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Relative Importance of Bottom-up vs. Top-down Controls on Size-structured Phytoplankton Dynamics in a Freshwater Ecosystem: I. Temporal and Spatial Variations of Size Structure

Sin, Yongsik* and Jongmin Kim[1]

(Division of Ocean System Engineering, Mokpo National Maritime University, Mokpo, Chonnam 530-729, Korea, [1]Youngsan-River Environment Research Laboratory, National Institute of Environmental Research, Sooncheon, Chonnam 540-930, Korea)

Temporal and spatial variations of size-structured phytoplankton (chlorophyll *a*) were investigated over an annual cycle (February-October, 2003) to elucidate phytoplankton dynamics in the Juam Reservoir, Chonnam. Physical properties were also measured to investigate the relationship between the properties and temporal and spatial variations of size structured phytoplankton using simple linear regression. Phytoplankton (chlorophyll *a*) were grouped into three size classes: micro-size (>20 μm), nano-size (3-20 μm) and pico-size (<3 μm) in this study. Physical properties included water temperature, light attenuation coefficients, PAR (photosynthetically active radiation) and turbidity. Maximum chlorophyll a was observed in April, 2003 in the lower region whereas a peak of chlorophyll *a* developed in October, 2003 in the upper region. Large cell-sized phytoplankton (micro-size class) were dominant in the events of the chlorophyll *a* peaks. Potential mechanisms in the physical properties affecting the size-structured phytoplankton dynamics in the Juam Reservoir were discussed.

Key words : bottom-up control, top-down control, size-structured phytoplankton, Lake Juam, potential mechanism

INTRODUCTION

One approach to a better understanding of phytoplankton dynamics is to categorize phytoplankton community into different size classes since cell size determines both the response of phytoplankton communities to environmental variation (Malone and Chervin, 1979; Takahashi and Bienfang, 1983; Gieskes and Kraay, 1986; Joint and Pomroy, 1986; Oviatt *et al.*, 1989; Glibert *et al.*, 1992; Armstrong, 1994; Hein *et al.*, 1995), and associated impacts on aquatic food web structure and fisheries (Walsh, 1976; Lenz, 1992; Painting *et al.*, 1993). Over various time scales watershed inputs to aquatic systems may change both the quality (size structure) and quantity (biomass) of primary producers. In turn, these changes resulting from environmental disturbance may impact nutrient and dissolved oxygen (DO) distributions as well as heterotrophic consumers in the water column. Since cell size affects sinking (Michaels and Silver, 1988) and transport rates, it will determine where ungrazed biomass accumulates and undergoes microbial processing by bacteria and protozoa which in turn

* Corresponding Author: Tel: +82-61-240-7054, Fax: +81-61-240-7284, E-mail: yongsik@mmu.ac.kr

influences oxygen dynamics (Jonas, 1992) and nutrient remineralization (Caron, 1991). Remineralized nutrients may subsequently support primary production (Kemp and Boynton, 1984).

Lake Juam was artificially formed in 1992 and has used for multiple purposes such as industrial and agricultural use as well as use of drinking water for Kwangju and Chonnam regions since construction of the reservoir. Phytoplankton blooms occasionally develop and degrade water quality of the reservoir causing increase of the cost for water treatment.

In past studies, phytoplankton were usually grouped into two size fractions: netplankton (20−200 μm) and nanoplankton (< 20 μm). In recent years picoplankton (0.2−2 μm), comprised of minute chroococcoid cyanobacteria and eukaryotic phytoplankton, have received attention in phytoplankton studies (Ray *et al*., 1989; Lacouture *et al*., 1990; Malone *et al*., 1991; Iriarte, 1993).

Youngsan−River Environment Research Laboratory, National Institute of Environmental Research has monitored chlorophyll *a* concentrations as a water quality parameter once per month since late−1990's in the reservoir. Results on phytoplankton community (species) have also been reported for the reservoir (Kim *et al*., 2001; Lee, 2002) but chlorophyll *a* content was not determined for the different size classes. The principal goals of this study were to: (1) examine temporal and spatial variations in chlorophyll *a* of various size classes of phytoplankton in Lake Juam; (2) identify mechanisms, especially physical properties controlling size structure dynamics.

MATERIALS AND METHODS

Study site and sample collection

Lake Juam is composed of the Bosung River, a subriver of the Sumjin River (Fig. 1). Surface area of the reservoir is 22 km^2 and hydraulic residence time is 0.36 year. Drainage area of the system is 1,010 km^2 and total population is 58, 553 (persons) based on the record from 1993 to 1994. Six stations along the axis of the Dongbok Stream and Bosung Rivers (Fig. 1) were sampled monthly over one annual cycle from February, 2003 to October, 2003. Samples were collected from 1 m below the surface and 1 m above the bottom using Nanssen bottle.

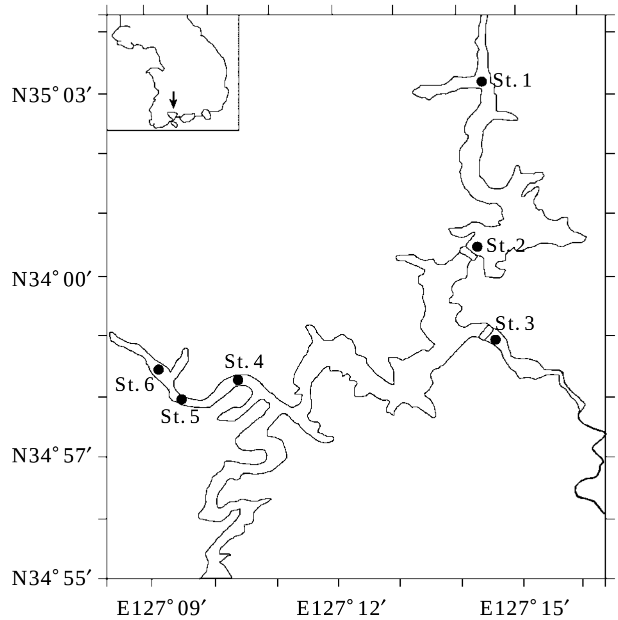

Fig. 1. Sampling stations in the lower (Stations 1, 2, 3) and upper (Stations 4, 5, 6) regions of Lake Juam.

Chlorophyll *a* measurement

In this study, phytoplankton were categorized into three size classes: micro−size (> 20 μm), nano−size (3−20 μm) and pico−size (< 3 μm). Phytoplankton were fractionated by filtration through 20 μm Nytex mesh (1−2 liters) and 3 μm PORETICS polyester membrane filters (1 liter) with minimal vacuum (< 150 μm Hg). For chlorophyll *a* determinations, 30 ml of non−fractionated whole water, 50 ml of 20 μm filtrate, and 100 ml of 3 μm filtrate were filtered through Whatman 25 μm GF/F glass fiber filters (0.7 μm) under vacuum (< 120 μm Hg). Sample filtration was performed in duplicate. The filters were placed in dark test tubes pre−filled with 8 ml extraction solution (90% acetone, 10% deionized water). After storage for 12 hrs at room temperature, fluorescence was measured on a Turner Designs10−AU Fluorometer. Chlorophyll *a* in each size fraction was determined by consecutive subtraction of the < 3 μm and < 20 μm fractions from whole water chlorophyll *a*.

Measurement of physical properties

A YSI Model 85 S−C−T Meter was used to measure in situ temperature during field sampling. A LICOR PAR Quantum Radiometer was used to measure solar and submarine irradiance at depths of 10, 35, 60, 85 and 110 cm. Light attenuation coefficients were calculated using Beer's Law, $I_z = I_o e^{-kz}$, where I_z is the intensity of light at z, the depth of interest, I_o is the intensity at the surface, and k is the attenuation coefficient of water. Turbidity was measured by Hydrolab Surveyor4 and water depth was measured using a scale marked on the HydroLab's line.

Other data collection and statistical analysis

Precipitation and duration of solar radiation data was collected from the Korea Meteorological Administration, Sooncheon, Chonnam. For the seasonal comparison, averages of data from winter (February), spring (March, April, May), summer (June, July, August) and fall (September, October) were reported. Simple linear regression analysis was employed to investigate correlationships between phytoplankton size class chlorophyll *a* and the various physical variables.

RESULTS

Physical characteristics: precipitation, photo−period, temperature, & water clarity

Precipitation for the period from January 2003 to October 2003 (Fig. 2A) displayed a seasonality similar to that of other areas in S. Korea; high during summer and low during winter. Monthly sum of photo−period data collected in Sooncheon also revealed a seasonal trend: highest during March and lowest during July (Fig. 2B). Photo−period of sampling date, April 21 was extraordinarily long.

Surface water temperatures at Stations 1, 2, 4 were highest during August and lowest during February whereas bottom water temperatures were highest during September and lowest during February (Fig. 3A, 3B, 3C). Surface water temperature slightly increased as upstream whereas temperature increased rapidly at bottom water. Evident seasonal pattern was observed for bottom water temperature at Station 4 (Fig. 3C) but bottom water temperature varied slightly at Station 1 (Fig. 3A). Severe stratification of water column was observed at Stations 1, 2 during warm season. Water turbidity of Station 1 peaked during April and had minimum during September (Fig. 3D). Similar pattern was observed for light

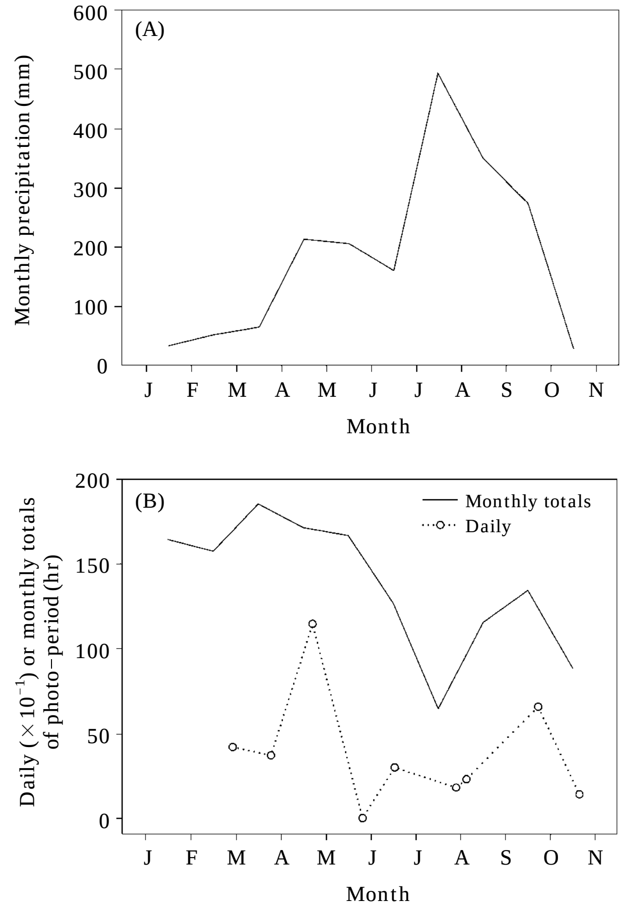

Fig. 2. Seasonal variations of monthly precipitation (rainfall) and daily/monthly totals of photo−period in Sooncheon, Chonnam.

attenuation coefficients (K_d). At Station 2 maximum turbidity and light attenuation coefficients were detected during March and minimum during September (Fig. 3E). Distribution of light attenuation coefficients generally followed that of turbidity except during June at Station 4 (Fig. 3F). The results showed that K_d was closely related with turbidity. Water depths at Stations 1, 2, 3 and 5 were 33, 22, 10, and 8 m respectively.

Temporal variations in chlorophyll *a*

At Station 1 total chlorophyll *a* concentrations in surface water were minimum during February and peaked during April (Fig. 4A). The concentration was extraordinary high (236 μg l^{-1}) in April. This same seasonal chlorophyll *a* signal characterized all phytoplankton size classes except nanophytoplankton size class at the station

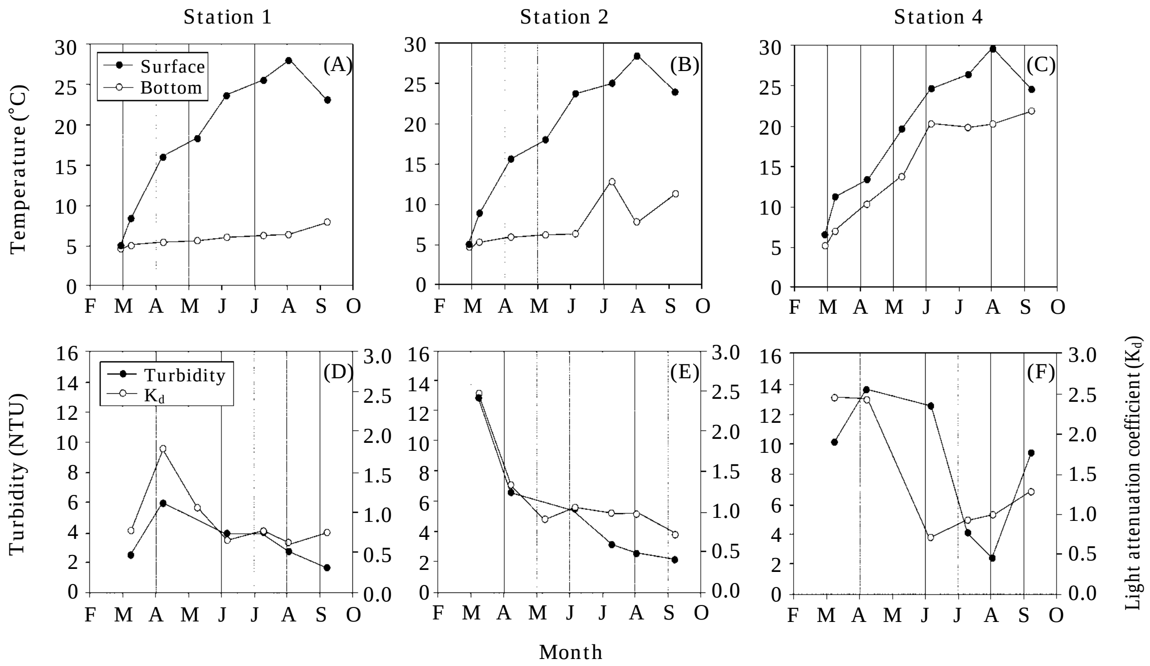

Fig. 3. Temporal distributions of water temperature, turbidity and light attenuation coefficients (K_d) at Stations 1, 2, 4.

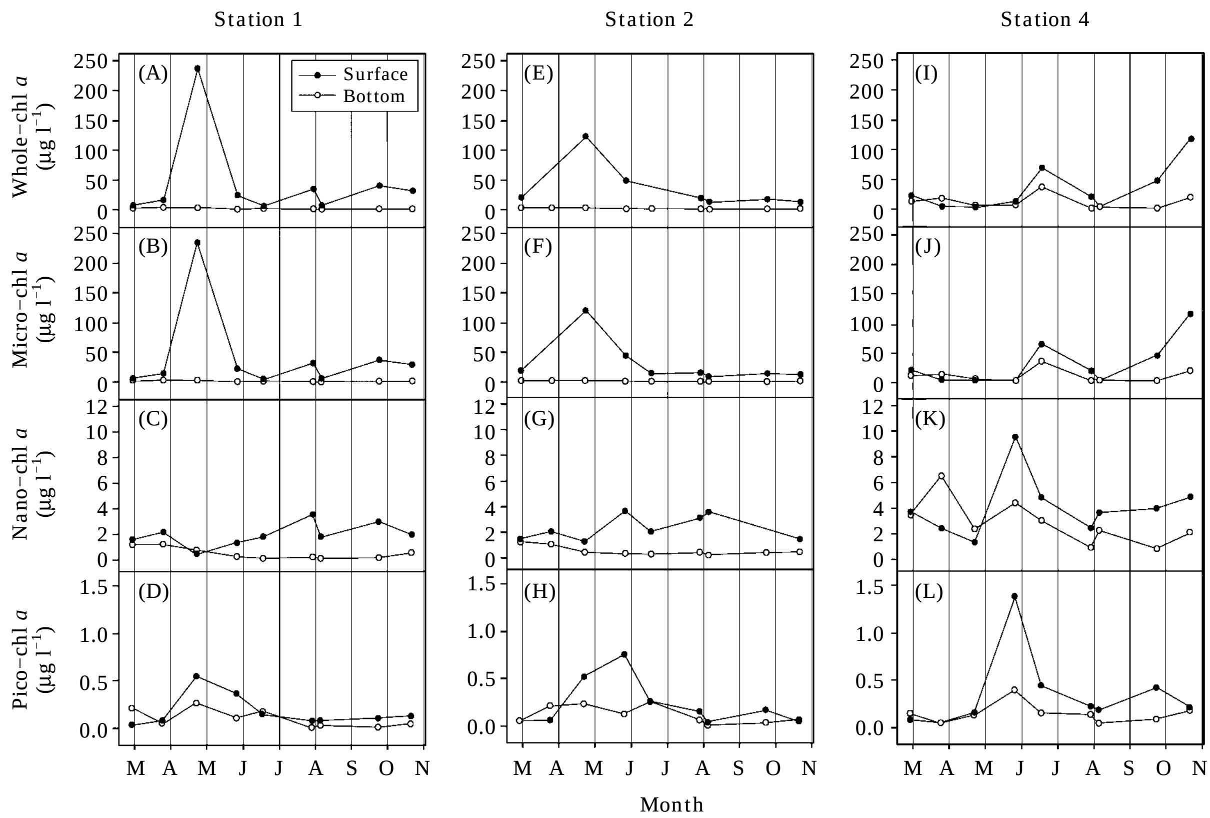

Fig. 4. Temporal variations of chlorophyll *a* in unfractionated water (whole-chl *a*), micro-sized chlorophyll *a* (micro-chl *a*), nano-sized chlorophyll *a* (nano-chl *a*), and pico-sized chlorophyll *a* (pico-chl *a*) at Stations 1, 2, 4 along the axis of Lake Juam.

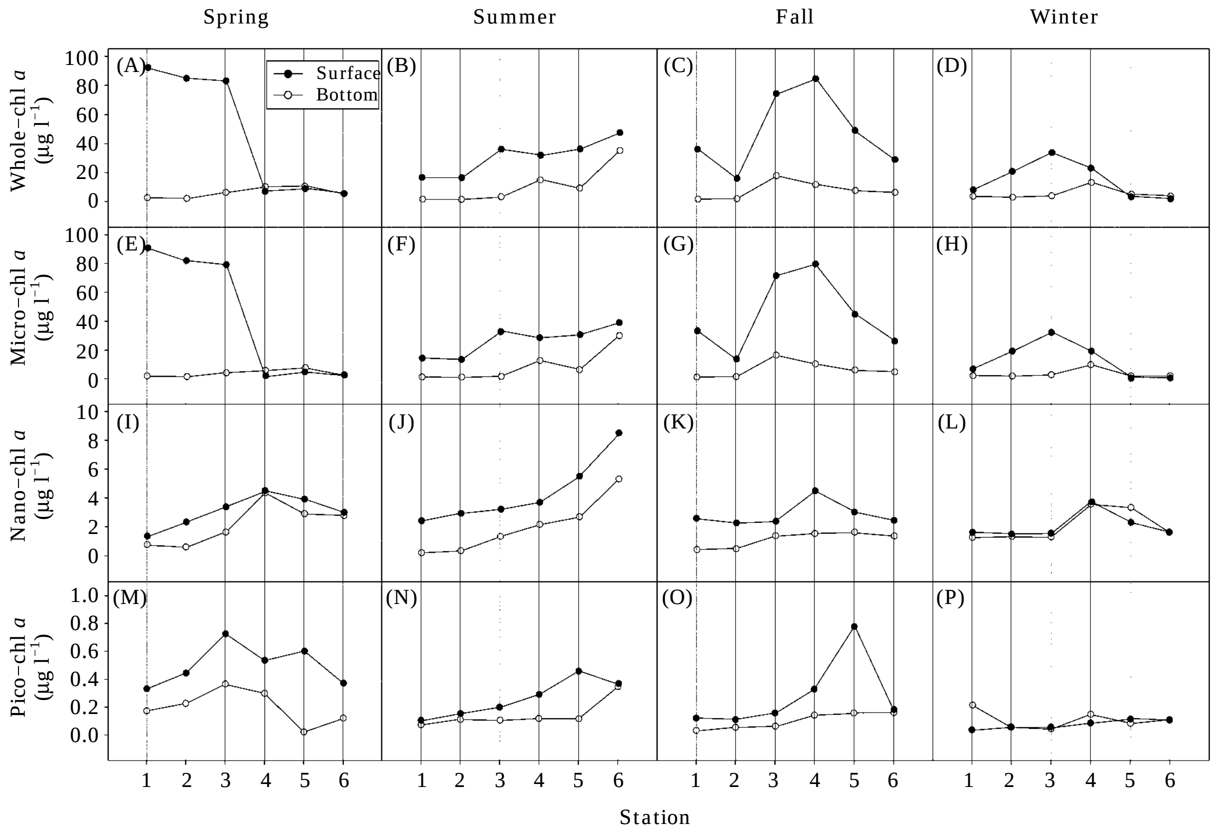

Fig. 5. Spatial variations of chlorophyll *a* in unfractionated water (whole-chl *a*), micro-sized chlorophyll *a* (micro-chl *a*), nano-sized chlorophyll *a* (nano-chl *a*), and pico-sized chlorophyll *a* (pico-chl *a*) during spring, summer, fall and winter.

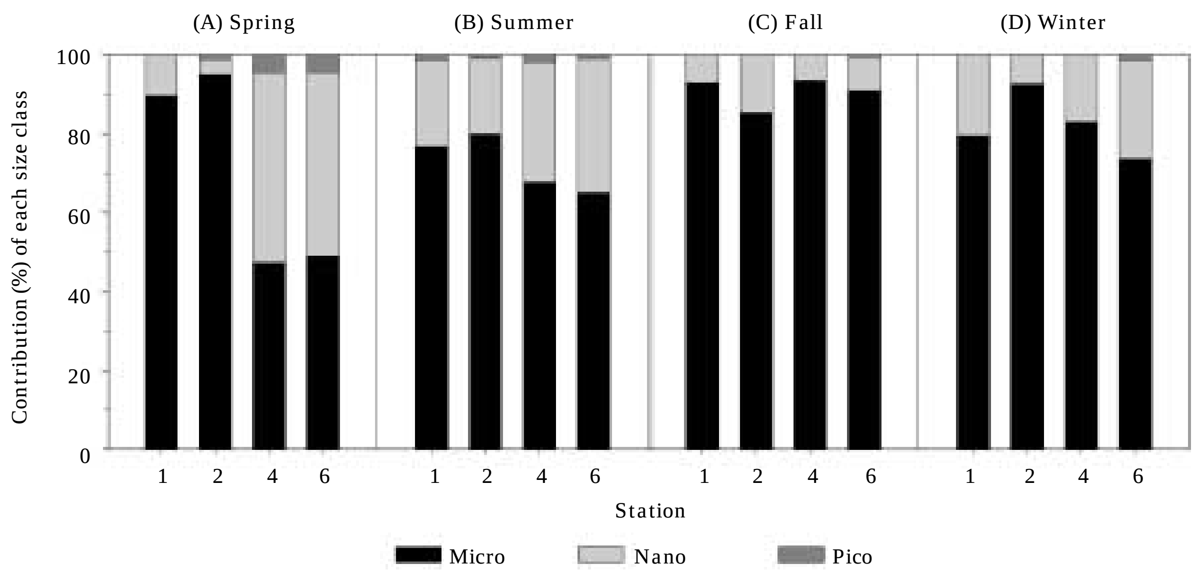

Fig. 6. Percentage contributions of three size classes (micro, nano and pico) to the total chlorophyll *a* in the surface water of the study sites of the Lake Juam.

(Fig. 4B, 4D). Biomass of nanophytoplankton size class was minimum when chlorophyll *a* for other size classes was peaked (Fig. 4C).

At Station 2, total chlorophyll *a* and micro-sized chlorophyll *a* in surface water were peaked in April and low during cold seasons (Fig. 4E, 4F). Similar seasonal variations were observed for pico-size class whereas no clear seasonality was observed for nano-size class (Fig. 4G, 4H).

At Station 4 showed a clear seasonality with a small-scaled summer bloom and larger-scaled fall bloom when other stations experienced low total chlorophyll *a* (Fig. 4I). Blooms were arbitrarily designated as episodes when chlorophyll *a* exceeded 50 μg l^{-1}. Chlorophyll *a* of microphytoplankton was highest during October and lowest during spring in surface water (Fig. 4J). Nanophytoplankton and picophytoplankton chlorophyll *a* had a seasonality with high concentrations during summer and low during spring (Fig. 4K, 4L). Magnitude of pico- and nano-sized phytoplankton peaks increased in the surface water as upstream. Bottom total and micro-sized chlorophyll *a* was generally high compared to those at other stations.

Spatial variations in chlorophyll *a*

Total and micro-sized chlorophyll *a* concentrations during spring revealed clear spatial pattern in surface water, low at upper regions but high at lower regions (Fig. 5A, 5E) whereas the opposite was observed during summer: high at upper regions but low at lower regions (Fig. 5B, 5F). Whole and micro-size classes had maximum chlorophyll *a* at Sation 4 during fall (Fig. 5C, 5G) and at Station 3 during winter (Fig. 5D, 5H). Nano-sized chlorophyll *a* concentrations were highest at Station 4 except during summer when they were highest at Station 6 (Fig. 5I, 5J, 5K, 5L) whereas pico-sized chlorophyll *a* were highest at Station 5 except during spring when maximum concentrations observed at Station 3 (Fig. 5M, 5N, 5O, 5P).

In the surface water at lower region (Stations 1, 2) the contribution of large cells (microphytoplankton) to total chlorophyll *a* was greatly higher than upper region (Station 4, 6) whereas the opposite characteristics were observed for smaller-sized cells (pico-, nano-sized) during spring (Fig. 6A). The similar pattern was observed during summer although difference of percentages between upper and lower regions decreased (Fig. 6B). No evident spatial variations of the percentage contribution were detected for all size classes during cold period including fall and winter (Fig. 6C, 6D).

Simple linear regression analysis

Table 1 shows results (r^2) of linear regression analyses of relationships between the chlorophyll *a* concentrations or contribution of various phytoplankton size classes and various physical properties of the Lake Juam, such as water temperature (T), light attenuation coefficient (K_d), PAR at 1 m water depth (PAR), Photo-period (Rad), and precipitation (Pr). Temperature was significantly ($\alpha = 0.05$) and negatively correlated with biomass of micro-size class at Station 2 whereas the opposite relationship was observed for nano- and pico-size classes at the station. The results suggest that growth of small cells such as nano- and pico-sized phytoplankton may be influenced by water temperature. Light attenuation coefficients were significantly (α =

Table 1. Results (r^2) of linear regression analyses of surface chlorophyll *a* (μg l^{-1}) or percent contribution by each size class (%) vs. water temperature (T, °C), light attenuation (K_d), PAR at 1 m water depth (PAR, μEin m^{-2} s^{-1}), photoperiod of sampling date (Rad), and precipitation (Pr, mm) during the sampling period. r^2 values less than 0.2 were omitted and denoted by '–'. Negative value denote negative relationship.

	Micro-size class					Nano-size class					Pico-size class				
	T	K_d	PAR	Rad	Pr	T	K_d	PAR	Rad	Pr	T	K_d	PAR	Rad	Pr
Station 1	–	0.69[b]	–	0.69[b]	–	–	−0.53[b]	0.56[b]	–	0.23	0.21	0.64[b]	−0.25	0.26	–
Station 2	−0.58[b]	0.32	–	0.54[b]	−0.29	0.55[b]	−0.28	–	–	0.45[a]	0.54[b]	−0.29	–	−0.24	0.37
Station 3	−0.27	0.76[b]	−0.32	–	−0.26	0.27	–	–	−0.22	0.25	0.28	0.67[b]	−0.28	–	0.25
Station 4	–	−0.22	0.23	–	–	–	−0.48[a]	0.43	−0.40[a]	–	–	−0.47[a]	0.43	–	–
Station 6	–			–	–	0.61[a]			–	–	–			−0.35	–

[a] $P < 0.1$
[b] $P < 0.05$

0.05) and positively correlated with chlorophyll *a* of micro−size and pico−size classes (especially at lower region) whereas the relationship was opposite for the nano−size class (α = 0.1). PAR was significantly positively correlated with chlorophyll *a* of nano−size class alone (α = 0.05). Photo−period was significantly positively correlated with chlorophyll *a* concentrations of micro−size class (α = 0.05) at Station 1 and 2 whereas it was negatively correlated with chlorophyll *a* concentrations of nano−size class (α = 0.1). In general, precipitation was negatively correlated with chlorophyll *a* of micro−size class and positively correlated with those of nano− and pico−size classes.

DISCUSSION

Results on seasonal and spatial distributions (Figs. 4, 5) revealed that larger phytoplankton (micro−sized) were more abundant in the lower region of the Lake Juam and biomass of smaller phytoplankton (nano− and pico−sized) decrease as downstream. Phytoplankton blooms were mainly predominated by large cells i.e. micro−size class throughout the sampling period. Percentage contribution of small cells especially pico−sized phytoplankton to total chlorophyll *a* concentrations was minor during the phytoplankton blooms whereas their percentage contributions increased when phytoplankton biomass was low. Chisholm similarly reported that the percentage of small cells in the phytoplankton population increased as total chlorophyll *a* decreased (Chisholm, 1992). These results suggest that Lake Juam may be eutrophic since large cells of phytoplankton can grow better than small−sized phytoplankton at high nutrient concentrations (Iriarte, 1994, Sin *et al*., 2000).

Fig. 3D−3F showed that accumulation of phytoplankton cells affected turbidity and light attenuation coefficients in surface water since the peaks of turbidity and light attenuation coefficients during spring concomitant with the phytoplankton blooms (see Fig. 4A, 4E). The result suggests that phytoplankton in Lake Juam interfered light penetration in the water column (i.e. self−shading (Kirk, 1994)). This scenario is supported by the positive correlationship between light attenuation coefficients and chlorophyll of micro− and pico−size classes in the lower region (Station 1, 2, 3) (Table 1). Similar relationship between K_d and chlorophyll *a* in the Lake Juam was reported by Kim *et al.* (2001). High turbidity and light attenuation coefficients at Station 2 during April (Fig. 4E) indicate that phytoplankton biomass probably was extraordinarily high during April when chlorophyll *a* data were not available for whole and micro−sized phytoplankton due to fluorometer reading exceeding the detection limit. Spring blooms of micro−size class developed in the lower region (Station 1, 2) appear to be derived from increase of photo−period (light availability) in the water column considering the significant and positive correlationship between the photo−period and chlorophyll *a* concentrations of micro−size class in the region (Table 1). Stratification in water columns initiated from March and sustained throughout the sampling period (Fig. 2A) as well as long horizontal residence time resulting from low river discharge and outflow from the dam during spring (Jung, 2002) appeared to maintain large cells of phytoplankton longer in the surface water at Stations 1 and 2 during the period of spring blooms. This suggests that growth of large cell phytoplankton (micro−size) is more likely limited by light in the lower region of Lake Juam. The results from regression analyses, i.e. negative correlationship between temperature and chlorophyll *a* concentrations indicate that temperature may be not a principal factor controlling the large cells (micro−sized) of phytoplankton dynamics.

For nano−size phytoplankton class, both temperature and light appeared to be important mechanisms governing the dynamics of nanophytoplankton since there were positive relationships between temperature, PAR (1 m water depth) and chlorophyll *a* concentrations, and a negative relationship between light attenuation coefficients and chlorophyll *a* concentrations (Table 1). For pico−size phytoplankton, temperature−dependent metabolism is most likely an important mechanism controlling the growth of small−sized cells since temperature was significantly(α = 0.05) and positively correlated with chlorophyll *a* concentrations. Light availability may be not a controlling mechanism for the pico−size class since light attenuation coefficients were significantly (α = 0.05) and positively correlated with chlorophyll *a* concentrations of the small cells and PAR was negatively correlated the concentrations in the lower region of Lake Juam (Table 1). The opposite relationships were observed between light attenuation coefficients, PAR and pico−sized chlorophyll *a* concentrations in the upper region of the lake indicating that controlling mechanims for pico−sized cells may be spacially changed in the Lake Juam (Table 1). In order to identify potential mechanims controlling the size structure of phytoplankton and determine relative importance of bottom−up and top−down controls in Lake Juam, required in the ecosystem scale are integrative analyses on sampling data including nutrient availability and grazing pressure of consumers. In a companion paper, we investigate the dynamics of size structure related to nutrient availability and grazing activity by herbivores.

In summary, we investigated the temporal and spatial variations of size−structured phytoplankton dynamics in Lake Juam and physical properties related to the variations of phytoplankton in the artificial lake. Phytoplankton blooms developed during spring in the lower region of the lake whereas small−scaled summer bloom and large−scaled fall bloom were observed in the upper region. The scales of phytoplankton blooms were higher in the lower regions than the upper region and predominated by large cells of phytoplankton (micro−sized). Growth of large cells appeared to be controlled by rather light availability than temperature−dependant metabolisms in the system. On the other hand, small−sized cells such as pico−size class were more abundant in the upper region than lower region and the growth of small−sized phytoplankton (pico−sized) is most likely controlled by temperature−dependant metabolisms. Light availability and temperature−dependant metabolism appeared to be principal mechanisms controlling the growth of intermediate−sized cells (nanophytoplankton). Although further data analyses on nutrient availability to size−structured phytoplankton and grazing activity of herbivores are required to present conclusions on the relative importance between bottom−up and top−down controls of size−structured phytoplankton dynamics in the Lake Juam, the results from this study provide useful information to better understand phytoplankton dynamics in the Lake Juam.

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< **국문적요** >

담수성 식물플랑크톤의 크기별 동태에 대한 상향식, 하향식 조절간의 상대적 중요도 조사: I. 크기구조의 시·공간적 변동

신 용 식*·김 종 민[1]

(목포해양대학교 해양시스템공학부, [1]국립환경연구원 영산강물환경연구소)

전남 주암호에서의 식물플랑크톤 동태를 파악하기 위해 2003년 2월부터 10월까지 식물플랑크톤 생체량(클로로필 *a*)의 크기별 시·공간적 변동과 제반 환경요인에 대해 조사하였다. 본 논문에서는 주암호와 같은 담수호에서 식물플랑크톤의 크기 구조가 계절적, 공간적으로 어떻게 변화하고 그러한 변화 속에서 물리적 요인들이 어떤 영향을 미치는지 회귀분석을 통해 파악하고자 하였다. 식물플랑크톤(클로로필 *a*)은 세 그룹 즉, 대형(micro-size $>20\,\mu$m), 소형(nano-size 3-20 μm) 마지막으로 초소형(pico-size, $<3\,\mu$m)으로 구분했다. 물리적 특성 파악을 위해 수온, 광소멸계수, PAR (photosynthetically active radiation), 수중 탁도등도 동시에 측정하였다. 최대치의 클로로필 *a*는 2003년 하류지역에서는 4월에 상류지역에서는 10월에 발생하였다. 식물플랑크톤의 대번성기에는 대부분 세포크기가 큰 대형(micro-size) 식물플랑크톤이 우세하였다. 주암호의 크기별 식물플랑크톤의 변동에 영향을 미칠 수 있는 물리적 특성들에 대해 논의하였다.