390 \text{ mg C/m}^2/\text{d}^{-1}$  in 1969 and  $1,810 \text{ mg C/m}^2/\text{d}^{-1}$  in 1970. These values were not significantly different from 1998-99 annual primary production of  $1,540 \text{ mg C/m}^2/\text{d}^{-1}$ . In 1969-70, Pawnee Reservoir exhibited maximum Secchi disk depths  $\geq 3$  meters, but during late summer months blue-green algal blooms limited Secchi disk depths to 0.5 meter or less. In the present study, inorganic suspended sediments limited Secchi disk depths to  $\leq 1$  meter. This increase in turbidity limited the euphotic zone to within 1 to 2 meters of the lake surface, shifting phytoplankton species composition toward species that could maintain their position in the

water column, mainly flagellated chlorophytes. Thus, sedimentation and associated abiotic sediment turbidity have been shown to be major determinants of phytoplankton species composition and biomass, and macroinvertebrate community composition, but annual primary productivity has not changed significantly over the past 35 years.

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## Introduction

Reservoirs constructed in the Midwest within the past 50 years were expected to have useful lifespans of about 100 years. However, many of these impoundments are already exhibiting signs of rapid reservoir aging due to sedimentation and nutrient loading (Popp & Hoagland, 1995). In the Midwest, sedimentation is a major factor causing aging in reservoirs due to high drainage area-to-lake surface area ratios and land use practices in their watersheds (Kimmel & Groeger, 1986; Thornton, 1990). Reservoirs located in agricultural watersheds where land use is primarily devoted to row crops are somewhat unique, due to the overriding influence of sedimentation and associated turbidity.

Sedimentation involves the accumulation of silts and clays in the sediments (Avnimelech, 1989) and is influenced by a variety of parameters (Bordovshiy, 1965) all of which generally lead to decreased reservoir volume (Popp et al., 1996). When sedimentation takes place in midwestern reservoirs where drainages are devoted to row crop agriculture, inputs of silts, clays and associated organic matter, the high turbidity associated with sedimentation also decreases the euphotic zone. As turbidity increases, light penetration decreases, causing the 1% level of subsurface irradiance to occur within two meters or less of the surface. In both turbid and clear waters, light is absorbed and scattered as it moves through the water column (Kirk, 1985). As a consequence of suspensoids in the water column, light in the blue wavelengths

(i.e. 400 nm) is attenuated more rapidly than light in the red wavelengths (i.e. 700 nm) (Grobbelaar, 1985). Therefore, inorganic suspensoids present in the water column cause primary productivity profiles to become compressed in turbid waters (Grobbelaar, 1985). Organisms such as planktonic algae must migrate into shallower waters to receive necessary light for photosynthesis or declines in primary productivity will result.

Kimmel & Groeger (1986) hypothesized that lakes and reservoirs age in relatively the same way, the main difference being in the relative rates of aging. This is attributable to the size of the watershed and land use practices in the reservoirs' or lakes' immediate drainage area (watershed). They hypothesized that after basin filling a period of high biological productivity would occur, termed "trophic upsurge", as a result of nutrients being leached from the newly formed reservoir bottom sediments. This period of high biological productivity would then be followed by a decline in biological productivity, termed "trophic depression", when the reservoir becomes shallow and wind mixed, therefore not allowing for anoxia in the profundal zone. "Trophic equilibrium" occurs after the initial spike of high biological productivity, and lake succession and cultural eutrophication periods, during which the reservoir's biological activity declines and remains at a lower level if external loading remains constant (Holz et al., 1997). Previous studies of benthic macroinvertebrates, zooplankton and phytoplankton biomass during trophic upsurge have supported Kimmel &

Groeger's (1986) hypothesis (Helzer, 1971; Hergenrader, 1980a, b; Hergenrader & Lessig, 1980, Holz et al., 1997). Few studies have examined reservoirs in the trophic equilibrium phase, due to a lack of long-term monitoring programs and the relatively young age of many reservoirs in the U.S.

The purpose of this study was to examine the effects of reservoir aging on primary productivity by comparing data from Andersen (1971) four years after Pawnee Reservoir was filled to present day levels. In previous studies documenting changes in response to aging in Pawnee Reservoir, (1) Popp & Hoagland (1995) reported that the total benthic invertebrate biomass declined by a factor of ten, 27 years after basin filling. (2) Popp et al. (1996) found that total zooplankton biomass increased by 3.9 times compared to samples collected 3-5 years after basin filling (i.e. trophic upsurge), and (3) Holz et al. (1997) found a decrease in the number of algal groups and a decline in algal species diversity. Species that could avoid flocc-forming sediments by optimizing their position in the photic zone via phototactic swimming were favored. The results presented here will be evaluated in light of Kimmel & Groeger's reservoir aging model.

## **Materials and Methods**

### *Study site*

Pawnee Reservoir is a shallow ( $z = 3.4$  m), eutrophic flood-control impoundment located approximately 20 km northwest of Lincoln, Nebraska, USA ( $40^{\circ} 51' N$ ,  $96^{\circ} 52' W$ ). Constructed by the U.S. Army Corps of Engineers in

1965, this 299-ha reservoir is located in a 9298-ha agricultural watershed where land use consists primarily of row crops and pasture. The reservoir is wind-mixed and stratifies weakly for only brief periods during the summer. This mixing also promotes sediment resuspension in the water column, resulting in turbid conditions throughout ice-free periods. Sedimentation has decreased water depth by an average of 2.7 m near the inflow and 3.0 m along the dam over the past 30 years (Popp & Hoagland, 1995). Additional physical and chemical data have been previously reported (Hergenrader, 1980a, b; Popp & Hoagland, 1995; Popp et al., 1996, Holz et al., 1998).

#### *Field collections*

Pawnee Reservoir was sampled bimonthly from June 29 to November 18, 1998 and from May 8 to July 28, 1999. Water samples were taken from two sites at the center of two east-west transects described by Hergenrader (1980a), which included one shallow and one deep water transect [for transect locations, see Fig. 1 in Popp & Hoagland (1995)]. Water samples were collected with a 3-L, non-metallic Van Dorn bottle, at the surface, 0.5 m and every meter thereafter until the 1% level of subsurface irradiance was reached. Glass-stoppered BOD bottles (300 ml) were filled with lake water from each sampling depth, returned to a covered box, and inoculated with 10  $\mu\text{Ci}$  of  $\text{C}^{14}$  labeled sodium bicarbonate ( $\text{Na}_2\text{H}^{14}\text{CO}_3$ , Dupont NEN, Boston, MA, USA). BOD bottles were then returned to the depth from which they were collected, and incubated for a period of four

hours starting at approximately 1000 h (Vollenweider, 1969). Three BOD bottles were incubated at each depth, including two light bottles and one dark bottle. The BOD bottles were attached to a 1-m square floating surface frame large enough not to shade the near-surface bottles, connected to a rope with clips at each meter and anchored on the lake bottom. Along with primary productivity measurements, pH (Fisher Accumet, model 1003, Pittsburgh, PA, USA), dissolved oxygen and temperature (Yellow Springs Instruments, model 55, Yellow Springs, OH, USA), alkalinity (Lind, 1985), light (spherical quantum sensor, model spqa 2015 and LI-1000 data logger, LiCor Inc., Lincoln, NE, USA) and Secchi disk depth were also collected on each sampling date.

#### *Laboratory analyses*

After incubation, a 60-ml aliquot from each bottle was filtered through a 47-mm, 0.45- $\mu\text{m}$  membrane filter (Metricel membrane filter GN-6, Pall Gelman Sciences, Ann Arbor, MI, USA), using a vacuum pump with no more than 0.3 atm of vacuum, to avoid cell damage (Wetzel & Likens, 1979). Before counting, the filters were acidified in a desiccation chamber with 3 ml of HCL for 10 min to remove any precipitated  $^{14}\text{C}$  (Wetzel, 1965). After acidification, the filters were placed into 20-ml polypropylene scintillation vials (VWR Scientific, So. Plainfield, NJ, USA) and filled with 20 ml of scintillation fluid (ICN Ecolite Plus, Costa Mesa, CA, USA). The filters were then counted on a liquid scintillation spectrometer

(model 1209 Rackbeta, Wallac Inc., Gaithersburg, MD, USA), with an efficiency of 96% for  $^{14}\text{C}$ .

Productivity was calculated by the following equation (Vollenweider, 1969):

$$^{12}\text{C available} = \frac{^{14}\text{C assimilated}}{^{14}\text{C available}} \times ^{12}\text{C available} \times K_{1,2,3}$$

$^{12}\text{C available} = \text{total carbonate alkalinity} \times \text{pH factor}$

$^{14}\text{C available} = ^{14}\text{C activity added} \times \text{counter efficiency}$

$^{14}\text{C assimilated} = (\text{total counts} - \text{background}) \times 1.06$

$K_1 = \text{a correction for the aliquot factor}$

$K_2 = \text{a time factor to reduce the measured activity to activity per hour}$

$K_3 = \text{a dimension factor to convert mg/l to mg/m}^3$

The values obtained using the above equation were then graphed using Sigma Plot (Version 4, Jandel Scientific, San Rafael, CA, USA), to convert the volumetric measurements to areal estimates of productivity using a mechanical planimeter to determine the area under the curve, to obtain  $\text{mg C/m}^2$  of lake surface area. This area was then compared proportionally with a known standard area of  $\text{mg C/m}^3/\text{time}$  versus depth drawn to the same scale. This value was converted to  $\text{mg C/m}^2/\text{day}$  by extrapolating the incubation values to daily values. Daily productivity rates were determined experimentally by conducting a series of

$^{14}\text{C}$  estimates over a 14-hr period (Wetzel, 1964). This was done by sampling the daily productivity by running a series of 4-h measurements from 0700 to 1000; 1000 to 1400; 1400 to 1800; and 1800 to 2100. Productivity is then converted to  $\text{mg C/m}^3/\text{day}$ . The area under the entire curve is integrated by planimetry and compared to an area of one representative 4-hr measurement. The ratio of the area of the fraction to the whole provided a factor by which the 4-h incubation period can be extrapolated to a daily value. The annual primary productivity was then estimated, by graphing the entire sampling year (195 days). The sampling period originally consisted of 222 days, but was cut short by interpolating a point on the graph to limit the sampling period to one sampling year. This was done to allow the comparison with Andersen (1971), in which primary productivity measurements were done on a yearly basis. The area under the curve was then compared with an area of known productivity (i.e.  $1000 \text{ mgC/m}^2/31\text{d}^{-1}$ ) and extrapolated to an annual value.

#### *Statistical analyses*

A one-way ANOVA was used to determine if significant differences existed between study periods for selected physical and chemical parameters (1968-1970 vs. 1998-1999). These analyses were based on differences between annual means. Primary productivity values at the two sites (dam and inflow) during the 1998-1999 study period were also compared using a one-way

ANOVA (SAS, 1989). All analyses were completed using SAS/STAT version 6 (SAS Institute Inc., 1989) and statistical significance was inferred at  $P < 0.05$ .

## Results

### *Physical and chemical conditions*

Mean summer pH values were not significantly different between the study periods 1998-99 and 1968-70 (Andersen, 1971), with pH values of 8.4 ( $\pm 0.5$ ) in 1998-99 and 8.3 during 1968-70 (Table 1). Mean pH values in 1998-99 also were not significantly different from 1992-93 data (Popp et al., 1996), with a mean of 8.4 ( $\pm 0.2$ ). Mean summer alkalinity was significantly different among the three study periods, as it decreased from 151 mg l<sup>-1</sup> in 1968-70, to 134 mg l<sup>-1</sup> in 1970-73, and then increased to 161 mg l<sup>-1</sup> in 1998-99 (Table 1). Water clarity declined, as Secchi disk depth was significantly different among the three study periods as it decreased from a 1968-70 summer mean of 187 cm to 65 cm in 1992-93, and a summer mean of 62.5 cm and 47.2 cm, for site 2 (dam) and site 1 (inlet) respectively, during the 1998-99 study period (Table 1). Turbidity was significantly different among study periods with a summer mean of 25.3 (+17.5) JTU in 1968-70, and 16.4 JTU and 10.3 JTU, for site 1 and site 2, respectively in 1998-99 (Table 1).

### *Primary Productivity (1968-70 vs. 1998-99)*

Primary production for daily rates of carbon fixation in 1970 ranged from a winter minimum of 264 mg C/m<sup>2</sup>/d<sup>-1</sup> to a summer maximum of



6,823 mg C/m<sup>2</sup>/d<sup>-1</sup>, with the summer peak in August (Andersen, 1971). During 1998-99, daily rates of carbon fixation ranged from a summer low of 1,019.9 mg C/m<sup>2</sup>/d<sup>-1</sup> during June 1999 to a summer maximum of 9,763.3 mg C/m<sup>2</sup>/d<sup>-1</sup> during August 1998 (Table 1). Annual primary production for the 1968-70 study was 1,390 mg C/m<sup>2</sup>/d<sup>-1</sup> in 1969, and 1,810 mg C/m<sup>2</sup>/d<sup>-1</sup> in 1970 (Andersen, 1971). These primary production estimates were not significantly different (Fig. 3) than those for 1998-99, with an annual primary production of 1,490 mg C/m<sup>2</sup>/d<sup>-1</sup> at site 1 (inlet) and 1,540 mg C/m<sup>2</sup>/d<sup>-1</sup> at site 2 (dam) (Fig. 2).

Algal species found by Holz et al. (1997) including the 16 chlorophytes, 9 bacillariophytes, 5 cyanophytes, 3 euglenophytes, and 4 "others", were similar to those found in 1998-99. The number of algal species found declined since the trophic upsurge phase; in 1968-69 there were 60 species of algae, including 25 chlorophytes, 19 bacillariophytes, 9 cyanophytes, 4 euglenophytes, and 4 "others"; in 1970-73 there were 47 species, including 18 chlorophytes, 16 bacillariophytes, 4 cyanophytes, 4 euglenophytes, and 5 'others'. However, this decline may not be significant because 1968-73 and 1990-92 enumerations were performed at different taxonomic levels (Holz et al., 1997).

## **Discussion**

### *Turbidity*

Since the reservoir was built over 31 years ago, reservoir conditions have changed significantly. The reservoir has changed from a relatively transparent,

eutrophic reservoir to one with high sediment turbidity, resulting in marked changes during ice-free periods. Relatively high turbidity in Pawnee Reservoir has been present since 1968-69, but the sources of this turbidity have changed. Prior to the mid-70's, periods of high turbidity were associated with seasonal algal blooms; thus cyanophyte blooms limited the light environment in Pawnee Reservoir. This is a marked change from the present, because now inorganic sediments are the major source of turbidity. A report by EA Engineering, Science and Technology, Inc. (1991) indicated that inorganic sediments have contributed significantly to water column turbidity, as a result of erodible soils in the watershed and shoreline erosion due to wave action in the reservoir.

Secchi disk depths have decreased significantly, from 1 to 2 meters or more to 0.5 meter or less during this period (Fig. 1). Inorganic turbidity causes incoming photons of light to be scattered and absorbed (Scheffer, 1998), thus affecting the underwater light environment (Kirk, 1985). Kirk (1985) noted that inorganic turbidity scatters and absorbs more light than biotic turbidity because of the surface area to volume differences between particles. The 1% subsurface irradiance depth in Pawnee Reservoir remained at ~2 meters during this study (Fig. 1). This affects the ratio of mixing to euphotic zone depth; algal cells mixed out of the euphotic zone where productivity losses due to respiration can occur if left in the aphotic zone for an extended period (Grobbelaar, 1992). Grobbelaar (1989) argued that the depth of the mixed layer is the most important factor

determining phytoplankton productivity in turbid environments, although this may not be the case in Pawnee Reservoir because of constant wind mixing, wave action due to recreational use, and the reservoir's relatively shallow depth.

Pawnee Reservoir could be classified as a polymictic reservoir during ice-free periods, i.e. seldom does the reservoir have a prominent thermocline.

Kimmel and Groeger (1986) predicted that primary productivity could increase for reservoirs undergoing rapid siltation. The associated increase in turbidity was found to have three distinct effects on phytoplankton, including light limitation of photosynthesis, removal of phytoplankton cells from the water column by flocculation with silt and clay particles, and nutrient stimulation of photosynthetic activity of phytoplankton remaining in the water column (Kimmel, 1981). The predicted increased productivity was due to desorption of organics from the silt and clay particles, increasing nutrient availability (Kimmel, 1981).

#### *Phytoplankton Community*

Inorganic turbidity associated with Pawnee Reservoir also has changed the phytoplankton community. What was once a reservoir dominated by cyanophytes making up 76% and 96% of the relative abundance in 1969 and 1970 (mainly *Microcystis aeruginosa*, *Aphanizomenon flos-aquae*, *Anabaena circinalis*)(Hergenrader, 1980a) is now characterized by flagellated chlorophytes which make up 39% of the relative abundance (*Chlamydomonas* spp. and unidentified flagellates were most abundant)(Holz et al., 1997). This change is

due in part to the over-riding influence of turbidity. Cuker (1987) showed that cyanophytes were most sensitive to clay loading whereas flagellated chlorophytes did not respond to inorganic suspended particles. Chlorophytes have the ability to avoid floc-forming sediments (Avnimelech et al., 1982), using phototactic swimming to maintain their position in the euphotic zone (Cuker, 1987).

Primary productivity in Pawnee Reservoir has remained constant between study periods, despite other impacts as a result of reservoir aging. During the 1969 and 1970 study period, annual primary productivity estimates were 1,390 mg C/m<sup>2</sup>/d<sup>-1</sup> and 1,810 mg C/m<sup>2</sup>/d<sup>-1</sup>, respectively. These values were not significantly different from the 1999 annual primary productivity estimate of 1,540 mg C/m<sup>2</sup>/d<sup>-1</sup>. A number of factors involved in the estimation of yearly primary productivity could explain the similarities between study periods. Daily rates of carbon fixation during 1969-70 (Fig. 3) ranged from a seasonal low of 148.01 mg C/m<sup>2</sup>/d<sup>-1</sup> to a seasonal high of 6,823.38 mg C/m<sup>2</sup>/d<sup>-1</sup>, whereas values in the present study ranged from 1,019.9 to 9,763.3 mg C/m<sup>2</sup>/d<sup>-1</sup> (Table 1). Nevertheless, the large differences in daily rates of carbon fixation resulted in similar annual values despite significant differences in "baseline" productivity when algal blooms were not present. It is interesting to note that seasonal highs during both study periods came during the month of August, likely due to cyanophyte blooms. This is consistent with species composition data for

eutrophic reservoirs in the midwestern region of the U.S. during the end of summer (Hergenrader, 1980a). Therefore, one might expect to see lower annual estimates in the absence of cyanophyte blooms; however, this does not explain why present primary productivity values are exceedingly high for this very turbid, light-limited eutrophic reservoir. Again, the shift from cyanophytes to motile chlorophytes may explain these differences.

### **Conclusion**

Based on Kimmel and Groeger's (1986) reservoir aging model (Fig. 4), it was expected that Pawnee Reservoir's primary productivity would have decreased over the 31-year period, (Fig. 4a). However, this was not the case, as there was no significant difference between annual phytoplankton primary productivity estimates from 1969-70 and 1999 (Fig. 3). While there are numerous factors controlling phytoplankton primary productivity in Pawnee Reservoir, sediment turbidity is a dominant influence. The euphotic zone in Pawnee Reservoir has decreased since it was impounded and corresponding Secchi disk depths have decreased. Andersen (1971) found a reservoir that was turbid during parts of the year due to a large increase of algal biomass during cyanophyte blooms. In the recent study, turbid conditions have existed during ice-free periods because of abiotic sediment turbidity which persists through the growing season. As a result, the euphotic zone has become a relative thin layer one to two meters from the surface, where a majority of Pawnee Reservoir's

primary productivity now occurs. Primary productivity has remained relatively constant because of algal species composition changes (i.e. shifting to flagellated chlorophytes) and because of the lack of dramatic cyanophyte blooms once characteristic of Pawnee Reservoir.

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TABLES

Table 1. Annual means of selected physical and chemical parameters of Pawnee Reservoir (standard deviation in parentheses) [range in brackets]

| Parameters                         | 1968-70                       | 1990-93                 | 1998-99                   |
|------------------------------------|-------------------------------|-------------------------|---------------------------|
| Dissolved Oxygen (ppm)             | 9.7 (9.0)<br>[0.01-13.6]      | 9.2 (1.4)<br>[6.4-14.1] | 7.6 (3.2)<br>[0.08-13.6]  |
| pH                                 | 8.1 (0.2)<br>[7.6-8.9]        | 8.4 (0.2)<br>[7.9-8.8]  | 8.4 (0.5)<br>[5.5-9.0]    |
| Secchi Depth (cm)                  | 163.0 (117.0)<br>[53.3-304.8] | 65.0 (15.0)<br>[34-125] | 62.5 (13.6)<br>[47-100]   |
| Alkalinity (as CaCO <sub>3</sub> ) | 142.5 (12.0)<br>[115-177]     | 182.0                   | 161.0 (17.1)<br>[140-205] |
| Turbidity (JTU)                    | 25.3 (17.5)<br>[9-59]         | ----                    | 10.3 (2.4)<br>[5.5-14.6]  |

Table 2. Primary productivity on each sampling date. Table shows conversion of 4 hr sampling dates (~10am - 2pm) to whole day primary productivity using a correction factor of 45.575 to interpolate the data to daily primary productivity

| Date/site    | mg C/m <sup>2</sup> /h <sup>-1</sup> | mg C/m <sup>2</sup> /d <sup>-1</sup> |
|--------------|--------------------------------------|--------------------------------------|
| 6.29.98 S-1  | 747.0                                | 6556.2                               |
| 6.29.98 S-2  | 501.2                                | 4398.9                               |
| 7.16.98 S-1  | 1004.0                               | 8811.9                               |
| 7.16.98 S-2  | 958.2                                | 8409.9                               |
| 7.29.98 S-1  | 588.7                                | 5166.9                               |
| 7.29.98 S-2  | 830.8                                | 7291.7                               |
| 8.25.98 S-1  | 905.5                                | 7947.3                               |
| 8.25.98 S-2  | 918.7                                | 8063.2                               |
| 9.15.98 S-1  | 1101.4                               | 9666.7                               |
| 9.15.98 S-2  | 1112.4                               | 9763.3                               |
| 9.19.98 S-1  | 501.2                                | 4398.5                               |
| 9.19.98 S-2  | 424.5                                | 3725.3                               |
| 10.13.98 S-1 | 489.4                                | 4295.3                               |
| 10.13.98 S-2 | 716.8                                | 6291.2                               |
| 11.17.98 S-1 | 300.9                                | 2640.9                               |
| 11.17.98 S-2 | 284.9                                | 2500.5                               |
| 5.8.99 S-1   | 187.9                                | 1649.2                               |
| 5.8.99 S-2   | 117.9                                | 1034.8                               |
| 5.19.99 S-1  | 163.6                                | 1435.4                               |
| 5.19.99 S-2  | 144.8                                | 1270.7                               |
| 6.9.99 S-2   | 116.2                                | 1019.9                               |
| 7.27.99 S-1  | 119.5                                | 1048.6                               |
| 7.27.99 S-2  | 143.7                                | 1261.4                               |

**FIGURES**

Figure 1. Secchi disk depths for 1998-99; site 1 (Inlet), site 2 (Dam), and Anderson (1971) site 2 (Dam). Also 1% subsurface irradiance for 1998-99 site 1 (Inlet)(●) and site 2 (Dam) (○) in centimeters.



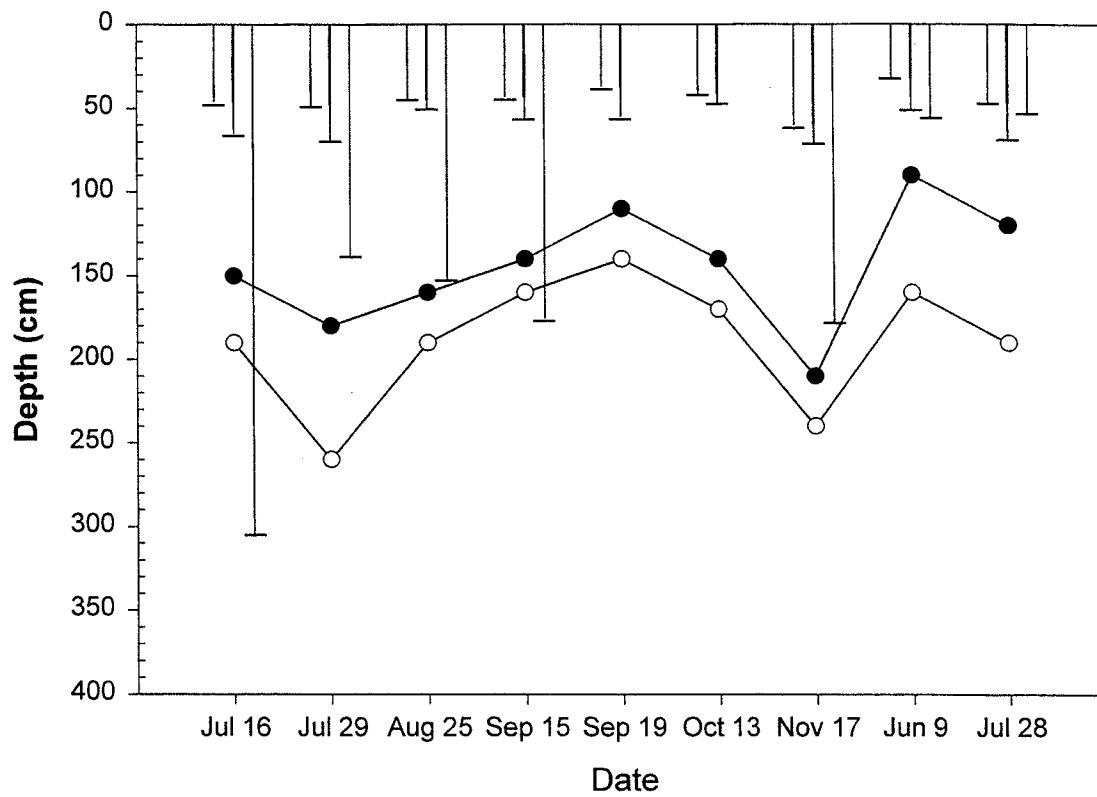


Figure 2. Annual primary productivity for Pawnee Reservoir; (a) site 1 & 2 mean,  
(b) site 1 (Inlet) & (c) site 2 (Dam)

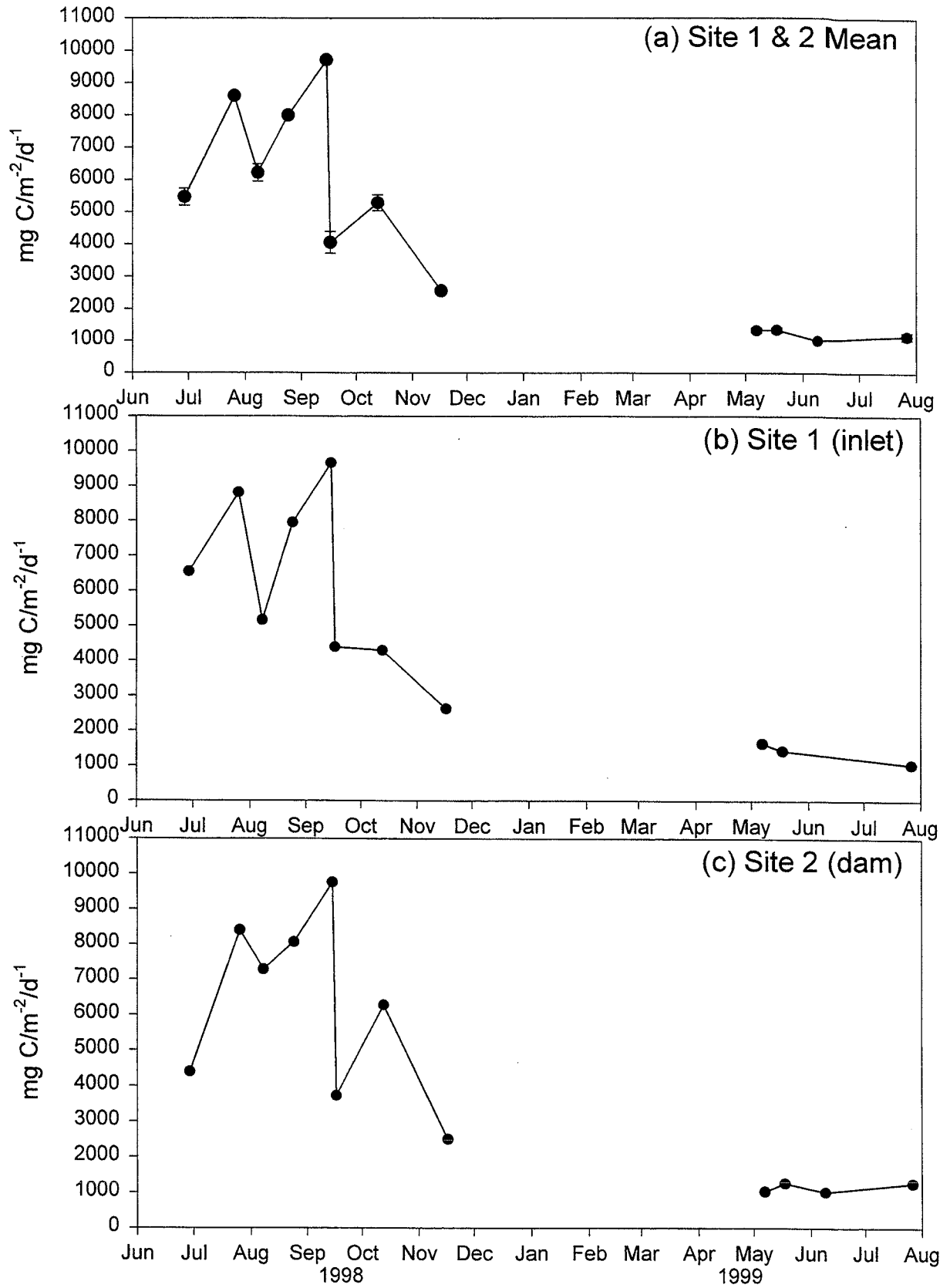


Figure 3. Annual primary productivity ( $\text{mg C/m}^2/\text{d}^{-1}$ ) comparison between 1969-70 ( $\blacktriangle$ ) and 1998-99 ( $\bullet$ )

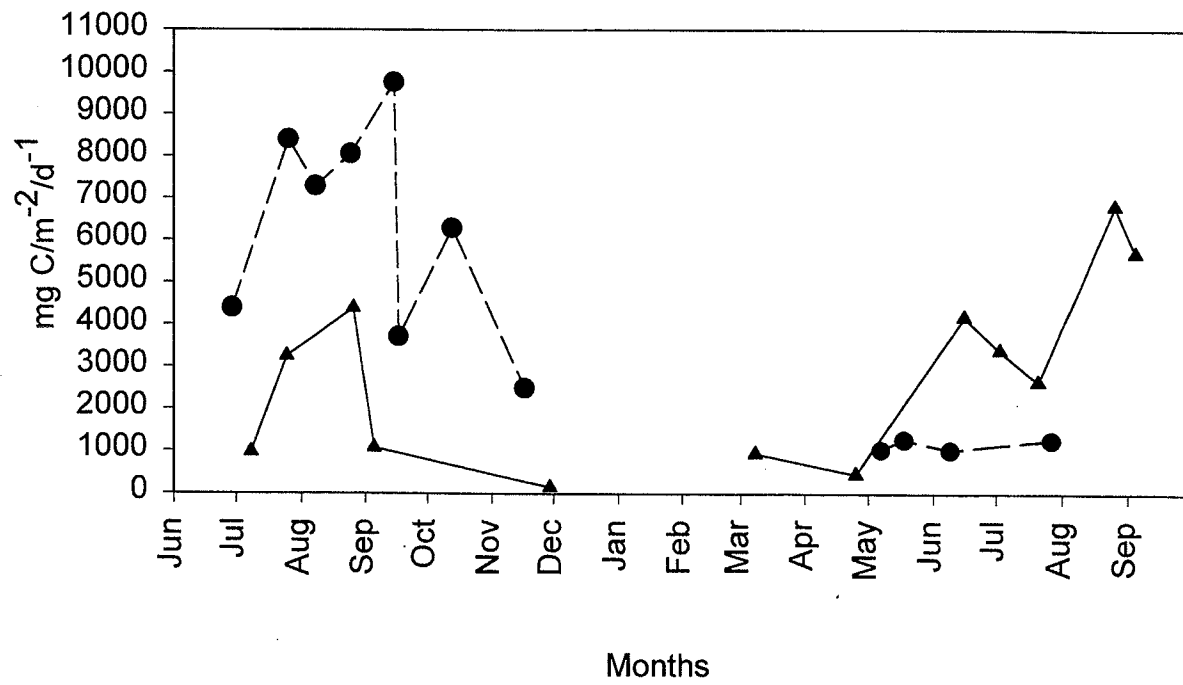


Figure 4. Models of water quality and phytoplankton productivity in response to reservoir aging: (a) modified from Kimmel and Groeger (1986) and (b) based on the results of Holz et al. (1997) and the present study in Pawnee Reservoir. The current model reflects changes in turbidity and productivity in Pawnee Reservoir from 1969-1999.

