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Characteristics and Inter-annual Variability of Zooplankton Dynamics in the Middle Part of the River (Nakdong River)

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낙동강 중류지점에서의 동물플랑크톤 동태의 연간 변이 및 특성 (낙동강). 김현우* · 장광현[1] · 주기재[2] (순천대학교 환경교육학과, [1]에히메대학교 해양환경연구센터, [2]부산대학교 생물학과)

낙동강 중류 지점에서 (왜관, 낙동강 하구언으로부터 175 km 상류 지점) 1998년 1월부터 2002년 12월까지 동물플랑크톤 군집 동태 및 환경요인 들과의 상관관계에 대해서 조사하였다. 조사지점에서의 동물플랑크톤의 계절별 변화와 연간 변화는 매우 뚜렷하였으며 (ANOVA, $p<0.01$), 1998년과 2002년을 제외하고는 1999년부터 2001년까지 3년 동안 유사한 동물플랑크톤 양상을 나타내었다. 조사기간 동안 연 평균 윤충류의 개체수는 43±76 ind. L^{-1} (평균±s.d., n = 118)이며, 요각류 (1.6±4.8 ind. L^{-1})와 지각류 (0.4±1.2 ind. L^{-1}) 순으로 나타났다. 윤충류 군집내에서는 *Brachionus* spp., *Polyarthra* spp., *Colurella* spp., *Keratella* spp.와 *Trichocerca* spp. 등이 우점하였다. 이러한 종들은 전체 총 윤충류의 개체수에 대한 상대 풍부도의 80% 이상을 차지하였다. 조사지점 내 총 동물플랑크톤 개체수는 봄과 가을에 급격히 증가 하였으며, 겨울 동안에는 낮은 개체수를 유지하였다. 여름기간 동안, 동물플랑크톤 동태는 수문학적 요인에 의해 크게 영향을 받는 것으로 파악된다. 조사구획 내 동물플랑크톤의 동태는 내적요인 (동물플랑크톤의 먹이상태, 예: 식물플랑크톤 생체량) 보다는 외적 요인 (강의 수문학적 요인)들에 의해서 보다 더 큰 영향을 받는 것으로 사료된다.

Key words : inter-annual variation, zooplankton, rotifer, hydrology, Nakdong river

Introduction

Insofar as characteristics of river segments reflect interactions among local geomorphology, climatic gradients and spatial and temporal scales of natural disturbances (Naiman *et al*., 1991), they can induce changes in plankton biomass and community structure (Ha *et al*., 1999; Kim *et al*., 2002; Kim *et al*., 2004). Zooplankton may form an important component of the biological communities in large rivers due to their high abundances and their ability to cycle nutrients through the aquatic environment (Kobayashi *et al*., 1998). Furthermore, hydrodynamics probably play a key role in determining zooplankton dynamics in a body of flowing water (Kim and Joo, 2000). The mean water residence time and dilution effects resulting from lateral inflows from tributaries, determine the opportunities for organisms to multiply in the water column (Kim *et al*., 2002). Although zooplankton may be important in the food web of river, most studies of zooplankton have been carried out in the river-reservoir hybrid systems and restricted to sections of the river such as the lower reaches (Benfield, 1990).

Numerous factors influence the zooplankton

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community in river ecosystems. The interactions between them are so complicated, and the relative importance of the factors varies. Furthermore, the transport of zooplankton biomass from middle stretches to downstream in the river could be more important factor in the zooplankton dynamics of discontinuous running−water environments such as regulated river. However, the potential variability in zooplankton community structure of middle stretches in river channels was little understood. In contrast to zooplankton dynamics associated with lakes and reservoirs in main river channels (Shiel and Walker, 1984; Walz and Welker, 1998; Kim *et al*., 2003), the condition for zooplankton development in the middle part of the river stretches could be different.

We investigated the zooplankton dynamics in the middle stretch in the regulated river ecosystem, considering following hypothesis: zooplankton development and community structure is mainly dependent on the interaction between external conditions (e.g., hydrological factors) and internal conditions (e.g., phytoplankton biomass).

Materials and Methods

1. Description of the study site

The river shows typical characteristics of large Korean rivers, being hydrologically regulated by a series of multipurpose dams in the headwater tributaries and middle part of the river, and by barrages in the estuary (length: 528 km, total drainage area: 23,818 km^2) (Fig. 1). The consistently high nutrient levels, along with high phytoplankton biomass, would classify the lower Nakdong River as hyper−eutrophic level (Kim *et al*., 1999; Kim *et al*., 2000; Kim *et al*., 2002). The sampling station (RK 175; river kilometer; above 175 km from the estuary dam) is situated in meandering stretches where weir has been built across the river to maintain a minimum depth in the channel and facilitate water supplies since 2000 (Fig. 1). At low discharge, many of these sand and gravel banks emerge and form strips near the shore or at the head of islands. The average partial retention time of the river water in the middle stretches between RK 145 and RK 180 is about 1.0 day (Kim *et al*., 2002), but retention time varies seasonally with regulated discharges. Average phytoplankton biomass (Chl. *a*) were $12.8 \pm 12.4\ \mu g\ L^{-1}$ from 1994 to 1998. The average concentration of TN and TP were 3.9 ± 1.5 mg L^{-1} and $141 \pm 75\ \mu g\ L^{-1}$, respectively from 1994 to 1999.

2. Sampling procedures, water quality analysis and climate data

Sampling was carried out in the middle Nakdong River on biweekly intervals from 1998 to 2002. Water samples were obtained from 0.5 m depth with a Van Dorn sampler, placed into 20 L sterile polyethylene bottles, and kept in the shade at ambient temperatures until return to the laboratory. Water temperature and dissolved oxygen were measured with a YSI Model 58 meter.

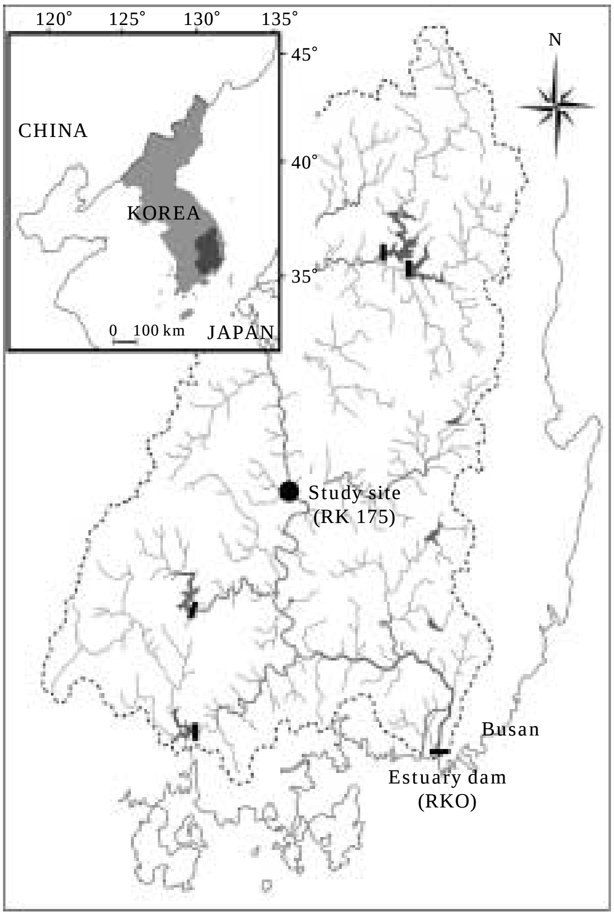

Fig. 1. Map showing the basin of the Nakdong River, major tributaries, and the study site (●: Waekwan, river kilometer 175 RK from the mouth of the river).

Turbidity was measured with Shaban model 200052. Conductivity was measured using a Fisher model 152 and alkalinity was measured by titration with 0.02 N H_2SO_4 to an end point of pH 4.5. The pH was measured using an Orion Model 407A meter. Phytoplankton biomass (Chl. *a*) was determined with a spectrophotometer using the monochromatic method described in Wetzel and Likens (2000). Local climate data (daily precipitation for the middle Nakdong river basin; Gumi) were obtained from the water management resources information system (Ministry of Construction and Transportation and Korea Water Resources Corporation).

3. Zooplankton sample collection and enumeration

For the determination of zooplankton density, 8 L samples of water were collected from 0.5 m depth. The collected water was filtered through a 35 μm mesh net, and preserved with 10% (final concentration) formalin. Zooplankton samples were gently mixed and aliquots of known volume were removed and enumerated until at least 300 animals were counted. Macrozooplankton (cladocerans and copepods) were counted at 50× magnification, and microzooplankton (rotifers) were counted at 100× magnification using an inverted microscope. Zooplankton were identified to genus or species level (with the exception of juvenile copepods and protozoa) according to Koste (1978), Smirnov and Timms (1983), Koste and Shiel (1987) and Bayly (1992).

4. Statistical analysis

Most of the data collected in this study were not normally distributed and it was not possible to correct this problem using transformations. Therefore, we used nonparametric statistics to analyze the data. A two-way nonparametric

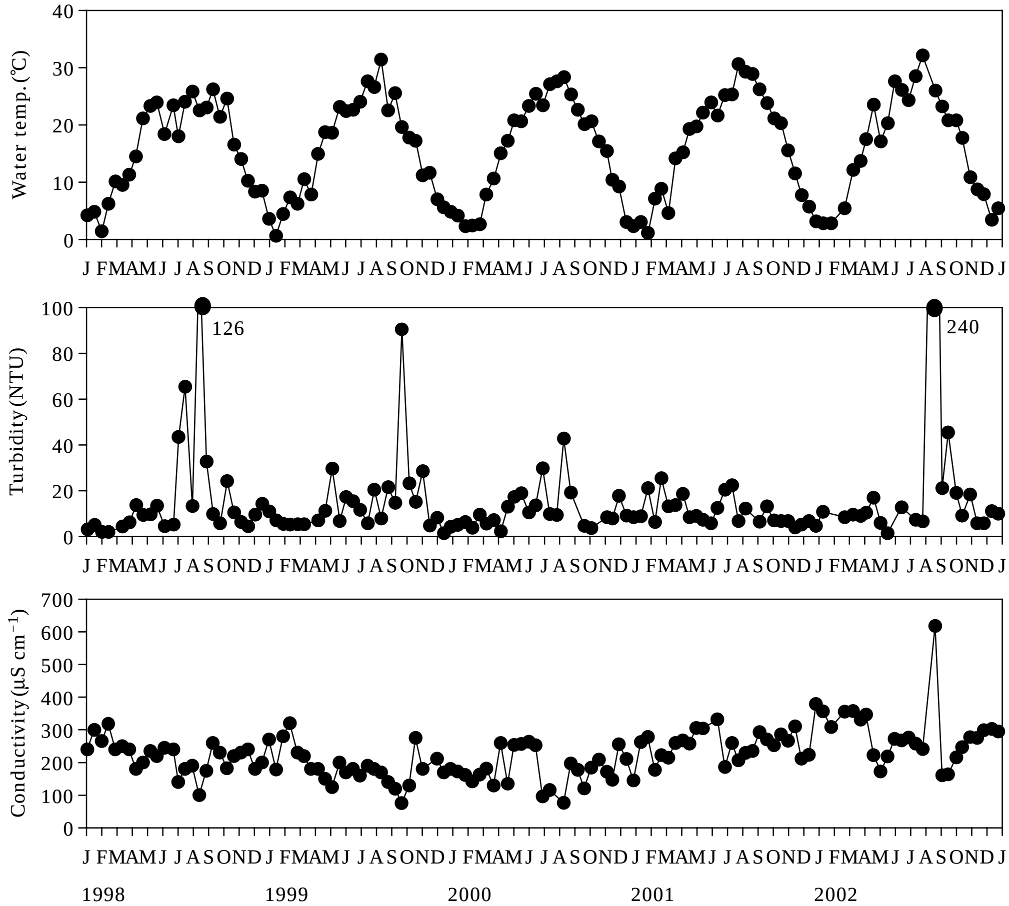

Fig. 2. Change in the basic limnological parameters (water temperature, turbidity, and conductivity) in the study site during the study period (Jan. 1998～Dec. 2002).

ANOVA was used to test for significant effects of season on the abundance of total zooplankton and major zooplankton communities. Significant differences were identified at 95% level.

Results

1. Characteristic of limnological properties and the hydrological regime

Water temperatures varied from 0.6 to 32.1°C (Table 1, Fig. 2). During spring (April ~ May) and winter (December ~ January), water temperatures were highly variable. Average pH and dissolved oxygen concentration was 7.6 ± 0.7 (5.9 ~ 10.1) and 10.8 ± 2.7 mg L^{-1} (6.1 ~ 19.7) during the study period (Table 1). Highest turbidities were observed in the summer except 2001, coincident with greater amounts of surface runoff (Fig. 3). Seasonal changes in conductivity were pronounced, with reductions occurring during summer flooding events except 2002 (Fig. 3).

In the middle part of Nakdong River basin, over 61% of the precipitation was concentrated in the summer (June ~ September) while low precipitation occurred from late fall to early spring (Fig. 3). Total rainfall amounts in 1998, 1999, 2000, 2001, and 2002 at the central part of the river basin were 744 mm, 1,180 mm, 1,103 mm, 744 mm and 1,327 mm, respectively (5 years average ± s.d. = 1,019 ± 283 mm). Total rainfall in 2002 was unusually high. Peak discharge occurred at the end of the wet season (June ~ September), while low discharges occurred in other periods of the year. There were distinct non-flooding phases. In the wet season flooding phase, water velocities sometimes were in excess of l m s^{-1}. Typically, there was a brief period of rising water in the summer, after which high discharge was maintained for several weeks.

Table 1. Means, standard deviations, and ranges of limnological parameters of the study site (Jan. 1998 ~ Dec. 2002).

	Unit	Study site (RK 175)
Temperature	°C	16.0 ± 8.6 (0.6 ~ 32.1)
pH		7.6 ± 0.7 (5.9 ~ 10.1)
Conductivity	μS cm^{-1}	225 ± 72 (76 ~ 618)
Alkalinity	mg L^{-1}	42 ± 14 (14 ~ 104)
Dissolved Oxygen	mg L^{-1}	10.8 ± 2.7 (6.1 ~ 19.7)
Dissolved Oxygen	%	108 ± 22 (58 ~ 180)
Turbidity	NTU	15 ± 25 (1.5 ~ 240)

2. The inter-annual variations of zooplankton community dynamics

The annual variation in total zooplankton abundance was significant (ANOVA, $p < 0.01$), displaying similar patterns in three years from 1999 to 2001 except 1998 and 2002. The timing and magnitude of zooplankton community occurrences appeared to be consistent across seasonal cycles. Zooplankton community in summer of 2001 and 2002 showed a contrast in abundance and development in the study site. During heavy rainfall events and floods in summer of 2002, total abundance decreased sharply (Fig. 3). Generally, after the flooding ended, total zooplankton abundance increased rapidly and recovered to pre-flood levels within 1 < month.

While macrozooplankton was restricted to young cyclops copepoids or small cladocerans (e.g., *Bosmina* and *Alona*), rotifers accounted for

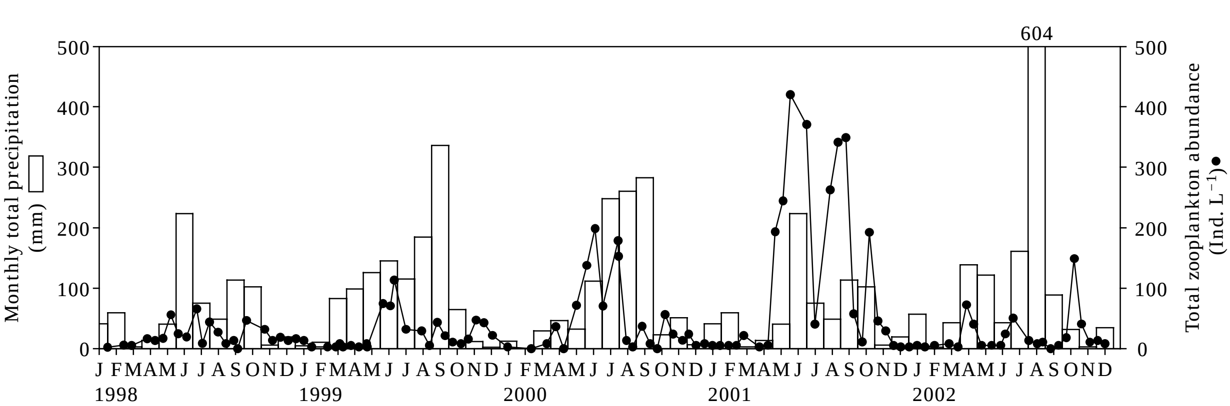

Fig. 3. Seasonal changes in total zooplankton abundances and changes of monthly total precipitation in middle basin of the river (Gumi: ~RK 195).

a large fraction of the total zooplankton abundances (Fig. 4). The annual average of microzooplankton abundance during the study period was 43±76 ind. L^{-1} (n = 118), followed by copepodids (1.6±4.8 ind. L^{-1}), small cladocerans (0.4 ±1.2 ind. L^{-1}). Cladocerans and copepods displayed similar seasonal trends as rotifers, but formed a minor part of the total zooplankton

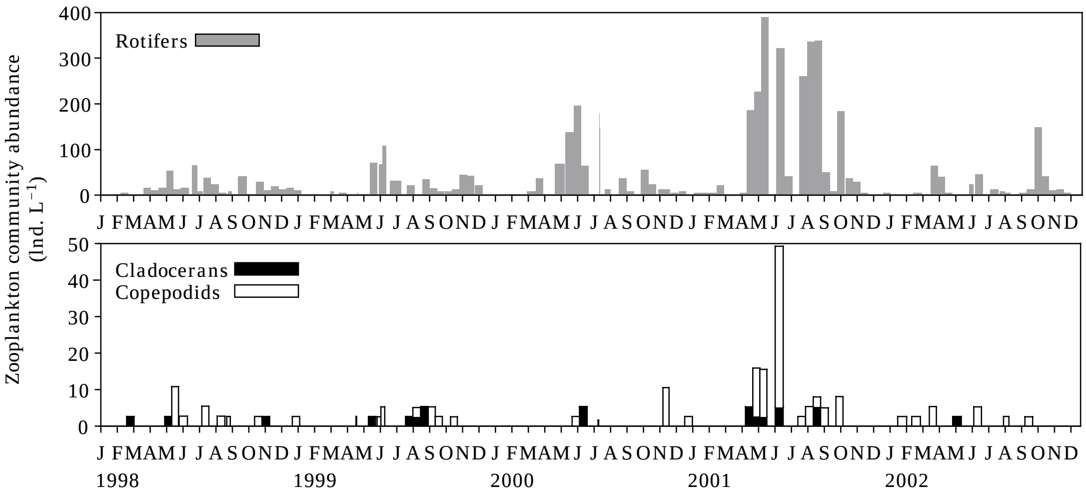

Fig. 4. Seasonal changes in rotifers and macrozooplankton community abundances in the study site (Jan. 1998～Dec. 2002).

Table 2. Dominant rotifers taxa over 1% of total zooplankton abundance in the study site (1998～2002).

Community	Taxa	1998 (n = 24)	1999 (n = 24)	2000 (n = 22)	2001 (n = 23)	2002 (n = 25)
Rotifers	*Brachionus angularis*	*	*	2.4	5.6	*
	Brachionus budapestinensis	*	*	2.6	*	*
	Brachionus calyciflorus	7.1	6.0	18.9	16.2	2.6
	Brachionus forficula	1.3	*	*	*	*
	Brachionus rubens	*	7.6	*	2.0	1.3
	Brachionus urceolaris	1.3	*	3.9	2.2	2.1
	Brachionus quadridentatus	1.2	3.0	1.1	*	*
	Colurella sp.	11.6	5.1	6.6	14.1	43.3
	Conochilus unicornis	*	*	*	1.1	*
	Filinia longiseta	3.8	2.5	6.2	*	*
	Hexarthra mira	*	*	3.0	*	*
	Keratella cochlearis	12.5	15.1	14.8	10.5	2.1
	Keratella quadrata	*	1.5	*	*	*
	Keratella valga	5.8	1.5	*	*	*
	Lecane sp.	3.8	1.0	1.1	1.1	*
	Lepadella oblonga	*	2.5	*	1.3	1.7
	Monostyla lunaris	3.2	2.5	*	*	*
	Notholca labis	2.4	1.0	*	*	*
	Philodina roseola	3.0	1.0	1.0	*	*
	Polyarthra sp.	20.9	19.7	16.5	28.8	17.5
	Pomphlx complanata	*	1.0	*	*	*
	Testudinella sp.	*	2.0	*	*	*
	Trichocerca sp.	10.6	15.2	12.8	8.4	13.7
	Trichotria tetractis	3.2	2.5	2.4	2.5	6.9
	Total No. of species	26	33	32	42	24

*indicate less than 1% of the total zooplankton abundance.

community (Fig. 4). Zooplankton occurrence with regard to abundance development was observed in the order of rotifer → macrozooplankton (cladocerans + copepodids) across the seasonal cycles.

3. The rotifer dynamics

Rotifers highly dominated the zooplankton community in the study site. In this part of the river, 42 species of rotifers were identified during 5 years (Table 2). The annual variations in rotifer abundance were significant (ANOVA, $p < 0.01$). The number of rotifer species in 2001 was much higher than that of other years (Table 2). Seasonal variations of total rotifer abundance were also significant. In spring and fall, high peaks of rotifer biomass were observed (Fig. 4).

Among the rotifers, *Brachionus* spp., *Polyarthra* spp., *Colurella* spp., *Keratella* spp., and *Trichocerca* spp. were the most common taxa. These species occupied more than 80% of the total rotifer abundance throughout the study period (Table 2). The most abundant were Brachionidae with 7 species of the genus *Brachionus* (*B. calyciflorus* and *B. rubens* were largely dominated). The genus *Polyarthra* represented up to 23% of the rotifer communities. The genus *Colurella*, *Keratella*, and *Trichocerca* contributed ~15%, ~12%, and ~10% of the total rotifer abundance, respectively.

Discussion

In comparison with zooplankton dynamics in the lower reaches of the river (Kim, 1999) and the three tributaries of the Nakdong River (Kim *et al*., 2004), there were notable differences in abundance and zooplankton community structure in study site. The annual average of total zooplankton abundance in the study site was much lower (43 ± 76 ind. L^{-1}, $n = 118$) than sites (e.g., Mulgum) in the lower reaches (Kim *et al*., 2003). De Ruyter Van Steveninck *et al*. (1992) explained that zooplankton could not maintain significant densities in the middle stretch of Rhine River, because reproductive rates cannot keep up with losses due to high flushing rates. Previous studies on zooplankton dynamics in the Nakdong River (Kim *et al*., 2004) reported that the river-reservoir hybrid system provided a stable environment for zooplankton reproduction and development and the high phytoplankton densities provide an adequate food sources to support the increasing zooplankton community (Kim and Joo, 2000). High phytoplankton biomass was considered to be one of the factors, which would lead to the high abundance of zooplankton in the river ecosystem (Kim *et al*., 2000). However, only a weak relationship existed between phytoplankton biomass and zooplankton abundances in 1998 observed in the study site.

On the other hand, climate and hydrological conditions, as a regulator of water flow, exerts an important control over fluvial communities (Admiraal *et al*., 1994). Previous study on zooplankton dynamics in the Nakdong River (Kim, 1999) also reported that local conditions (e.g., dilution rate and advective effects form major tributaries) might induce seasonal and longitudinal changes of zooplankton abundance. However, hydrologic parameters more clearly explained the seasonal and inter-annual variations of zooplankton dynamics in this study (Fig. 3).

Community structure of the middle stretch was also different from that of the lower part. In contrast to the lower part (Kim *et al*., 2004), large zooplankton like *Daphnia* was not observed in all samples, and small cladocerans (e.g., *Bosmina* and *Alona*) and rotifers were numerically dominant. Among the numerous rotifer taxa, *Brachionus* spp., *Polyathra* spp., *Colurella* spp., *Keratella* spp., and *Trichocerca* spp. were the most common in the study site. Different from cladocerans which require more time to reproduce, rotifers have very short generation time (Walz, 1995). The several species of dominant rotifers in the river channel are among the fastest growing taxa recorded in the literature (Bennet and Boraas, 1989). Rotifers are considered to be opportunistic r-strategists with a great reproductive potential (Allan, 1976). Such rapid growth is necessary to maintain positive net growth when flushing rate is relatively high in the middle stretch of the river.

Among the numerous rotifer taxa, *Brachionus* spp., *Polyathra* spp., *Colurella* spp., *Keratella* spp., and *Trichocerca* spp. were the most common in the study site. An increase in total rotifers density may indicate advancing eutrophication (Gannon and Stemberger, 1978). The high rotifer densities may indicate a high rate of energy transfer between the producers and herbivores in the lower Nakdong River (Kim *et al*., 1999).

Kim *et al.* (2002) also reported that microzooplankton was able to decrease phytoplankton concentration down to 50% in 1.2 days and bacteria in 1.5 days. Generally, *B. angularis, B. calyciflorus, K. cochlearis* and *A. fissa* (which are dominant in the lower Nakdong River) are indicators of eutrophy (Peiler and Berzins, 1989). However, the difference in total rotifer abundance (N_{mean}: less than 50 ind. L^{-1}) and dominant species, especially *Colurella* spp. and *Trichocerca* spp. between the study site and downstream (Kim, 1999) indicates that grazing by rotifers could not seriously impact phytoplankton biomass and bacteria in the study site. Considering these results on zooplankton dynamics in a river system, we suggest that branched rivers with man-made structures such as dams induce complexity in natural landscape and studies of this nature provide some insight into their ecological complexity.

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Abstract

The dynamics of zooplankton community and its relationship with environments were studied at the middle stretch (Waekwan, RK; river kilometer; above 175 km from the estuary dam) of large regulated river, Nakdong River from 1998 to 2002. There were distinct inter-annual variations and seasonal changes in total zooplankton abundance in the study site (ANOVA, $p<0.01$), displaying similar pattern in three years from 1999 to 2001 except 1998 and 2002. The annual average rotifers abundance during the study period was 43 ± 76 ind. L^{-1} (mean$\pm$s.d., $n=118$), followed by adult copepodids (1.6 ± 4.8 ind. L^{-1}), and small cladocerans (0.4 ± 1.2 ind. L^{-1}). Among the rotifers, *Brachionus* spp., *Polyarthra* spp., *Colurella* spp., *Keratella* spp., and *Trichocerca* spp. were the most common taxa. These species occupied more than 80% of the total rotifer abundance throughout the study period. Total zooplankton abundance rapidly increased in spring and fall and remained low throughout the winter. During summer, zooplankton dynamics seemed to be largely affected by hydrological parameters. Overall, rather the external factors (hydrological factors of the river) than internal factors (food condition for zooplankton such as phytoplankton biomass) appear to be responsible for changes in zooplankton dynamics in the middle stretch of the river.

References

Admiraal, W., L. Breebaart, G.M.J. Tubbing, B. van Zanten, E.D. de Ruijter van Steveninck and R. Bijkerk. 1994. Seasonal variation in composition and production of planktonic communities in the lower River Rhine. *Freshwat. Biol.* **32**: 519-531.

Allan, J.D. 1976. Life history patterns in zooplankton. *Am. Nat.* **110**: 165-180.

Bayly, I.A.E. 1992. 'The Non-marine Centropagidae (Copepoda: Calanoida) of the World.' Guides to the Identification of the Microinvertebrates of the Continental Waters of the World. No. 2. (SPB Academic Publishing: The Hague)

Benfield, L.A. 1990. The composition and distribution of zooplankton in the lower Waikato River, New Zealand. M.S. thesis. University of Waikato, Hamilton, New Zealand. 120pp.

Bennett, W.N. and M.E. Boraas. 1989. A demographic profile of the fastest growing metazoan: a strain of Brachionus calyciflorus (Rotifera). *Oikos* **55**: 365-369.

De Ruyter Van Steveninck, E.D., W. Admiraal, L. Breebaart, G.M.J. Tubbing and B. van Zanten. 1992. Plankton in the River Rhine: structural and functional changes observed during downstream transport. *J. Plankton Res.* **14**: 1351-1368.

Gannon, J.E. and R.S. Stemberger. 1978. Zooplankton (especially crustaceans and rotifers) as indicators of water quality. *Trans. Am. Micros. Soc.* **97**: 16-35.

Ha, K., E.A. Cho, H.W. Kim and G.J. Joo. 1999. Microcystis bloom formation in the lower Nakdong River, South Korea: importance of hydrodynamics and nutrient loading. *Mar. Freshwater Res.* **50**: 89-94.

Kim, H.W. 1999. Water quality, plankton community dynamics, and trophic regulation in the microbial food web by zooplankton in a hypertrophic river (Nakdong River, Korea). -Ph. D. dissertation, Pusan National University, Pusan, 230pp.

Kim, H.W. and G.J. Joo. 2000. The longitudinal distribution and community dynamics of zooplankton in a regulated large river: a case study of the Nakdong River (Korea). *Hydrobiologia*. **438**: 171−184.

Kim, H.W., K.H. Chang, K.S. Jeong and G.J. Joo. 2003. The spring metazooplankton dynamics in the river−reservoir hybrid system (Nakdong River, Korea): Its role in controlling the phytoplankton biomass. *Korean J. Limnol.* **36**: 420−426.

Kim, H.W., K.H. Chang, W.−K. Shin, G.−H. La, K.−S. Jeong and G.J. Joo. 2004. Population dynamics of predator (*Asplanchna* spp.) and its impact on herbivorous rotifers community in three tributaries of the Nakdong River (S. Korea). *Korean J. Limnol.* **37**: 385−393.

Kim, H.W., S.−J. Hwang and G.J. Joo. 1999. Grazing rates of rotifers and their contribution to community grazing in the Nakdong River. *Korean J. Ecol.* **22**: 337−342.

Kim, H.W., S.−J. Hwang and G.J. Joo. 2000. Zooplankton grazing on bacteria and phytoplankton in a regulated large river (Nakdong River, Korea). *J. Plankton Res.* **22**: 1559−1577.

Kim, H.W., S.−J. Hwang, K.H. Chang, M.H. Jang, G.J. Joo and N. Walz. 2002. Longitudinal difference in zooplankton grazing on phyto− and bacterioplankton in the Nakdong River (Korea). *Internat. Rev. Hydrobiol.* **87**: 281−293.

Kobayashi, T., R.J. Shiel, P. Gibbs and P.I. Dixon. 1998. Freshwater zooplankton in the Hawkesbury −Nepean River: comparison of community structure with other rivers. *Hydrobiologia* **377**: 133−145.

Koste, W. 1978. Rotatoria. Die Radertiere Mitteleuropas. Ein Bestimmungswerk begrundet von Max Voigt, 2nd edn. (Borntrager: Stuttgart, Vol. 1, Textband 673p., Vol. 2. Textband 234p.)

Koste, W. and R.J. Shiel. 1987. Rotifera from Australian inland waters II. Epiphanidae and Brachionidae (Rotifera: Monogononta). Invertebrate Taxonomy 1, 949−1021.

Naiman, R.J., J.A. Stanford and H. Decamps, 1991. The application of ecological knowledge to river management. In What large rivers for the future? Meeting of the 'Ministere de l'Environement', Orlecans, France, 55pp.

Peiler, B. and B. Berzins. 1989. On choice of substrate and habitat in brachionid rotifers. *Hydrobiologia* **186/187**: 137−144.

Shiel, R.J. and K.F. Walker. 1984. Zooplankton of regulated and unregulated rivers: The Murray−Darling river system, Australia, *in*: Regulated rivers− *In*: A. Lillehammer and S.J. Saltveit (eds.), Univ. Oslo., pp. 263−270.

Smirnov, N.N. and B.V. Timms. 1983. A revision of the Australian Cladocera (Crustacea). Records of the Australian Museum Supplement **1**: 1−132.

Walz, N. 1995. Rotifer populations in plankton communities: Energetics and life history strategies. *Experientia* **51**: 437−453.

Walz, N. and M. Welker. 1998. Plankton development in a rapidly flushed lake in the River Spree system (Neuendorfer See, Northeast Germany). *J. Plankton. Res.* **20**: 2071−2087.

Wetzel, R.G. and G.E. Likens. 2000. Limnological Analyses, 3rd edn. Springer−Verlag. New York. 429p.

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