

# Reservoir Response to the Asian Monsoon with an Emphasis on Longitudinal Gradients

Kwang-Guk An<sup>a</sup> and John R. Jones  
*Department of Fisheries and Wildlife Sciences  
University of Missouri  
Columbia, MO 65211-7240 USA*

## ABSTRACT

Measured responses to monsoon inflow into Taechung Reservoir, Korea support loading theory. During an intense monsoon in 1993 there was nearly twice the total phosphorus (TP) and three times the non-volatile suspended sediments (NVSS) relative to a weak monsoon in 1994. Across both monsoon seasons, water residence time was negatively correlated with TP and NVSS ( $r > -0.92$ ). Despite lower TP levels, volumetric chlorophyll values (Chl) were larger by ~45% during the weak monsoon. This increased response to the limiting nutrient was attributed to longer residence time and reduced suspended load. The reservoir showed sharp longitudinal zonation during the intense monsoon in 1993 with a light limited riverine zone created by strong advective inflow. With a downlake decline in the suspended load the photic depth doubled and autochthonous production became important. Within the transition and lacustrine zones Chl was responsive to nutrients and volatile solids dominated the seston. An interflow resulted in weak stratification and moved oxygenated water, at mid-depths in the water column, the length of the mainstem. During the weak monsoon in 1994 there was no apparent riverine zone within the sampled reach and lacustrine conditions dominated. High yields of Chl per unit of TP suggested bloom conditions were sustained throughout the reservoir. Low flow resulted in strong stratification and the anoxic zone extended through > 30% of the water column within the lacustrine zone. These data demonstrate that large inter-annual differences in water quality and associated longitudinal gradients within an individual reservoir are regulated by monsoon intensity.

## INTRODUCTION

The summer monsoon in Asia accounts for 50-70% of the annual precipitation (Watts 1969), and evidence suggests it is a major factor determining external loading and temporal patterns in lakes of the region. Studies, conducted mostly in subtropical South Asia, show that during the monsoon there is a reduction in algal levels, likely in response to suspended sediment and reduced water residence time. In some cases, phosphorus increases in response to external loading (Jones et al. 1997). These changes result in sharp seasonal patterns tied to the cyclic monsoon climate.

Monsoon intensity will also directly influence longitudinal patterns and limnological processes within mainstem reservoirs. Longitudinal gradients in physical, chemical and biological factors occur along a continuum from inflow to the dam (Thornton et al. 1981). An established heuristic model divides this continuum into three zones: a headwater, riverine reach, dominated by fluvial inputs; a lake-like lacustrine zone with nutrient limitation; and, an intermediate transition zone where autochthonous production becomes important (Kimmel and Groeger 1984). These zones are not discrete and change from predominately lacustrine conditions during low inflow to riverine-dominance during spates (Thornton et al. 1990). Thus, flood events such as the monsoon reset these processes and patterns.

<sup>a</sup>Present address: Department of Environmental Science and Engineering,  
Ewha Womans University, Seoul 120-750, South Korea

Our study evaluated how monsoon inflow influenced limnology and longitudinal patterns within the mainstem of Taechung Reservoir, Korea during 1993 and 1994. Precipitation during monsoon 1993 was > 2.5 times greater than monsoon 1994, and the sharp contrast illustrates how inflow determines processes and longitudinal zonation in an individual reservoir.

## METHODS AND MATERIALS

*Sampling Sites and Sample Collection:* Taechung Reservoir, South Korea (36°50' N, 127° 50'E) was formed December 1980 by impounding the Keum River about 150 km upstream from its estuary (Fig. 1). Nine mainstream sites were sampled to represent conditions along the longitudinal axis. Herein, we use "location X km" to represent the position of a given site relative to the dam. Surface water samples were collected three times during monsoon (July - August) 1993 and on four occasions during 1994.

*Analytical Methods:* Water samples were covered on ice, and either preserved or analyzed within 12 - 36 hours. Secchi transparency, temperature and dissolved oxygen (YSI Model 51B meter) were measured in the field, and specific conductance (YSI Model 33) was measured in the laboratory. Total nitrogen (TN) was measured by second derivative after a persulfate digestion (Crompton et al. 1992). Total phosphorus (TP) was determined using ascorbic acid after persulfate oxidation (Prepas and Rigler 1982). Total suspended

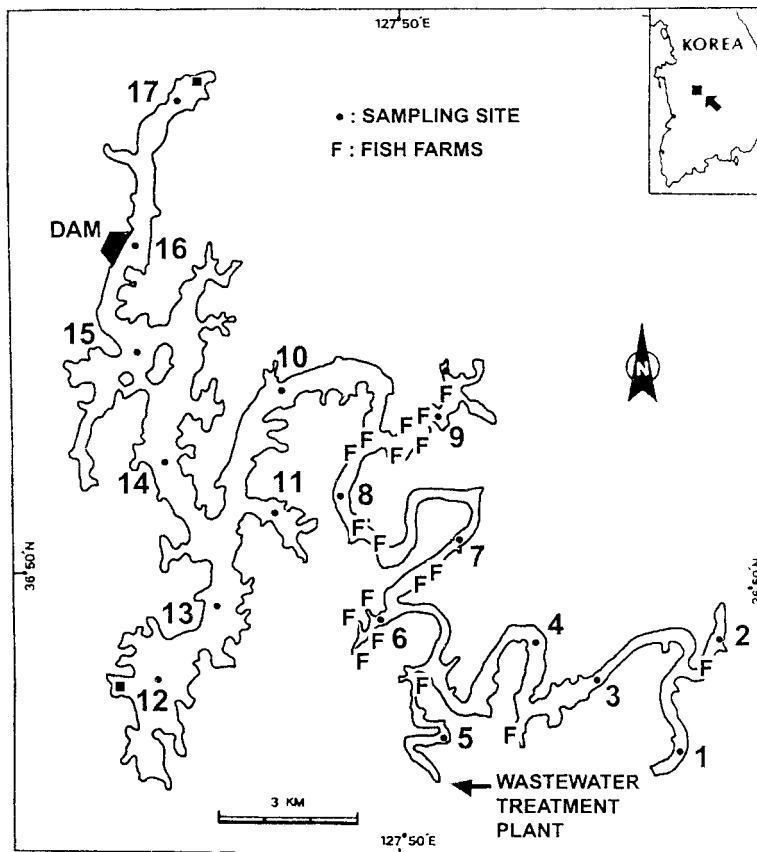


Figure 1. Map of Taechung Reservoir showing sampling sites.

solids were determined by using preweighed Whatman GF/C filters. Filters were weighed after drying at 103°C for one hour. Non-volatile suspended solids (NVSS) were determined by combustion at 550°C for one hour (A.P.H.A. 1985), and volatile suspended solids (VSS) were determined by difference. Chlorophyll (Chl) was measured spectrophotometrically (Beckman Model DU - 65) after extraction in hot ethanol (Sartory and Grobbelaar 1984). Nutrient analyses were performed in triplicate; suspended solids and Chl were measured in duplicate. Water Residence Time (WRT in days, Knowlton and Jones 1990) was estimated using lake surface area, volume and inflow on each sampling date. Precipitation and evaporation were not included in the estimate of WRT.

*Monsoon Hydrology:* Annual precipitation at the reservoir averaged 1100 mm during 1981 - 1994. The major difference in rainfall between 1993 and 1994 occurred during the monsoon. Precipitation during July-August 1993 was 660 mm, and monsoon 1994 rainfall was only 251 mm.

Total inflow in 1993 was four times that of 1994 ( $0.83 \times 10^9 \text{ m}^3$ ), and summer inflow in 1993 was eight times greater than summer 1994. In 1993, daily outflow ranged from a peak of  $995 \text{ m}^3 \text{ sec}^{-1}$  in August to a base flow of  $31 \text{ m}^3 \text{ sec}^{-1}$  in February. In contrast, peak instantaneous outflow in 1994 was  $83 \text{ m}^3 \text{ sec}^{-1}$  and the lowest was  $2 \text{ m}^3 \text{ sec}^{-1}$ . Mean water level was 71 m (MSL) in 1993 and 66.2 m in 1994. Lake stage during the monsoon was > 10 m greater in 1993 than 1994.

## RESULTS

### Physical Conditions and Hydrology

Longitudinal patterns in Taechung Reservoir varied dramatically with monsoon intensity. During monsoon 1993, water residence time (WRT) averaged 24 d, ranging from 3 d at the uppermost site to 35 d at the dam (Fig. 2a). Within the riverine zone (37-50 km, sites 1, 2, and 4) WRT was less than a week, and this reach composed 25% of the reservoir area. The downlake lacustrine zone in 1993 (0-6 km, sites 10,14,15 and 16) composed 60% of the area. The transition zone (7-27 km, sites 7, 8), where WRT was ~ 10 days, occupied the mid-reach. In contrast, during monsoon 1994 WRT ranged from 10 d at the uppermost site to 120 d at the dam (Fig. 2e). Within the upper 25% of the reservoir WRT averaged 10 to 14 d; this matches WRT within the 1993 transition zone. Downlake lacustrine conditions dominated the reservoir in 1994.

### Conditions During an Intense Monsoon (1993)

Inflow during the July-August monsoon 1993 resulted in a mixed layer ( $Z_m$ ) that averaged 7.2 m across the entire reservoir but decreased in thickness from 12.3 m in the headwaters to 4.6 m at the dam. Below the mixed layer, a nearly isothermal interflow, 2 - 3 °C cooler than the upper strata, dominated the water column to a depth of about 32 m (Fig. 3a). On average there was a decrease of ~ 3 °C in the upper 10 m of the reservoir during the monsoon (Fig. 2b). Below the interflow layer there was a sharp temperature cline of > 10 °C (Fig. 3a). Oxygen values < 3 mg/L were limited to strata below the interflow layer within the lacustrine zone (Figs. 2c and 3c).

Conductivity measurements, 30% smaller than downlake values (Fig. 2d), clearly characterized the extent of the riverine zone above a plunge point (located at ~ 37 km). A sharp increase in conductivity below this point marked the transition zone. Within the riverine zone NVSS averaged >18 mg/L and composed 85% of TSS, and Secchi values were ~ 0.5 m (Figs. 4a and 4b). Given deep mixing and allochthonous particulates within this reach, the ratio of the mixing depth ( $Z_m$ ) to the photic depth was >10 ( $Z_m:Z_p$  Fig. 4c). Algal response to phosphorus was low in the riverine reach (Chl:TP was  $\leq 0.13$ , Fig. 5d) where rapid flushing and light-limitation were likely important. Non-algal turbidity values were >1 (Fig. 4d,  $T_{na} = (1/\text{Secchi} - 0.025 * \text{Chl})$ , Walker 1986) which is consistent with conditions dominated by allochthonous particulates and light-limitation.

There was a strong downlake gradient in the suspended load such that within the lacustrine zone NVSS was < 5% of the uplake concentration. At the dam, VSS composed two-thirds of TSS, indicating a downlake switch to autochthonous materials in the suspended solids. Secchi depth in the lacustrine zone was about five times that in the riverine. With downlake declines in mineral turbidity and a shallower mixing depth, the  $Z_m:Z_p$  ratio changed from > 4 to < 2 within the transition zone. Within the lacustrine zone  $Z_m:Z_p$  was  $\leq 1$  (Fig. 4c).

Total nitrogen (TN) averaged >1.6 mg/L at all sites, and peaked slightly mid-lake (Fig. 5a) where fish farms and a wastewater disposal plant may locally influence water

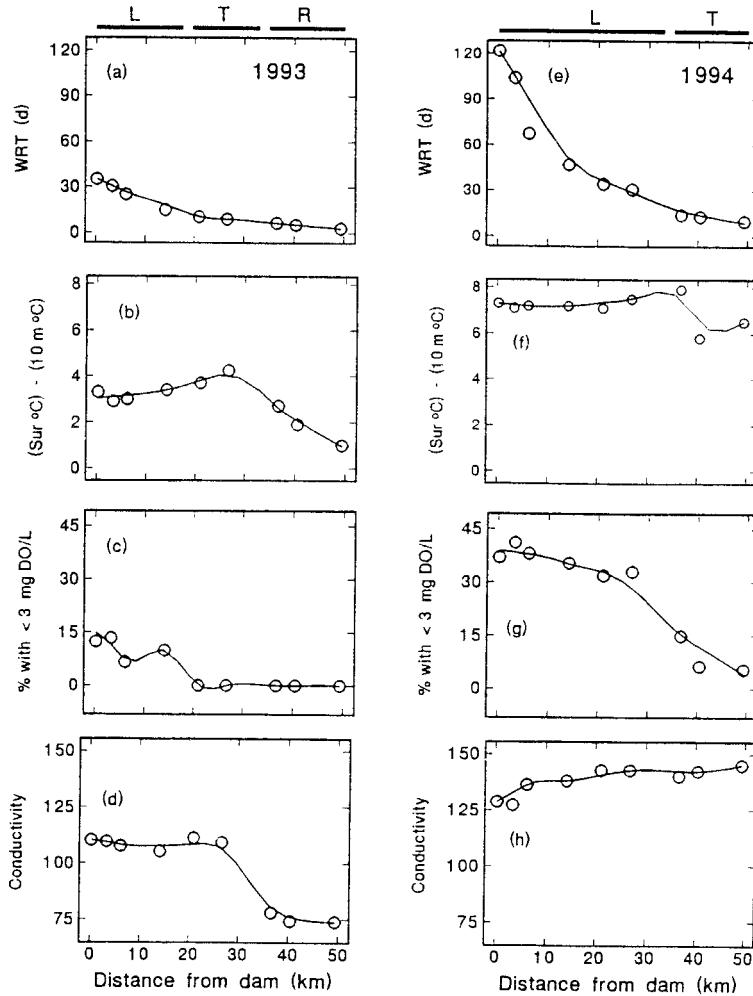


Figure 2. Longitudinal gradients in water residence time (WRT), temperature change within the top 10 m (surface temperature minus temperature at 10 m), % of the water column with dissolved oxygen concentrations < 3 mg L<sup>-1</sup>, and conductivity (as  $\mu\text{S}/\text{cm}$ ) along the mainstream sites, and functional zones during monsoon 1993 and 1994. Each data point indicates a seasonal mean ( $n \geq 3$ ) during July – August in 1993 and 1994, and the longitudinal gradient was characterized using locally-weighted sequential smoothing (LOWESS; Cleveland 1979). Letters R, T and L indicate the riverine, transition, and lacustrine zones, respectively.

quality, but lower TN values in late monsoon inflow also contributed to the pattern. Total phosphorus values in the riverine zone were  $> 100 \mu\text{g/L}$  (Fig. 5b), and a downlake decline to  $< 30 \mu\text{g/L}$  was strongly correlated with a concurrent decline in NVSS ( $r = 0.985$ ,  $p < 0.001$ ,  $n = 9$ ) and inversely correlated with WRT ( $r = -0.90$ ,  $p < 0.001$ ,  $n = 9$ ). The ratio of TN:TP was 15 in the riverine zone but increased to  $> 50$  in the lacustrine reach, reflecting lower TP values downlake and an increase in phosphorus limitation. Chl peaked at  $\sim 25 \mu\text{g/L}$  within the transition zone (Fig. 5c). Within the transition-lacustrine reach Chl was strongly correlated with TP ( $r = 0.87$ ,  $p < 0.001$ ,  $n = 6$ ) and the yield of Chl per unit of TP (Chl:TP) was  $\geq 0.4$ , which indicates algal biomass responded to the phosphorus supply (Fig. 5d, Walker 1986).

#### Conditions During a Weak Monsoon (1994)

Greatly reduced inflow during monsoon 1994 resulted in strong stratification; the epilimnion ( $Z_m$ ) averaged 2.3 m (Fig. 3b). Surface temperature near the dam during July-August 1994 ( $29.6^\circ\text{C}$ ) was  $5.4^\circ\text{C}$  warmer than during monsoon 1993. Below the epilimnion, temperatures declined sharply with depth. On average there was a decrease of  $> 7^\circ\text{C}$  in the upper 10 m of the reservoir during the monsoon (Fig. 2f), and the magnitude of density change within this depth was about three times greater than during monsoon 1993. At depths between 18 and 30 m within the water column, water temperatures were  $\sim 13^\circ\text{C}$  cooler in mid-July-August 1994 than during 1993 (Fig. 3b). Oxygen values  $< 3 \text{ mg/L}$  in the bottom waters extended throughout the reservoir (Figs. 2g and 3d) and accounted for  $> 30\%$  of the volume within the lacustrine zone.

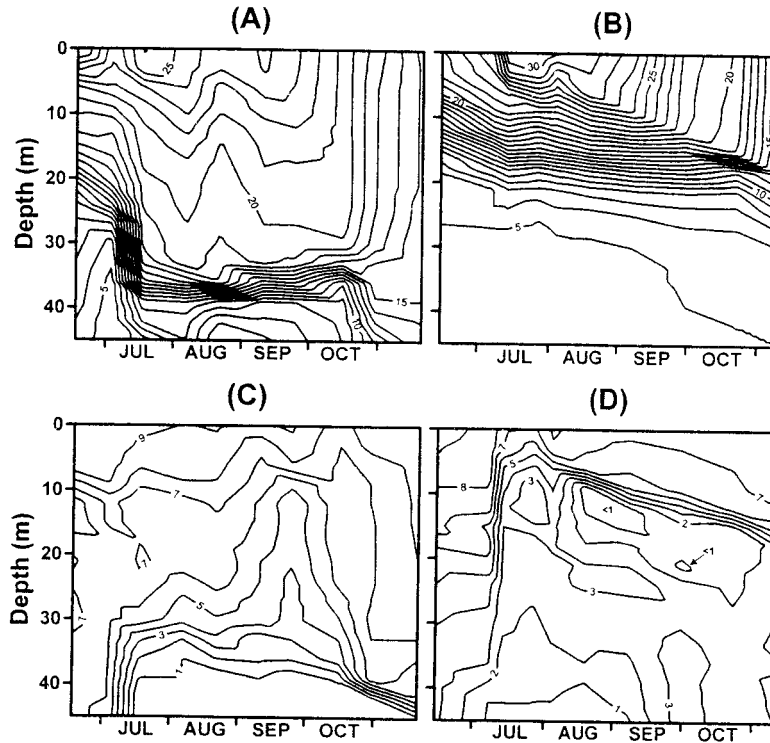


Figure 3. Isopleth diagrams of temperature in the water column ( $^\circ\text{C}$ ) during 1993 (A) and 1994 (C), and dissolved oxygen in the water column ( $\text{mg L}^{-1}$ ) during 1993 (B) and 1994 (D). Data were collected at a sampling site near the dam.

Drought during monsoon 1994 resulted in two functional zones within the sampled reach; a transition zone uplake and lacustrine conditions throughout the lower 75% of the reservoir. Relative to monsoon 1993, TP and NVSS declined by ~ 50 and 75%, respectively, while conductivity and Secchi transparency increased by ~ 35% and 20%, respectively (Figs. 4 and 5). These between year differences were larger uplake than at sites near the dam. With shallower stratification and greater water clarity in 1994, the photic zone exceeded the mixing depth at all sampling sites (Fig. 4g) and there was no indication of light limitation by allochthonous particulates anywhere in the mixed layer (Fig. 4h).

There were modest longitudinal gradients in nutrients and suspended load along the main axis during monsoon 1994 (Figs. 4 and 5). On average NVSS was about three times

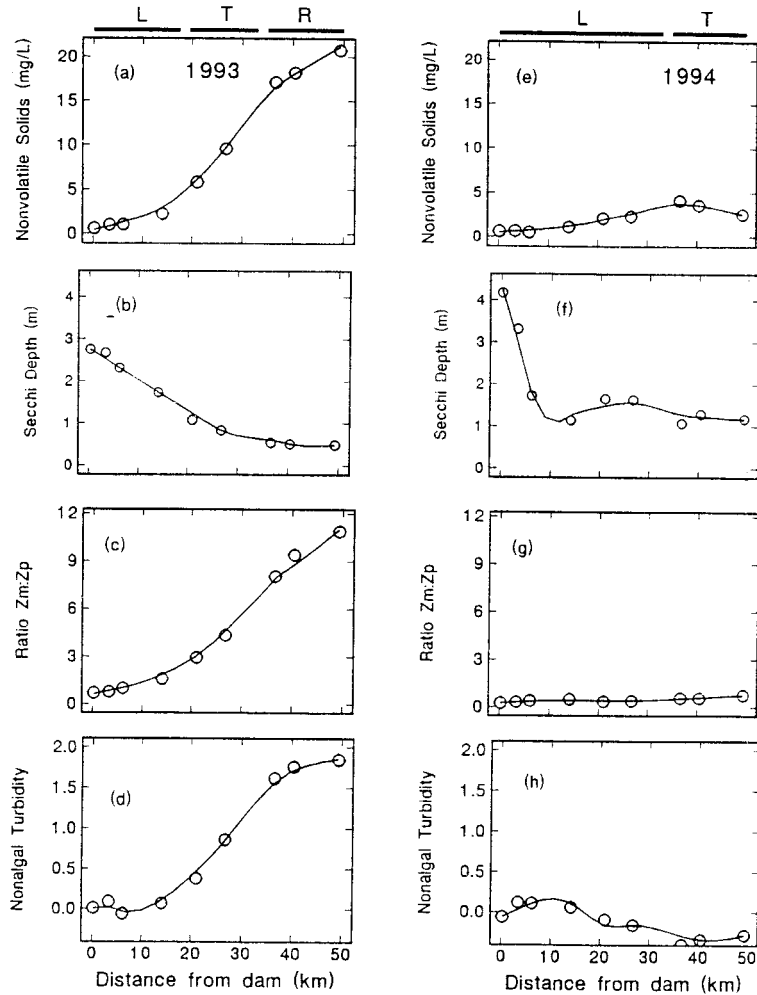


Figure 4. Longitudinal gradients in nonvolatile suspended solids, Secchi depth, ratio of the mixing depth to the photic depth ( $Z_m:Z_p$ ), and nonalgal turbidity ( $T_{na} = (1/\text{Secchi} - 0.025 * \text{Chl})$ , Walker 1986) along the mainstream sites and functional zones during monsoon 1993 and 1994. Each data point indicates a seasonal mean ( $n \geq 3$ ) during July – August in 1993 and 1994 and longitudinal gradient was characterized using locally-weighted sequential smoothing (LOWESS; Cleveland 1979). Letters R, T and L indicate the riverine, transition, and lacustrine zones, respectively.

greater in the transition zone than downlake (Fig. 4e), and there was a switch from dominance of TSS by mineral turbidity uplake (NVSS>VSS) to dominance by autochthonous materials within the lacustrine zone (VSS>NVSS). TP decreased by about three-fold downlake. TN values peaked mid-lake (Fig. 5e) and declined downlake to  $\leq 1.4$  mg/L. Ratios of TN:TP were 35 to 40 uplake and  $>80$  near the dam. Within the mainstem Chl averaged  $\sim 30$   $\mu\text{g/L}$  in 1994, this was  $\sim 45\%$  greater than 1993 levels (Fig. 5c and g). At headwater sites, monsoon 1994 Chl was about three times larger than in 1993. In 1994 Chl was highly correlated with TP ( $r = 0.95$ ,  $p < 0.001$ ,  $n = 9$ ) and ratios of Chl:TP were near unity (Fig. 5d).

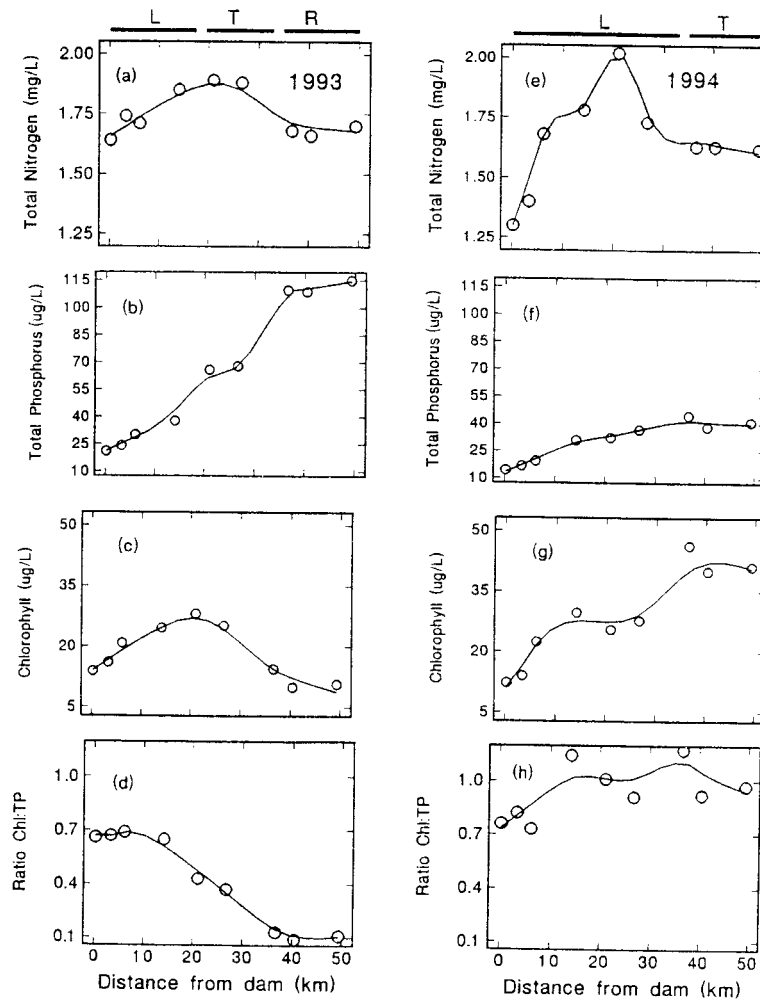


Figure 5. Longitudinal gradients in total nitrogen, total phosphorus, chlorophyll, and ratio of chlorophyll to total phosphorus, along the mainstream sites and functional zones during monsoon 1993 and 1994. Each data point indicates a seasonal mean ( $n \geq 3$ ) during July – August in 1993 and 1994 and longitudinal gradient was characterized using locally-weighted sequential smoothing (LOWESS; Cleveland 1979). Letters R, T and L indicate the riverine, transition, and lacustrine zones, respectively.

## DISCUSSION

Measured responses to monsoon inflow into Taechung Reservoir were consistent with loading theory (Edmondson 1961, Vollenweider 1976) – that being, external input determines in-lake concentrations of nutrients and suspended materials, and values are greater in wet years than dry ones. During the intense monsoon in 1993 the reservoir had nearly twice the TP and over three times the NVSS content relative to the weak monsoon in 1994. Across both monsoon seasons, WRT showed a strong negative correlation with both TP and NVSS at the sampled sites (log transformed data,  $r > -0.92$ ,  $p < 0.0001$ ,  $n=18$ ), thereby demonstrating the role of external inputs. Despite lower TP levels, volumetric Chl measurements were larger by ~ 45% during the weak monsoon. This response is consistent with studies showing that high levels of suspended solids in wet years, and associated abiotic factors, weaken the relation between nutrients and algal biomass (Jones and Knowlton 1993, Jones et al. 1997). When expressed on an areal basis, however, differences between years were modest. Deep mixing in excess of the photic depth in 1993 resulted in areal Chl values of  $130 \text{ mg} \cdot \text{m}^{-2}$  while in 1994 the photic depth contained  $110 \text{ mg} \cdot \text{m}^{-2}$ .

Spatial heterogeneity was also consistent with reservoir patterns determined by watershed runoff – sharp longitudinal zonation was measured during the intense monsoon but not when inflow was weak. In 1993 the reservoir clearly showed a typical riverine zone with short WRT and limnological characteristics created by strong advective inflow. Values of NVSS  $>10 \text{ mg/L}$  (Jones and Knowlton 1993), values of  $T_{na} >1$  (Walker 1986) and ratios of  $Z_m:Z_p >10$  (Grobelaar 1985) within the riverine zone exceeded published criteria used to identify light limitation. Within this reach the yield of Chl per unit of TP was only ~ 15 % of levels expected in natural lakes (Jones and Bachmann 1976); reduced Chl:TP yields of this magnitude are typical of inflows with allochthonous particulates (Jones and Novak 1981). The 1993 transition zone, where WRT was about 10 d, was positioned below a plunge point. On average, there was a decline of ~ 2  $\mu\text{g/L}$  TP and ~ 0.4  $\text{mg/L}$  NVSS per km and concurrent doubling of the photic depth along the mainstem during 1993. With loss of the suspended load, nutrient limitation and autochthonous production became increasingly important. Within the transition zone Chl values matched the relationship to TP found in natural lakes (Jones and Bachmann 1976), and this Chl-TP fit extended the entire length of the lacustrine zone which occupied the lower 60% of the reservoir in 1993. Among the sampled sites, the proportion of VSS in the seston (VSS/TSS) was strongly correlated with WRT ( $r = 0.96$ ,  $p < 0.001$ ,  $n = 9$ ), demonstrating a downlake increase in autochthonous production. This sequence of changes along the length of Taechung Reservoir matches the hypothetical model for reservoir processes in which the downlake loss of suspended load and increased transparency favor nutrient regulation of algal growth (Kimmel et al. 1990).

During monsoon 1994 advective inflow was not sufficient to establish distinguishable riverine zone within the sampled reach, giving the reservoir the characteristics of a tributary reservoir with long-residence time (Kimmel et al. 1990). Light limitation was not indicated either by the suspended load or physical measurements ( $Z_m:Z_p$  and  $T_{na}$ ) at any of the sampling sites, and yields of Chl per unit of TP near unity suggest bloom conditions were sustained throughout the reservoir during monsoon 1994 (Jones and Bachmann 1976, White et al. 1985). Bluegreen algae dominated the algal assemblage during monsoon 1994 and may have contributed to this high Chl:TP ratio (An and Jones 2000). Advective nutrient supply to the headwaters was demonstrated by modest longitudinal gradients in most water quality variables. Downlake declines in phosphorus and suspended solids averaged ~ 0.5  $\mu\text{g/L}$  TP and  $< 0.1 \text{ mg/L}$  NVSS per km. These decreases were similar to gradients during pre-monsoon 1993 (Jones et al. 1997). Uplake measurements fit the characterization of a transition zone with strong algal response to nutrients and sedimentation of the suspended load. Below this point, lacustrine conditions



dominated Taechung Reservoir in 1994. This zonation is consistent with low flow, modest advective input, and compression of riverine and/or transition zones to a small, uplake portion of the basin (Kimmel et al. 1990).

Temperature and oxygen in Taechung Reservoir differed during these years of contrasting flow. Inflow in 1993 was sufficient to form a cool density current that reduced temperatures in the water column below pre-monsoon values, weakened stratification, and transported water with DO between 5 and 7 mg/L downlake. This contrasts with the classic pattern (Cole and Hannan 1990) that during high flow hypolimnetic waters are discharged and replaced by warmer layers from above causing greater temperatures and greater oxygen uptake in a high flow year. The massive density current and short WRT in 1993 swamped this process. In 1994 low flow resulted in strong stratification and the anoxic zone extended into the headwaters.

Data from Taechung Reservoir show that the content of nutrients and suspended solids and longitudinal zonation is dynamic spatially and temporally in response to monsoon intensity. Low algal response to nutrients in the headwater riverine zone and an interflow dominated the limnology of the mainstem during the intense monsoon, while bloom conditions occurred in lake-like conditions during the weak monsoon. We anticipate that during an average monsoon, the interflow will be less developed and the riverine zone will extend further downlake as a prominent feature of longitudinal zonation.

#### ACKNOWLEDGEMENTS

Support for this study was provided by KEPOC, Korea and Whemiller Fellowship at the University of Missouri. We thank Jin-Won Seo, Jai-Ku Kim, Ju-Hee Yeon for field help, Matthew Knowlton for valuable comments, and Wuk-Hee Hong, Hee Mock Oh, Dong-Il Seo, Shin-Sok Choi for field and laboratory support.

#### LITERATURE CITED

- An, K. -G. and J. R. Jones. 2000. Factors regulating bluegreen dominance in a reservoir directly influenced by the Asian monsoon. *Hydrobiologia* 432:37-48.
- A.P.H.A. 1985. Standard methods for the examination of water and wastewater. 16th ed. New York, American Public Health Association. 874-1133 pp.
- Cleveland, W.S. 1979. Robust locally weighted regression and smoothing scatterplots. *J. Am. Stat. Assoc.* 74: 829-836.
- Cole, T. M., and H. H. Hannan. 1990. Dissolved oxygen dynamics (Chapter 4). In: Thornton, K. W. et al. (ed.): *Reservoir Limnology: ecological perspectives*. John Wiley & Sons, New York. p. 71-108.
- Crumpton, W.G., T.M. Isenhardt, and P.D. Mitchell. 1992. Nitrate and organic N analyses with second-derivative spectroscopy. *Limnol. Oceanogr.* 37: 907-913.
- Edmonson, W. T. 1961. Changes in Lake Washington following an increase in the nutrient income. *Verh. Internat. Verein. Limnol.* 14:167-175.
- Grobbelaar, J.U. 1992. Phytoplankton productivity in turbid waters. *J. Plankton Res.* 7:653-663.
- Jones, J.R. and M.F. Knowlton. 1993. Limnology of Missouri reservoirs: An analysis of regional patterns. *Lake and Reserv. Manage.* 8:17-30.
- Jones, J.R., M.F. Knowlton, and K-G. An. 1997. Developing a paradigm to study and model the eutrophication process in Korean reservoirs. *Korean J. of Limnol.* Vol. 30-Supplement: 463 - 471.
- Kimmel, B. L., Lind O. T. and Paulson, L. H. 1990. Reservoir primary production (Chapter 6). In: Thornton, K. W. et al. (ed.): *Reservoir Limnology: Ecological Perspectives*. John Wiley & Sons, New York. p. 133-194.

- Kimmel, B.L. and A.W. Groeger. 1984. Factors controlling primary production in lakes and reservoirs; In: *Lake and Reservoir Management*. U.S. EPA-440/5-84-001. p 277-281.
- Lind, O. T., T. T. Terrel, and B. L. Kimmel. 1993. Problems in reservoir trophic-state classification and implications for reservoir management. In: *Comparative Reservoir Limnol. and Wat. Qual. Manage.* Kluwer Academic Publishers. in Netherlands. p. 57-67.
- Prepas, E.E., and F.A. Rigler. 1982. Improvements in qualifying the phosphorus concentration in lake water. *Can. J. Fish. Aquat. Sci.* 39: 822-829.
- Sartory, D.P., and J.U. Grobbelaar. 1984. Extraction of chlorophyll-a from freshwater phytoplankton for spectrophotometric analysis. *Hydrobiol.* 114:177-187.
- Soballe, D.M., B.L. Kimmel, R.H. Kennedy, and R.F. Gaugush. 1992. Lentic systems; reservoirs. In: *Biodiversity of the southeastern United States - Aquatic communities*, Hackney, C.T., S.M. Adams, and W.H. Martin (eds), John Wiley & Sons, Inc.
- Vollenweider, R. A. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. *Mem. Ist. Ital. Idrobiol.* 33:53-83.
- Walker, W.W., Jr. 1986. "Empirical methods for predicting eutrophication in impoundments. Report 4. Phase III: Applications manual," Technical Report E-81-9, prepared by William W. Walker, Jr., Environmental Engineer, Concord, Mass., for the US Army Engineer Waterways Experiment Station, Vicksburg, Miss. p. IV 1-73
- Watts, I.E.M. 1969. Climates of China and Korea. In: *Climates of Northern and Eastern Asia*. Arakawa, H. (ed.), Elsevier Publishing Co., Inc., Printed in Netherland. p. 24.
- White, E., K. Law, G. Payne and S. Pickmere. 1985. Nutrient demand and availability among planktonic communities – an attempt to assess nutrient limitation to plant growth in 12 central volcanic plateau lakes. *New Zealand J. Mar. Freshwat. Res.* 19:49-62.