Secondary Productivity of Pelagic Zooplankton in Lake Paldang and Lake Cheongpyeong

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ABSTRACT: We estimated monthly and annual secondary productivity of pelagic zooplankton in Lake Paldang and Lake Cheongpyong. Secondary productivity was calculated by combining estimated zooplankton biomass and biomass-specific productivity for each site and depth from March to November 2008. In addition to somatic production, we measured production of eggs and exuviae for three dominant species: *Daphnia galeata*, *Bosmina longirostris*, *Cyclops* sp. In terms of biomass, *B. longirostris* was dominant in Lake Paldang in April and May, *B. longirostris* showed explosive biomass growth, especially in May. In June and July, *B. longirostris* and *D. galeata* were both dominant. Lake Cheongpyeong showed much lower zooplankton biomass than Lake Paldang. In August, there was little or no biomass in both lakes probably due to heavy rain. The Gyeongan River contributed most of the secondary productivity and *B. longirostris* contributed the most secondary productivity in Lake Paldang. *D. galeata* also contributed in the Gyeongan River, the South Han River and at the Paldang Dam in spring and fall. Overall, Lake Cheongpyeong showed lower secondary productivity than Lake Paldang. *B. longirostris* made the largest contribution to secondary productivity in the Cheongpyeong Dam area while *D. galeata* contributed the most near Nami Island. Somatic production constituted ~80% of the total secondary productivity (the sum of somatic, egg and exuvia production) for *D. galeata* and *B. longirostris*. Although production-to-biomass (P/B) ratios were usually <<1, *B. longirostris* sometimes showed very high P/B ratios, probably due to fish predation. *D. galeata* showed much lower P/B ratios than *B. longirostris* after the summer at most sites.

Key words: *Bosmina longirostris*, Lake Cheongpyeong, Lake Paldang, production-to-biomass ratio, secondary productivity, zooplankton

INTRODUCTION

The Han River watershed covers 23% of the land area of South Korea, and is the most congested and industrialized area of the country, being inhabited by 40% of the country's population. The watershed is managed by national and regional governments (Han River Environment Research Center 2008), as it supplies potable water for approximately 24 million people. Accordingly, the Han River watershed has many man-made reservoirs, which are categorized into two types: lake-like water bodies and river-like water bodies (Kong et al. 1996). As energy flow and nutrient cycling patterns in aquatic systems may change according to the characteristics of the water body, management policies for water quality conservation should be based on scientific data on energy flow and nutrient cycling patterns (Han River Environmental Research Center 2008). Since the dynamics of important nutrients such as nitrogen and phosphorus are related to the flow of energy in the ecosystem, studies on energy flow in aquatic ecosystems are essential for water quality management in the Han River watershed (Han River Environmental Research Center 2008).

Energy in pelagic ecosystems flows from phytoplankton, the primary producers, to the zooplankton consumers through classical food chain and microbial food web pathways (Weisse and Stockner 1993). The efficiency of energy transfer between the zooplankton and phytoplankton shows much variability (Hilbricht-Ilkowska 1977). Energy transfer efficiencies at this interface appear to be dependent on seston food quality (Müller-Navarra et

al. 2000). Seston food quality includes prey size, secondary metabolites, digestion efficiencies and nutritional quality. (Müller-Navarra and Lampert 1996). Understanding energy transfer from primary producers to the higher trophic levels is very important for understanding a wide range of phenomena such as whole lake responses to eutrophication (Reimann and Christoffersen 1993, Weisse and Stockner 1993), and the transfer of toxic substances through food webs (Turner and Tester 1997), and for estimating the maximum sustainable harvest in fisheries (Baumann 1995, Pauly and Christensen 1995). Energy transfer efficiency between primary producers and herbivorous zooplankton is usually expressed as the ratio of secondary productivity to primary productivity, which is highly variable, ranging from 1% to 30% (Hilbricht-Ilkowska 1977).

Therefore, estimation of secondary production is an important step toward understanding energy transfer from primary producers to the higher trophic levels.

In this study, we estimated monthly and annual mean pelagic secondary productivity in Lake Paldang and Lake Cheongpyeong by measuring zooplankton biomass and zooplankton growth in the lab. Our results provide useful data that can be used to assess energy flow and nutrient dynamics models, and should contribute to the management of water quality in the Han River watershed.

MATERIALS AND METHODS

Study sites and sample collection

Lake Paldang is a man-made reservoir built in 1973 for hydro-power generation and to secure the water supply. It covers 23,800 km^2 of watershed area, is a mean of 6.5 m in depth, and has a 5-day average hydraulic residence time (Shin et al. 2007). Three rivers flow into Lake Paldang: the North Han River from the north, the South Han River from the east, and the Gyeongan River from the south (Fig. 1). We collected zooplankton samples for measurement of biomass and productivity from Sambong on the North Han River (site PD-L3), Walkesa on the South Han River (site PD-L2), Kwang Dong Bridge on the Gyeongan River (site PD-L4) and at the Paldang Dam (site PD-L1) (Fig. 1).

Lake Cheongpyeong is also a man-made reservoir, and was built in 1944 (Choi 2005). It covers 9,921 km^2 of watershed area, and is a mean of 24.0 m in depth (Choi 2005, Lee and Han 2005). We collected zooplankton samples for measurement of biomass and productivity from the Cheongpyeong Dam (site CP-L1), Nami Island (site CP-L2), and Go-seong ri (site CP-L3) (Fig. 1).

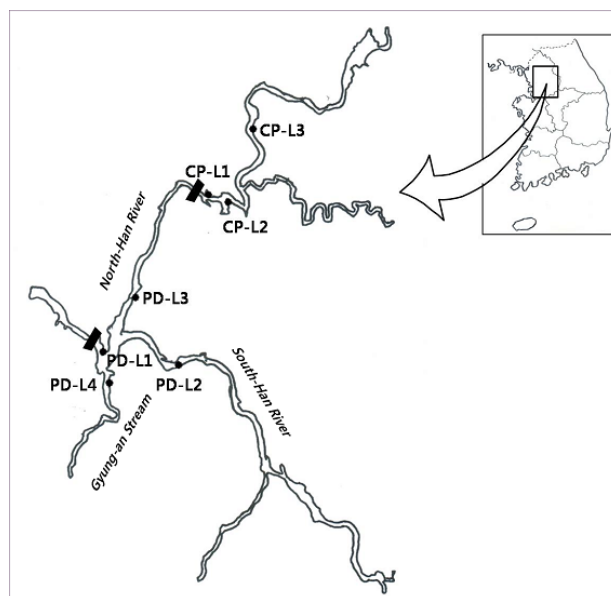We collected zooplankton samples using 12-L Schindler traps (61 μm) to estimate zooplankton biomass monthly

Fig. 1. Map of the sampling sites in Lake Paldang and Lake Cheongpyeong. PD-L1 indicates the Paldang Dam sampling site, PD-L2 the South Han River sampling site, PD-L3 the North Han River sampling site, PD-L4 the Gyeongan River sampling site, the Cheongpeong Dam sampling site, CP-L2 the Go-sung ri sampling site, and CP-L3 the Nami Island sampling site.

from March to November 2008. Samples were collected from Lake Paldang and Lake Cheongpyeong at the following depths: PD-L1 (0 m, 2 m, 5 m, 10 m, 20 m), PD-L2, PD-L3 (0 m, 5 m, 10 m), PD-L4 (0 m, 5 m), CP-L1 (0 m, 2 m, 5 m, 10 m, 20 m), CP-L2 (0 m, 10 m, 20 m), and CP-L3 (0 m, 5 m, 10 m). Samples were fixed with Lugol's solution in 60 mL plastic bottles.

Zooplankton Biomass

We counted the numbers and measured the lengths of dominant zooplankton species using a counting chamber under a dissecting microscope (Nikon, model SMZ800). For dominant species, the lengths of more than 200 individuals were measured and dry weights were estimated using length-weight relationships obtained from each sampling sites in this study (Table 1). If zooplankton numbers were too high to permit each individual to be counted or measured, aliquots of the samples were counted and measured. To estimate biomass for non-dominant species, we multiplied the numbers counted by the average dry mass (Table 2), which, in turn, was converted into the carbon-based biomass by multiplication by the average carbon content of zooplankton (0.4). In addition, we counted the number of eggs and exuviae for the three dominant zooplankton species (*Daphnia galeata*, *Bosmina longirostris*, and *Cyclops* sp.) and measured their

Table 1. Length(L)-weight(W) relationships for important zooplankton species obtained from sampling sites in this study in October, 2008

Site	Species			
	Daphnia	*Cyclops*	*Bosmina*	Calanoids
Lake Paldang				
PD-L1	$\ln W=1.71+2.53\times\ln L$	$\ln W=2.82+1.74\times\ln L$	$\ln W=3.40+2.35\times\ln L$	$\ln W=2.51+2.72\times\ln L$
PD-L2	$\ln W=1.95+1.90\times\ln L$	$\ln W=3.04+1.61\times\ln L$	$\ln W=3.40+2.35\times\ln L$	$\ln W=2.51+2.72\times\ln L$
PD-L3	$\ln W=1.47+3.05\times\ln L$	$\ln W=2.76+2.35\times\ln L$	$\ln W=3.40+2.35\times\ln L$	$\ln W=2.51+2.72\times\ln L$
PD-L4	$\ln W=1.71+2.53\times\ln L$	$\ln W=2.82+1.74\times\ln L$	$\ln W=3.99+4.19\times\ln L$	$\ln W=2.51+2.72\times\ln L$
Lake Cheongpyeong				
CP-L1	$\ln W=1.11+2.55\times\ln L$	$\ln W=2.58+2.09\times\ln L$	$\ln W=3.40+2.53\times\ln L$	$\ln W=2.51+2.72\times\ln L$
CP-L2	$\ln W=1.15+2.69\times\ln L$	$\ln W=2.33+2.17\times\ln L$	$\ln W=3.40+2.53\times\ln L$	$\ln W=2.51+2.72\times\ln L$
CP-L3	$\ln W=1.29+2.62\times\ln L$	$\ln W=2.51+3.18\times\ln L$	$\ln W=3.40+2.53\times\ln L$	$\ln W=2.51+2.72\times\ln L$

Table 2. Average dry mass for various zooplankton from the literature

Species	Dry Weight (µg)	Reference
Daphnia	12	Dumont et al. 1975
Bosmina	2.19	Dumont et al. 1975
Cyclops	30.63	Dumont et al. 1975
Bosminopsis	0.59	Kobayashi et al. 1996
Diaphanosoma	0.57	Kobayashi et al. 1996
Ceriodaphnia	4	Dumont et al. 1975
Moina	0.92	Matsumura-Tundisi 1989
Eudiaptomus	8.5	Dumont et al. 1975
Chydorus	1.17	Kobayashi et al. 1996
Asplancha	0.525	Bottrell et al. 1976
Pleosoma	0.1	Bottrell et al. 1976
Trichocerca	0.16	Kobayashi et al. 1996
Testudinella	0.05	Bottrell et al. 1976
Lecane	0.004	Kobayashi et al. 1996
Kellicottia	0.25	Bottrell et al. 1976
Lepadella	0.15	Kobayashi et al. 1996
Macrothrix	10	Guntzel et al. 1992
Harpacticoid	5	Goodman 1980
Leptodora	11.05	Adrian & Deneke 1996
Branchionus	0.4	Kobayashi et al. 1996
Anuraeopsis	0.07	Kobayashi et al. 1996
Keratela	0.07	Kobayashi et al. 1996
Polyarthra	0.4	Kobayashi et al. 1996
Filinia	0.45	Kobayashi et al. 1996
Nauplii	0.093	Kobayashi et al. 1996

masses. We used a microbalance (Perkin Elmer AD-6, 0.1 µg resolution) to weigh the zooplankton, eggs and exuviae.

Secondary productivity measurement

The "growth rate approach" is a popular method for estimation of zooplankton secondary productivity (SPR) (Kimmerer 1987, Poulet et al. 1995). In the growth rate approach, somatic production (P_{growth}) is estimated as the sum of stage-specific or age-specific growth rate (g_i) multiplied by the biomass of each stage or age (B_i) for each age or stage as in equation (1) (Poulet et al. 1995). Stage-specific growth rate is calculated as the mean increase in individual dry mass from before (W_{mini}) to after (W_{maxi}) incubation divided by incubation time (D_i) as in equation (2).

$$P_{growth} = \Sigma g_i B_i \tag{1}$$

$$g_i = (\ln W_{maxi} - \ln W_{mini}) / D_i \tag{2}$$

The method for measuring size-specific daily growth is described in the next section. Recently, Cauchie et al. (2000) suggest that zooplankton SPR should include egg production (P_{egg}) and exuvia production (P_{exuvia}) in addition to somatic production (P_{growth}) as in equation (3).

$$SPR = P_{growth} + P_{egg} + P_{exubia} \tag{3}$$

In this study, we estimated zooplankton secondary productivity based on somatic production (P_{growth}), egg production (P_{egg}) and exuvia production (P_{exuvia}) for the dominant five zooplankton species. For rotifers or other macrozooplankton, we estimated SPR by calculating the ratio of production estimates from the literature to biomass (P:B) (Table 3). Rotifers and other macrozooplankton are shown as 'others' in the figures and tables in the Results.

Measurement of size specific daily growth

We measured size-specific daily growth (g_i) every month after laboratory incubation for three of the five dominant species: *D. galeata*, *B. longirostris*, *Cyclops* sp., *Diaphanosoma* sp. and calanoid copepods. We collected

Table 3. Daily production-to-biomass (P/B) ratios from the literature (Straile 1998)

Plankton component	Annual average P/B (day^{-1})
Rotifers	0.13
Herbivorous crustaceans	0.05
Carnivorous crustaceans	0.07

12 L of water from each depth at each site, and filtered the sample through 61 μm mesh. Water from different depths was mixed into one composite water sample for zooplankton incubation. We incubated 10 individuals of various sizes without eggs for three days and five individuals with eggs for seven to eight days using 20 ml glass vials. Zooplankton incubation was conducted with the appropriate photo-period and water temperature for each sampling date using temperature/light controlled growth chambers (Hanbaek, Model HB-302S-4H). For the incubation temperatures, we used the hyperlimnion water temperature for the daytime temperature and the epilimnion temperature for nighttime temperature under the assumption of diel vertical migration of zooplankton.

Measurement of egg production

For three major zooplankton species, *D. galeata*, *B. longirostris* and *Cyclops* sp., egg production was calculated by counting egg numbers per individual per unit volume (N_{egg}), multiplied by average dry mass for just-hatched neonates (W_{egg}), and divided by egg development time (D_{egg}) as in equation (4).

$$P_{egg} = N_{egg} \times W_{egg} / D_{egg} \qquad (4)$$

Egg number (N_{egg}) was obtained by counting eggs in the field samples. Dry masses for just-hatched neonates were measured and converted into carbon-based biomasses. The average egg mass (W_{egg}) was 0.0126 μg for *D. galeata*, 0.0086 μg for *B. longirostris*, and 0.0041 μg for *Cyclops* sp. Average egg development time (D_{egg}) was measured by incubating zooplankton with eggs.

Measurement of exuvia production

During zooplankton incubation, we counted the exuviae of each species per individual and calculated exuvia production as the mean weight of exuviae multiplied by the number of exuvia for each species per day. The average exuvia dry mass measured in this study was 0.0133 μg for *D. galeata*, 0.0093 μg for *B. longirostris*, and 0.0061 μg for *Cyclops* sp.

Secondary productivity estimation

We made length-weight equations for the dominant zooplankton species in each site in October 2008. We assumed that daily biomass-specific secondary productivity, which is equivalent to the ratio of daily production to biomass (P/B), decreases as zooplankton grow, and developed regression equations for the relationship between biomass-specific secondary productivity and zooplankton biomass for the three dominant species every month. We estimated secondary productivity by combining zooplankton biomass and biomass-specific productivity for each site and depth from March to November, 2008. Depth-specific secondary productivity was averaged weighted by depth.

RESULTS

Seasonal dynamics of dominant zooplankton biomass

In PD-L1 in Lake Paldang, the zooplankton community was dominated by *B. longirostris* except in June and July 2008 (Fig. 2). In May in particular, *B. longirostris* had a very high mean biomass of 546 μg DW L^{-1}. *D. galeata* was among the dominant species in June and was the dominant species in July, while *Cyclops* sp. was important, but not dominant all year round. In PD-L2, *B. longirostris* was also the dominant species, with very high biomass in April (2234 μg DW L^{-1}) and October (350 μg DW L^{-1}). PD-L3 showed relatively lower zooplankton biomasses compared with other sites in this study. PD-L3 was dominated by *B. longirostris* in April and by *D. galeata* in May and June. Notably, calanoid copepods and *B. longirostris* were the dominant species in PD-L3 in November. PD-L4 was dominated by *B. longirostris* in April and November and by *D. galeata* in May and June. All sites showed very low zooplankton biomass in August, mainly due to heavy rains in that month. Zooplantkon showed the highest biomass at 0-5 m depth, which was a mixed layer, although considerable zooplankton biomass also existed below 10 m depth in Lake Paldang (data not shown).

In Lake Cheongpyeong, zooplankton biomass was lower overall compared to Lake Paldang. *D. galeata* dominated the zooplankton communities in CP-L1, CP-L2, and CP-L3 in June and July, while *B. longirostris* dominated the communities in other months in spring and fall. As in Lake Paldang, all sites in Lake Cheongpyeong showed very low zooplankton biomass in August, mainly due to heavy rain.

Seasonal secondary productivity

Among the dominant species, *B. longirostris* and *D. galeata* showed high seasonal variability in secondary
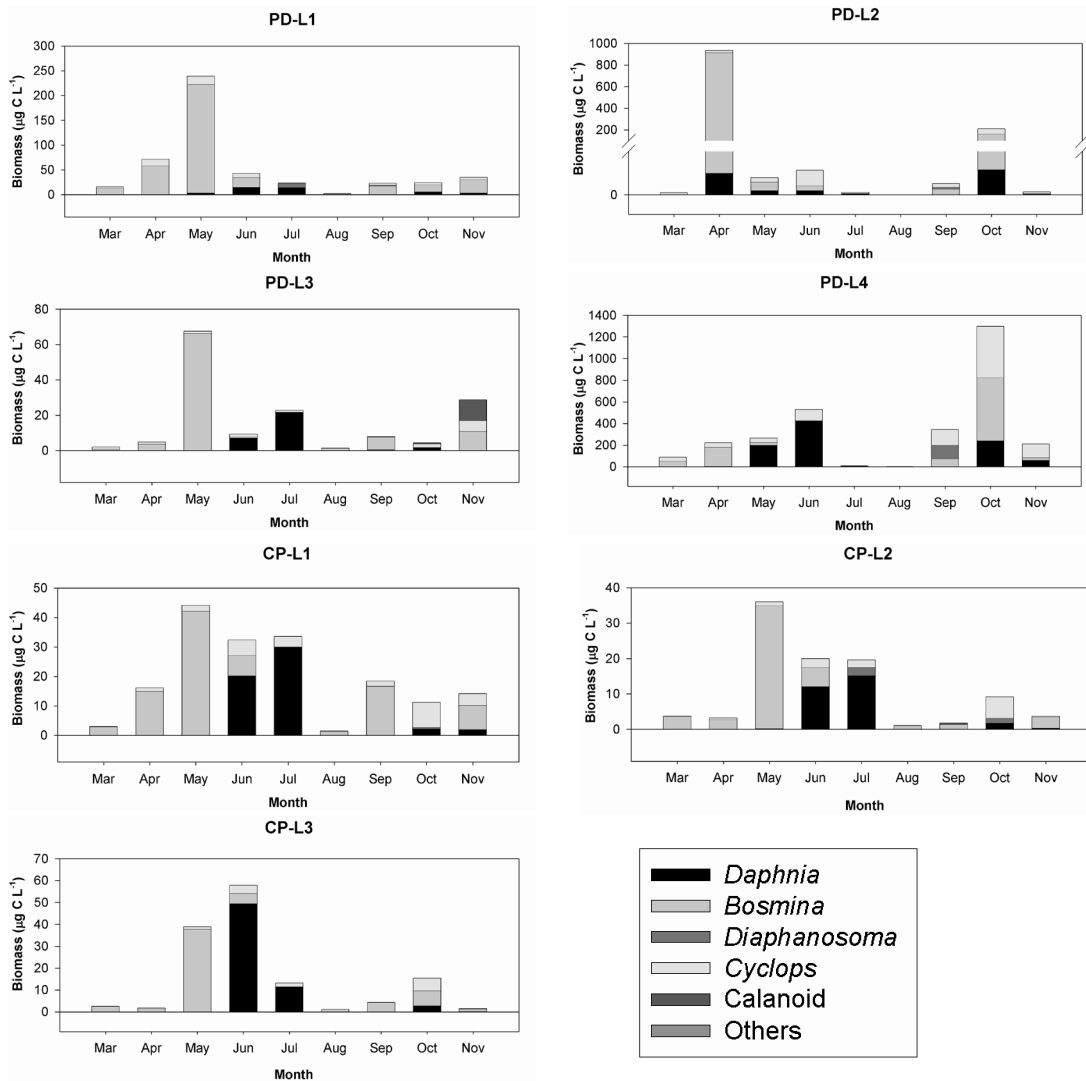
Fig. 2. Seasonal dynamics of the biomass of five major zooplankton species averaged over different depths in Lake Paldang and Lake Cheongpyeong in 2008.

productivity in Lake Paldang (Fig. 3). Overall, *B. longirostris* contributed the most to secondary production in PD-L1 while in PD-L2, it had the highest secondary productivity only in April and October. In PD-L3, *B. longirostris* contributed the most to secondary productivity in July and September, and in PD-L4, it contributed the most in April, September and October. In contrast, *D. galeata* showed the highest secondary productivity in May in PD-L2 and PD-L4 and in June in PD-L3 and PD-L4. *Cyclops* sp. showed relatively low secondary productivity. Secondary productivity was highest in the mixed layer due to a higher zooplankton biomass. However, PD-Ll, which was the deepest site, sometimes showed high secondary productivity in the middle or deeper depths.

In Lake Cheongpyeong, variability in secondary productivity was not high, with a range of 11-18 µg C L^{-1} day^{-1} (Fig. 3). However, the zooplankton species

that were most important contributors to secondary production were different at each sampling site. In CP-L1, *B. longirostris* was almost the sole contributor to secondary productivity except for June, when *D. galeata* dominated and October, when *Cyclops* sp. was dominant. In CP-L2 and CP-L3, *D. galeata* dominated secondary production in June and July. Like sites in Lake Paldang, all sites in Lake Cheongpyeong showed very low zooplankton secondary productivity in August due to low biomass after heavy rain. Overall, secondary productivity showed a similar seasonal pattern of variation to biomass. However, *B. longirostris* was exceptional in that they dominated zooplankton biomass with very low secondary productivity in May in CP-L2 and CP-L3 , and decreased their biomass in June.

Annual Secondary Productivities

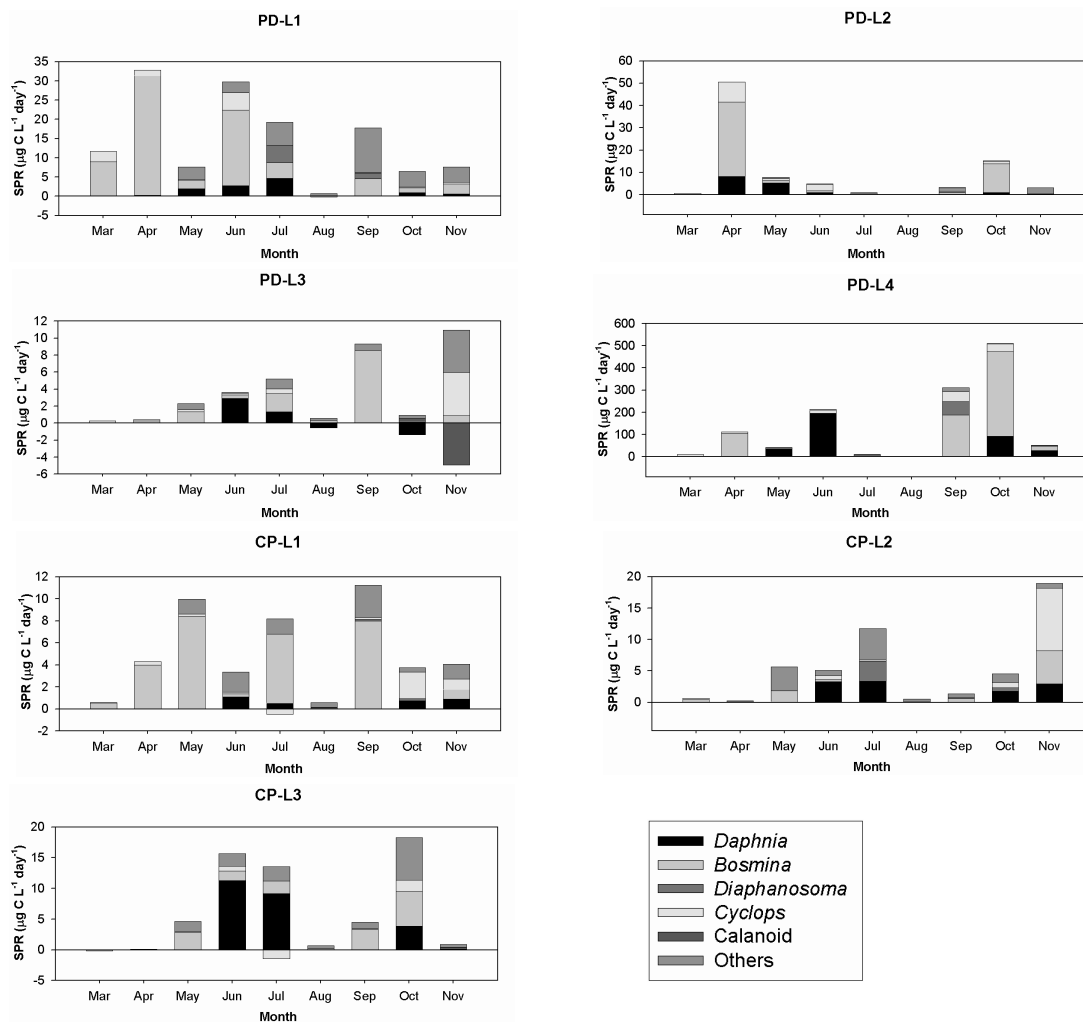Annual average daily water column secondary

Fig. 3. Seasonal dynamics of the secondary productivity of five major zooplankton species averaged over different depths in Lake Paldang and Lake Cheongpyeong in 2008.

Table 4. Annual average daily secondary productivity (μg C L^{-1} day^{-1}) for each sampling site. Averages indicate averages weighted by water volume covered by each site (water volume fraction for PD-L1: 0.283, PD-L2: 0.367, PD-L3: 0.295, PD-L4: 0.055)

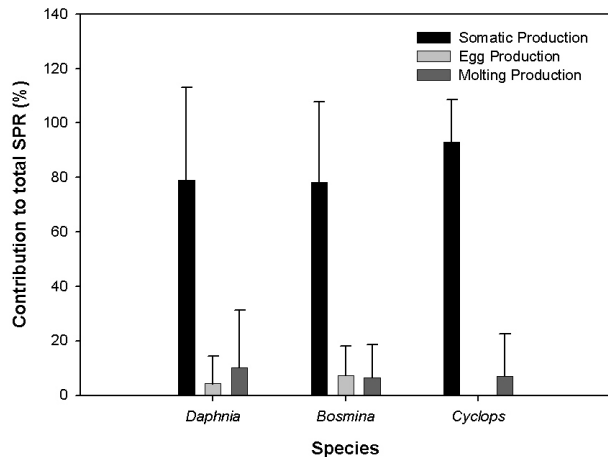| Site	Daily Secondary Productivity					
	Daphnia	*Bosmina*	*Diaphanosoma*	Cyclopoid	Others	Total
Lake Paldang						
PD-L1	1.3	8.2	0.7	1.1	3.6	14.9
PD-L2	1.7	5.5	0.1	1.7	0.6	9.6
PD-L3	0.3	1.5	0.0	0.7	0.9	2.9
PD-L4	39.7	76.8	7.0	13.5	3.5	140.4
average	3.3	9.0	0.6	1.9	1.7	16.5
Lake Cheongpyeong						
CP-L1	0.4	3.1	0.0	0.4	1.1	5.1
CP-L2	1.3	1.0	0.4	1.3	1.4	5.4
CP-L3	2.7	1.7	0.0	0.2	1.7	6.3
average	1.5	1.9	0.1	0.6	1.4	5.6

Fig. 4. Contributions to total secondary productivity (SPR) of somatic growth production, egg production and molting (exuvia) production by the dominant species: *Daphnia galeata*, *Bosmina longirostris*, and *Cyclops* sp. in Lake Paldang and Lake Cheongpyeong in 2008.

productivity for the PD-L4 site averaged 140.42 μg C L^{-1} day^{-1}, which represented ~47% of the total secondary production from all 4 sites in Lake Paldang sampled (Table 4). *B. longirostris* contributed 44-57% of the total secondary production from the five major zooplankton species. *D. galeata* was the second-most important contributor to zooplankton production in Lake Paldang.

In Lake Cheongpyeong, the three sampling sites showed similar average daily water column secondary productivity: the secondary productivity in CP-L3 was 34% of the total from the three sites, while CP-L1 and CP-L2 represented 29% and 27% of the total, respectively (Table 4). *B. longirostris* was by far the most important producer in CP-L1, while *D. galeata* and *Cyclops* sp. made similar contributions in CP-L2 and *D. galeata* was also important in CP-L3.

Somatic production, egg production and exuvia proudction

We estimated egg and exuvia production in addition to somatic growth production for dominant zooplanton species such as *D. galeata*, *B. longirostris* and *Cyclops* sp. (Fig. 4). Somatic production contributed ~80% of the total secondary productivity in *D. galeata* and *B. longirostris*. However, in *Cyclops* sp., somatic production contributed >90% of the total estimated secondary productivity, probably due our difficulty in finding their eggs.

Production to biomass ratio

Zooplankton production to biomass (P/B) ratios were usually <<1, indicating that they produce less carbon than

their body mass in a day (Fig. 5). However, *B. longirostris* sometimes showed very high P/B ratios of up to ~126 in July. *D. galeata* showed similar P/B ratios to *B. longirostris* in spring months. However, in July and September, *D. galeata* showed very low P/B ratios in most sites.

DISCUSSION

The results from our study show that cladocerans made the most important contribution to secondary production and that PD-L4 produced the highest amount of matter in Lake Paldang and Lake Cheongpyeong in 2008. The importance of cladocerans as producers may result from their dominance in terms of biomass (Fig. 2). Among cladocerans, *B. longirostris* was particularly important in terms of both biomass and production, especially in the spring months. *D. galeata* also contributed a considerable amount to total production, usually after the *B. longirostris* production peak in the spring.

Although overall patterns of secondary production appeared to follow the seasonal dynamics of biomass patterns, variation in biomass could not always explain secondary productivity patterns in this study (Fig. 2, Fig. 3). For example, *B. longirostris* biomass was very high in May in PD-L3, while their secondary production was relatively low. *B. longirostris* biomass then dropped in the following month in PD-L3. Therefore, comparisons of secondary production and biomass can provide useful information about the population dynamics of certain zooplankton species.

We examined the relationships between biomass and production further using P/B ratios (Fig. 5). In this study, zooplankton P/B ratios showed substantial variation among zooplankton species and sampling sites. Usually, the P/B ratios were <<1, but *B. longirostris* showed very high P/B ratios in July. We interpret this extremely high P/B ratio of *B. longirostris* as being due to lower biomass caused by fish predation. If our interpretation is correct, then unusually high P/B ratios may indicate a high level of energy flow to higher trophic levels, such as fish (Benke 1998). P/B ratios were very different for the dominant zooplankton species, especially in summer months, suggesting species-specific differences in sensitivity to unknown substances during this period. Further study will be required to determine what specific factors lowered the P/B ratios of *D. galeata* in Lake Paldang and Lake Cheongpyeong in those months.

In this study, we measured egg production and exuvia production in addition to somatic growth production to estimate total secondary productivity (Fig. 3). Although some variation was observed, somatic production
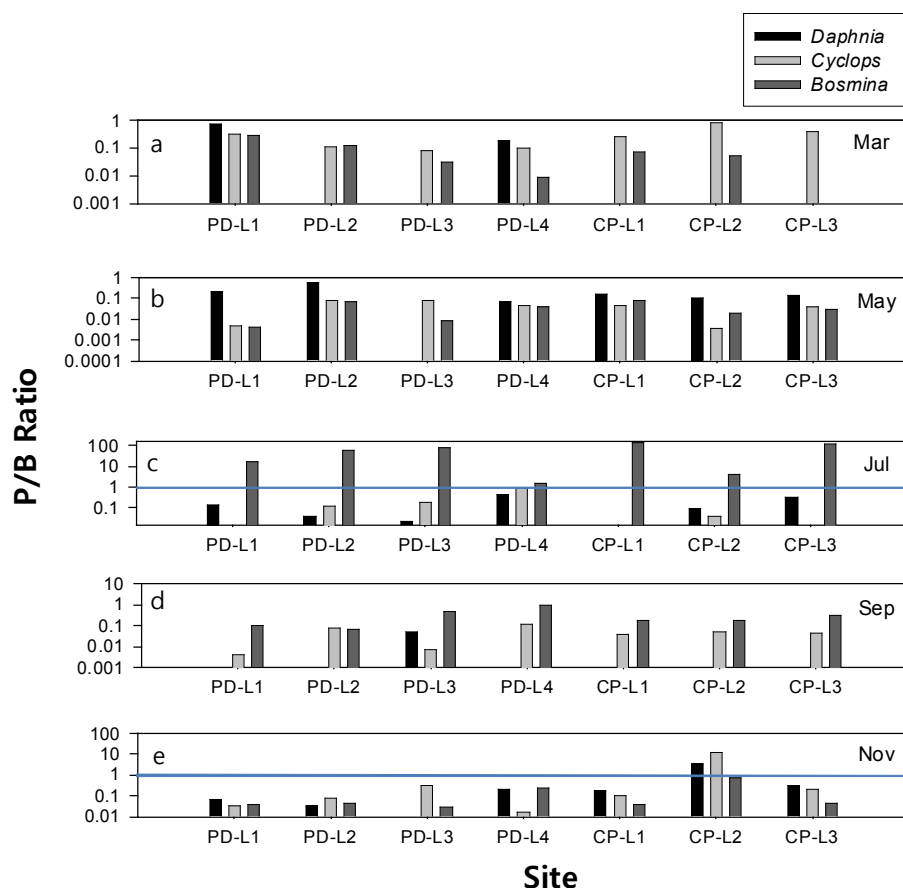
Fig. 5. Production to biomass (P/B) ratios of three dominant species: *Daphnia galeata*, *Bosmina longirostris*, and *Cyclops* sp. in Lake Paldang and Lake Cheongpyeong in 2008.

generally contributed ~80% of the total secondary production of *D. galeata*, *B. longirostris*, and *Cyclops* sp. However, a recent study reported that exuviae production contributed 20- 40% of total daily proudction (Cauchie et al. 2000). The relative contributions of somatic, egg and exuvia production showed seasonal variability. In practical terms, it may be possible to estimate secondary productivity efficiently by measuring only somatic growth and projecting total secondary productivity by multiplying by appropriate coefficients for egg and exuvia production. However to maximize the efficiency of estimation, information about seasonal variation in the relative contributions of somatic, egg and exuvia production in various water bodies would be necessary.

Secondary production data are very important for analyses of energy flow and nutrient dynamics in freshwater pelagic ecosystems (Park and Goldman 2008). For energy flow studies, secondary production data can be combined with primary production data to assess ecological efficiency (Hilbricht-Ilkowska 1977). Such ecological efficiency data, combined with food quality indices such as carbon-to-phosphorus ratios and

essential fatty acid contents, would prove very useful for future analyses of energy flow and nutrient cycles in lake ecosystems (Han River Environmental Research Center 2008).

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