



Stable carbon isotope signatures of zooplankton in some reservoirs in Korea

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Abstract

Dissolved organic carbon (DOC) concentrations and zooplankton and particulate organic matter (POM) $\delta^{13}\text{C}$ values were measured in five reservoirs in Korea. Zooplankton $\delta^{13}\text{C}$ and POM $\delta^{13}\text{C}$ showed large range from -33‰ to -22‰ and a significant difference among the reservoirs. One eutrophic reservoir, Lake Masan, showed unique characteristics with the highest zooplankton density, the highest $\delta^{13}\text{C}$, and the highest DOC. Zooplankton $\delta^{13}\text{C}$ was similar to POM $\delta^{13}\text{C}$, implying that zooplankton occupies substantial portion of POM or that zooplankton isotopic composition is related to selective grazing and assimilation of food sources from bulk POM. Except Lake Masan zooplankton $\delta^{13}\text{C}$ values were negatively correlated to DOC concentration in four reservoirs with mostly forest land use. This pattern can be probably attributed to intensive agricultural land use in the watershed of Lake Masan compared to the mostly forest land use in the other watersheds. Understanding the relationship between zooplankton $\delta^{13}\text{C}$ values and the origin of organic matter associated with watershed characteristics will be valuable to better understand trophic relationships in reservoirs in the summer monsoon region.

Key words: DOC, POM, stable carbon isotopes, watershed, zooplankton

INTRODUCTION

Small reservoirs are important for use as agricultural water supplies, flood control and power generation in many areas throughout the east-Asia monsoon region. These reservoirs provide opportunities for comparative studies of patterns and processes in small lake ecosystems in a variety of climatic and landscape settings. Perhaps the most distinctive characteristic in the typical seasonal pattern in lakes and reservoirs in Korea is the input of large amounts of allochthonous nutrients and organic matter during the summer monsoon (Lee et al. 2013). In Korea, monsoon rainfall can occur from July to September, with the other seasons generally being much

drier. During intense monsoon rain events, the nutrient and organic matter inputs to reservoirs from watersheds increases dramatically with increases in stream discharge. The input of large amounts of allochthonous nutrients and organic matter can greatly impact the biology and chemistry of reservoirs, even for a substantial period following the summer monsoon (here referred to as post-monsoon) (Kim et al. 2000, Li et al. 2008, Lee et al. 2013). The elevated inputs of nutrients and organic matter often results in post-monsoon cyanobacteria blooms (especially *Microcystis* spp.) and high chlorophyll-*a* concentrations (Kim et al. 2000, Lee et al. 2010).

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In general, phytoplankton is a preferred food source for zooplankton, but zooplankton may not be able to directly use only phytoplankton as a food source because some cyanobacteria are inedible and the elevated POM concentration likely results from the increase in input of terrestrial organic matter during the monsoon season (Lee et al. 2013, De Kluijver et al. 2012). Some cyanobacteria can be unsuitable as a food source for herbivorous zooplankton and inhibit not only feeding ability but also zooplankton growth (Chen et al. 2005).

Seasonal changes in the zooplankton community in some temperate lakes are associated with increases in *Microcystis* abundance (Kim et al. 2000, Lee et al. 2010). The typical temporal pattern in zooplankton dominance is a sudden change from cladocerans to small zooplankton such as copepods or rotifers with the appearance of *Microcystis* (Kim et al. 2000, Lee et al. 2010). In some lakes, the seasonal variation in zooplankton $\delta^{13}\text{C}$ values can be explained by changes in the relative proportions of phytoplankton and terrestrial organic matter in zooplankton diets (Grey et al. 2000, Gu et al. 2006). In lakes where a significant fraction of the organic matter originates from the watershed, zooplankton isotopic composition provides information about the contribution of carbon from allochthonous sources to the lake versus carbon derived via primary production in the lake. Studies using stable isotopes have shown that zooplankton production is supported by both allochthonous and autochthonous sources of carbon, with the higher fraction of carbon from autochthonous sources in more eutrophic lakes (Del Giorgio and France 1996, Schindler et al. 1997, Grey et al. 2000). Some studies have concluded that zooplankton production in temperate lakes may acquire a large fraction of their energy from allochthonous inputs through heterotrophic activity (Pace et al. 2004, Rautio et al. 2011, Cole et al. 2011). Therefore, we can gain some insight to the pathways of carbon transfer by comparing differences in zooplankton grazing activity, which probably plays an important role in mediating the transfer of terrestrial carbon to higher trophic levels.

The zooplankton community regulates energy flow from producers to upper trophic levels in lake ecosystems (Jeppesen et al. 2003, Hessen 2008, Santana et al. 2009). Analysis of zooplankton stable isotope composition can be useful because zooplankton have short turnover times and respond rapidly to environmental changes (Browne 1981, Schindler et al. 1997).

Using carbon stable isotopes to follow the flow of carbon in food webs has two advantages over other methods. First, the ratio of ^{13}C and ^{12}C in a consumer's tissue

reflects relatively long-term diet because stable isotopes effectively integrate the consumer's feeding history. Second, consumer tissue stable isotope composition reflect only materials actually assimilated and incorporated into tissue, as opposed to the total material ingested, as long as the gut contents are removed before analysis.

In this study, we compared zooplankton and POM $\delta^{13}\text{C}$ values with DOC concentration in five reservoirs which are impacted by the elevated loads of nutrients and organic matter received during the summer monsoon season in Korea. In reservoirs with large inputs of nutrients and organic matter during summer monsoon storms, zooplankton $\delta^{13}\text{C}$ values are likely most closely controlled by selective zooplankton grazing in the post-monsoon season (Kankaala et al. 2010, De Kluijver et al. 2012). The reservoirs selected for this study commonly experience cyanobacteria blooms following the monsoon season (post-monsoon). The objective of this study was to investigate the differences in zooplankton $\delta^{13}\text{C}$ and POM $\delta^{13}\text{C}$ values and the relationship between zooplankton $\delta^{13}\text{C}$ values and DOC concentration among five reservoirs with different proportions of agricultural land use in their watersheds.

MATERIALS AND METHODS

Study sites

We surveyed five reservoirs, including oligo-mesotrophic (BG, Byeokgye; JY, Jinyang; KP, Keumpung) and eutrophic reservoirs (JS, Jusan; MS, Masan) (Fig. 1). The reservoirs are largely (greater than 70%) surrounded by hardwood forest except for MS (Table 1). MS is located in an agricultural area. The watershed of JS is mostly forested, without major anthropogenic activity. MS has about 42% of the total watershed as forest land, compared with the other watersheds having <20% of their watershed area used for agriculture (Table 1).

Field sampling and analysis

Water samples for nutrient analysis were collected at the surface (0.1 m depth) during the post-monsoon season (September through October 2009). At each site, the following water quality parameters were measured in situ: pH meter (Denver Instrument Company, Arvada, CO, USA), YSI 55 dissolved oxygen meter (YSI Inc., Yellow Springs, OH, USA), and 2100P turbidimeter (Hach Co., Ames, IA, USA). Dissolved organic carbon (DOC), total

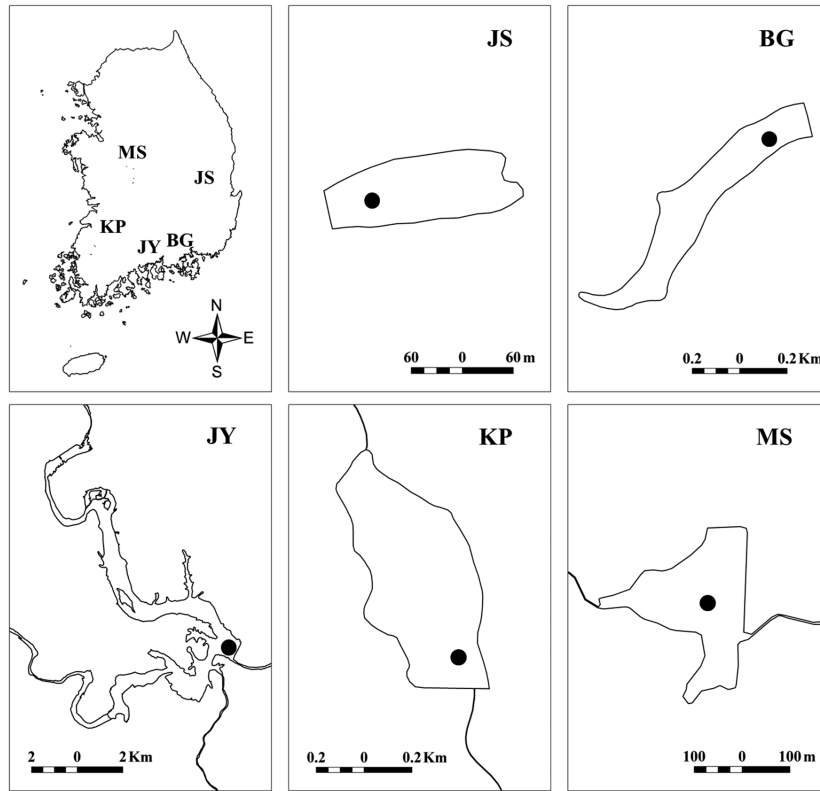


Fig. 1. Location of the study sites. JS, Jusan; BG, Byeokgye; JY, Jinyang; KP, Keumpung; MS, Masan.

phosphorus (TP) and total nitrogen (TN) concentrations were measured in the laboratory on unfiltered samples. Samples for determination of TP and TN concentrations were acidified with 18N H₂SO₄ and refrigerated until analysis. TP concentration was measured using the ascorbic acid method according to APHA (1998). TN concentration was measured by cadmium reduction after digestion with persulfate (APHA, 1998). DOC concentrations were measured using a TOC-5000A analyzer (Shimadzu, Kyoto, Japan). Chlorophyll-*a* concentrations (Chl-*a*) were mea-

sured after extraction with 90% acetone on GF/F filters (Whatman, Kent, UK).

Stable isotope analysis

Samples for zooplankton analysis were collected near the center of each reservoir using a net for a Schindler-Patalas trap with a 63µm Nitex mesh (Wildco, Yulee, FL, USA) for zooplankton. A separate sample was collected for phytoplankton analysis using a Van Dorn sampler

Table 1. Location and land use in the watersheds of study reservoirs

Lake	Location	Dry field (%)	Paddy field (%)	Forest (%)	Miscellaneous (%)
JS	N36°21'75" E129°11'34"	-	-	100.0	-
BG	N35°25'58" E128°13'09"	0.9	1.0	93.4	4.7
JY	N35°09'34" E128°01'27"	12.3	8.2	74.6	4.9
KP	N35°24'56" E127°23'57"	11.6	6.1	71.7	10.6
MS	N36°46'27" E126°58'46"	25.6	19.8	42.0	12.6

(Wildco) at the surface (0.1 m). To separate zooplankton from suspended particulate matter, samples were kept refrigerated and separated by gravity in a 3 L cylinder for 12 hours and filtered using a 200 µm mesh sieve and a distilled water rinse.

POM samples were collected using a Van Dorn sampler at discrete depths. Samples were pre-filtered through a 45 µm mesh net to remove zooplankton and then filtered using pre-combusted (450°C) GF/F filters. Phytoplankton samples were concentrated in the field using the plankton net with a 63 µm mesh (Wildco). The bulk phytoplankton which settled to the bottom of a cylinder was separated from suspended particulate organic matter and zooplankton with 200 µm and 45 µm mesh nets. Samples for stable isotope analysis were freeze dried and pulverized with a mill. Sediment samples were fumigated in desiccator (1 N HCl) for 4 hours and dried at 45 °C to remove inorganic carbon.

Carbon stable isotope composition was analyzed using an Isoprime (GV Instruments) Isotope Ratio Mass Spectrometer (IRMS) coupled with an Elementar Vario EL Cube Elemental Analyzer (EA) (Isoprime Ltd., Cheadle, UK). The stable isotope results are presented as the difference between the sample and an international standard (VPDB, Vienna Pee Dee Belemnite): $X (\text{‰}) = [R_{\text{sample}}/R_{\text{standard}} - 1] \times 10^3$, where X is the parts per thousand (‰) difference from a standard. R is the ratio of heavy (¹³C) to light isotope (¹²C). The precision for repeated sample measurement was better than ±0.3‰.

Statistical analyses

SigmaPlot ver. 11.0 (Systat Software Inc., San Jose, CA, USA) was used for statistical analyses. Regression analysis was used to test the relationships between DOC and isotopic composition of POM and zooplankton.

RESULTS

Reservoir chemistry

The surface water pH of the study reservoirs ranged from 6.0 to 9.1 and DO concentrations ranged from 2.2 mg/L to 14.3 mg/L (Table 2). The range of surface water pH in KP and JS (pH 6.0-6.7) was slightly lower than in the other reservoirs (pH 6.8-9.1). These two reservoirs also had the low DO concentrations (2.2-8.5 mg/L). DOC concentrations varied from 2.2 mg C/L to 5.2 mg C/L, with JS and MS having the high DOC concentrations (Table 2).

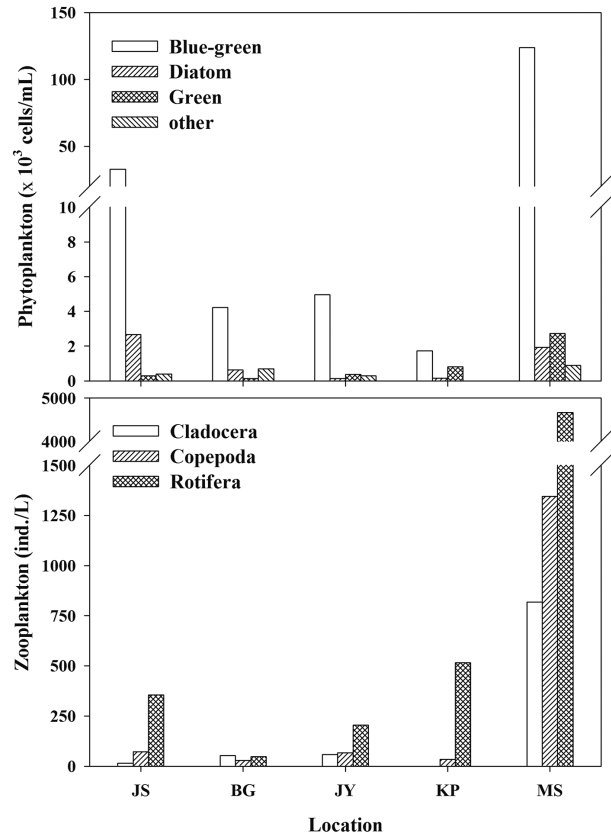


Fig. 2. Phytoplankton and zooplankton populations in the study reservoirs.

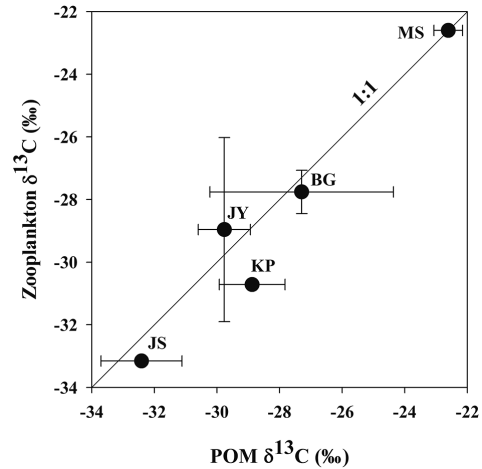
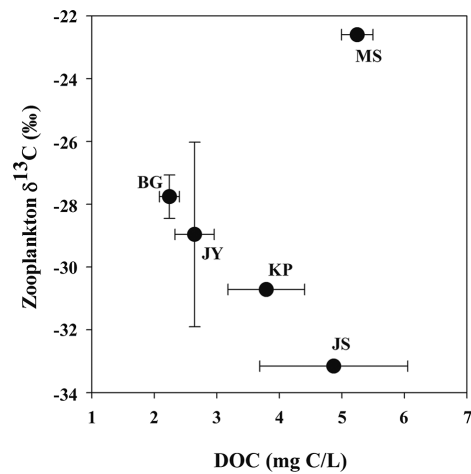
The Chl-*a* concentrations of surface waters ranged from 6 mg/L to 26.5 mg/L, except in MS showing 95.2 ± 12.0 (mean ± SD) mg/L in Table 2.

Zooplankton and phytoplankton communities

Zooplankton and phytoplankton density was mainly composed of rotifera and blue-green algae (cyanobacteria), respectively (Fig. 2) in all reservoirs. The dominant zooplankton species in JS, BG, and KP were the copepods (*Cyclops vicinus*, *Thermocyclops* sp., and *Mesocyclops* sp.). The zooplankton community in MS and JY were dominated by a kind of rotifera (*Asplanchna* sp.) and copepoda (*Eodiaptomus* sp.), respectively. The dominant phytoplankton were cyanobacteria species such as *Chroococcus minutus* (sites BG and JY), *Phormidium* sp. (site MS), *Microcystis* sp. (site JS) and *Coelosphaerium* sp. (site KP). The predominant feature of seasonal succession in the phytoplankton community is the occurrence of cyanobacteria blooms after summer monsoon.

Table 2. Water chemistry of the study reservoirs (SD, Secchi disc transparency; DO, dissolved oxygen; DOC, dissolved organic carbon; Chl-*a*, chlorophyll *a*; TN, total nitrogen; TP, total phosphorus concentration)

Date	Lake	Maximum Depth (m)	Watershed area (km ²)	Surface area (km ²)	SD (m)	DO (mg/L)	pH	DOC (mg C/L)	Chl- <i>a</i> (mg/m ³)	TN (mg/L)	TP (mg/m ³)
Sep/14	Jusan (JS)	7.8	2	0.02	1.0	5.6 ± 2.4	6.4 ± 0.3	4.9 ± 1.1	22.6 ± 7.4	1.06 ± 0.88	42 ± 9
Sep/17	Byeokgye (BG)	13.0	10	0.20	3.5	6.7 ± 2.9	7.3 ± 0.4	2.3 ± 0.2	5.5 ± 4.2	0.57 ± 0.14	14 ± 6
Sep/17	Jinyang (JY)	7.5	2,285	23.6	2.7	6.0 ± 1.8	7.5 ± 0.2	2.8 ± 0.4	5.8 ± 2.7	0.84 ± 0.05	23 ± 8
Oct/16	Keumpung (KP)	9.5	11	0.50	0.9	5.5 ± 2.3	6.3 ± 0.3	3.8 ± 0.6	26.5 ± 8.0	1.39 ± 1.11	36 ± 16
Sep/18	Masan(MS)	2.5	18	0.80	0.6	10.4 ± 2.5	8.5 ± 0.5	5.1 ± 0.2	95.2 ± 12.0	1.63 ± 0.18	114 ± 11

**Fig. 3.** Comparison of zooplankton $\delta^{13}\text{C}$ and POM $\delta^{13}\text{C}$ in the study reservoirs.**Fig. 4.** Relationship between zooplankton $\delta^{13}\text{C}$ and DOC concentration in the study reservoirs.

Relationship of zooplankton $\delta^{13}\text{C}$ and POM $\delta^{13}\text{C}$ among reservoirs

Zooplankton $\delta^{13}\text{C}$ values and POM $\delta^{13}\text{C}$ values ranged from -33.2‰ to -22.6‰, from -32.4‰ to -22.6‰, respectively (Fig. 3). There was a positive relationship between zooplankton $\delta^{13}\text{C}$ values and POM $\delta^{13}\text{C}$ values (Fig. 3). For the four reservoirs with relatively higher proportion of forested land use (BG, JY, JS and KP), zooplankton $\delta^{13}\text{C}$ values were negatively related to DOC concentration. Zooplankton $\delta^{13}\text{C}$ values differed between MS and JS despite having similar DOC concentrations (Fig. 4).

DISCUSSION

Relationship between zooplankton $\delta^{13}\text{C}$ and POM $\delta^{13}\text{C}$

This general difference we found in zooplankton $\delta^{13}\text{C}$ values is similar to the results of previous studies showing higher zooplankton $\delta^{13}\text{C}$ values in reservoirs affected by agricultural inputs than in reservoirs surrounded by forested land (Gu et al. 1994, Yoshioka et al. 1994). Zooplankton $\delta^{13}\text{C}$ values were significantly higher in MS with the major land use as agricultural land than in the other reservoirs with mostly forested land use (Figs. 2 and 3). Bacterial utilization of allochthonous organic matter derived from the watershed introduces a carbon source for zooplankton production, which may replace carbon sources such as phytoplankton production as a carbon source for zooplankton in reservoirs with forested land use (Salonen and Hammar 1986). Jones et al. (1999) reported that zooplankton $\delta^{13}\text{C}$ showed a significant trend towards greater ^{13}C enrichment with increasing Chl-*a* concentration in the forest oligotrophic lakes in southern Finland. This is because phytoplankton $\delta^{13}\text{C}$ values are affected by primary production, the isotopic composition of CO_2 and pH. Phytoplankton $\delta^{13}\text{C}$ values are high in lakes with high Chl-*a* concentration compared to others with low Chl-*a* concentration and thus zooplankton in these lakes have higher $\delta^{13}\text{C}$ values reflecting the isotopic composition of phytoplankton which zooplankton feed.

Our findings support the idea that zooplankton $\delta^{13}\text{C}$ values are useful indicators of food source and watershed land use (Del Giorgio and France 1996, Jones et al. 1999). Studies from other regions provide examples of the relationship between the stable isotopic composition of lake and reservoir biota and trophic conditions. For example, in several subarctic lakes, zooplankton $\delta^{13}\text{C}$ values were lower than in urban eutrophic lakes (Rautio and Vincent 2007).

In our study, zooplankton $\delta^{13}\text{C}$ values and POM $\delta^{13}\text{C}$ values were positively correlated (Fig. 3). The difference between zooplankton $\delta^{13}\text{C}$ values and POM $\delta^{13}\text{C}$ values in the five reservoirs was small, indicating that zooplanktons directly utilize POM as a food source. Hou et al. (2013) investigated the relationship between zooplankton $\delta^{13}\text{C}$ values and POM $\delta^{13}\text{C}$ values in eighteen lakes in China and found a positive correlation, also indicating the dependence of zooplankton on POM in their diet.

The phytoplankton community in our study reservoirs is dominated by blue-green algae (cyanobacteria) (Fig. 2). If inedible cyanobacteria are dominant in the phytoplank-

ton community, then zooplankton need to selectively graze for other edible food sources. During cyanobacteria blooms, POM $\delta^{13}\text{C}$ values may be higher than other phytoplankton $\delta^{13}\text{C}$ values (Vuorio et al. 2006). Lee et al. (2010) showed that after an increase in *Microcystis* abundance, macrozooplankton such as *Daphnia galeata* and *C. vicinus* disappeared and the microzooplankton (*Bosmina longirostris*) and rotifer populations were significantly reduced in eutrophic lakes (Kim et al. 1999, Lee et al. 2013). In our study, the small difference between zooplankton $\delta^{13}\text{C}$ values and POM $\delta^{13}\text{C}$ values might be explained by differences in the proportion of autochthonous and allochthonous inputs and the isotopic composition of phytoplankton which zooplankton feed on (Cole et al. 2011).

The lower zooplankton $\delta^{13}\text{C}$ values compared to food sources such as bulk POM in these reservoirs is similar to the pattern found for lakes worldwide and reflects the importance of allochthonous inputs (Del Giorgio and France 1996, Grey et al. 2000). Some studies have indicated that the relative depletion in ^{13}C of pelagic consumers compared to their POM as food source in lake ecosystems reflects the food selectivity of zooplankton for phytoplankton rather than the bulk POM, which has higher $\delta^{13}\text{C}$ values due to the presence of terrestrial detritus (Del Giorgio and France 1996, France et al. 1997). Most allochthonous organic matter is more refractory compared to autochthonously produced POM (Tranvik 1989).

In our study, the values of zooplankton $\delta^{13}\text{C}$ and POM $\delta^{13}\text{C}$ values between two reservoirs, MS and JS clearly showed different patterns (Fig. 3). This pattern is similar to the results from Jones et al. (1999) showing that zooplankton $\delta^{13}\text{C}$ values differed with the trophic conditions of the lakes they studied.

In reservoir JS, we found that zooplankton $\delta^{13}\text{C}$ values and POM $\delta^{13}\text{C}$ values were low even though Chl-*a* concentrations in JS were higher than in the other reservoirs with mostly forest land use. POM can include phytoplankton, allochthonous organic matter, protozoa and bacteria. Phytoplankton $\delta^{13}\text{C}$ values are affected by CO_2 availability, the isotopic composition of CO_2 and growth rate (Doi et al. 2006, Gu et al. 2006). Some studies have found that elevated dissolved CO_2 concentrations and low pH resulted in a low phytoplankton and zooplankton $\delta^{13}\text{C}$ values (Rau 1978, Yoshioka et al. 1994, Lee et al. 2011). Lakes with a high proportion of forest land use in their watersheds such as the four of the reservoirs (JS, BG, JY and KP) in this study are likely to be more heterotrophic ecosystems, receiving considerable inputs of allochthonous organic matter. Other studies have shown that the biomass and productivity of heterotrophic plankton

(bacteria and zooplankton) are often much greater than that of phytoplankton (Hessen et al. 1989, Del Giorgio et al. 1997). Many lakes can have high respiration rates of zooplankton and low P/R ratios (the ratio between gross production and community respiration) (Del Giorgio and Peters 1994, Lee et al. 2011). Del Giorgio and Peters (1994) have reported that plankton community respiration was larger than productivity in oligo- and mesotrophic lakes, indicating the importance of external sources of organic matter. Low plankton P/R ratios show the overwhelming contributions of watershed-derived particulate organic matter as a source of CO₂ (Cole et al. 2011). CO₂ produced from the decomposition of terrestrial organic matters might also be expected to have lower plankton δ¹³C values.

In general, a high rate of CO₂ uptake by primary producers will result in an increase in pH and a switch in inorganic C speciation from aqueous carbon dioxide, as a dissolved gas (CO_{2(aq)}) to HCO₃⁻ (Gu et al. 2006). Uptake of respired CO_{2(aq)} will cause phytoplankton δ¹³C values to become isotopically depleted in ¹³C (lower phytoplankton δ¹³C values) compared to it of phytoplankton using inorganic carbon which has not been previously assimilated (Keough et al. 1996, Lee et al. 2011). Rautio and Vincent (2007) showed that regional differences in POM δ¹³C values could be also explained by pH, with primary producer δ¹³C values showing higher values in lakes with high alkalinity and pH than in others. This mechanism could provide a clue for the low zooplankton δ¹³C values in reservoir JS in our study.

Our finding that zooplankton δ¹³C values are negatively related to DOC concentration agrees with results of other studies in humic lakes. Zooplankton δ¹³C values decrease with increasing DOC concentration and increase with increasing productivity and phytoplankton biomass (France et al. 1997, Lennon et al. 2006). Li (2007) also showed that zooplankton δ¹³C values decreased with increasing DOC concentration. This is explained by zooplankton utilization of ¹³C-depleted food sources such as methanotrophic bacteria, and therefore, less consumption of phytoplankton and/or POM with higher δ¹³C values. Methanotrophic bacteria can be an important carbon source for filter feeders feeding zooplankton in agricultural reservoirs (Cry 1998). However, in our study, copepods dominated in four agricultural reservoirs, though not in Lake Masan (MS), and utilized preferable particulate organic matter (e.g., phytoplankton).

Some of the methane is oxidized to CO₂ at the metalimnetic oxic-anoxic interface and is partly incorporated into microbial biomass. Phytoplankton can utilize inorganic carbon derived from methanotrophic bacteria, with lower

δ¹³C values (as mentioned above). Allochthonous inputs of POM and DOC to reservoirs can be mineralized and affect zooplankton δ¹³C values through the food web. In our study reservoirs, MS, unlike the other reservoirs, is most likely to have a high proportion of DOC derived from autochthonous sources (phytoplankton production).

CONCLUSION

In our study of five agricultural reservoirs (JS, BG, JY, KP and MS), zooplankton δ¹³C showed large variation from -33‰ to -22‰. One eutrophic reservoir, Lake Masan, had a pattern different from the other reservoirs, showing that zooplankton δ¹³C decreased with increasing DOC concentration. With this exception, the results of this study are consistent with results of other studies showing an inverse relationship between zooplankton δ¹³C values and DOC concentrations (France et al. 1997, Jones et al. 1999, Lennon et al. 2006, Persaud et al. 2009). In this study, the difference in zooplankton δ¹³C values between Lake Jusan and Lake Masan is most likely caused by differences in sources of organic matter related to the difference in the land use in the watershed (Jones et al. 1999). Future studies on reservoirs in Korea should further investigate carbon sources and elemental stoichiometry together with stable isotope techniques to understand the relationships between watershed characteristics and trophic conditions.

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LITERATURE CITED

- APHA, AWWA, WEF. 1998. Standard Methods for the Examination of Water and Wastewater, 20th ed. American Public Health Association, Washington, DC.
- Browne RA. 1981. Lakes as islands: biogeographic distribu-

- tion, turnover rates, and species composition in the lakes of central New York. *J Biogeography* 8: 75-83.
- Chen FZ, Xie P, Tang HJ, Liu H. 2005. Negative effects of *Microcystis* blooms on the crustacean plankton in an enclosure experiment in the subtropical China. *J Environ Sci* 17: 775-781.
- Cole JJ, Carpenter SR, Kitchell J, Pace ML, Solomon CT, Wetzel B. 2011. Strong evidence for terrestrial support of zooplankton in small lakes based on stable isotopes of carbon, nitrogen, and hydrogen. *Proc Natl Acad Sci USA* 108: 1975-1980.
- Cyr H. 1998. Cladoceran- and copepod- dominated zooplankton communities graze at similar rates in low-productivity lakes. *Can J Fish Aquat Sci* 55: 414-422.
- Del Giorgio PA, Cole JJ, Cimbleris A. 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. *Nature* 385: 148-151.
- Del Giorgio PA, France RL. 1996. Ecosystem-Specific patterns in the relationship between zooplankton and POM or microplankton $\delta^{13}\text{C}$. *Limnol Oceanogr* 41: 359-365.
- Del Giorgio PA, Peters RH. 1994. Patterns in planktonic P:R ratios in lakes: influence of lake trophy and dissolved organic carbon. *Limnol Oceanogr* 39: 772-787.
- De Kluijver A, Yu J, Houtekamer M, Middelburg JJ, Liu Z. 2012. Cyanobacteria as a carbon source for zooplankton in eutrophic Lake Taihu, China, measured by ^{13}C labeling and fatty acid biomarkers. *Limnol Oceanogr* 57: 1245-1254.
- Doi H, Zuykova EI, Kikuchi E, Shikano S, Kanou K, Yurlova N, Yadrenkina E. 2006. Spatial changes in carbon and nitrogen stable isotopes of the plankton food web in a saline lake ecosystem. *Hydrobiologia* 571: 395-400.
- France RL, Del Giorgio PA, Westcott KA. 1997. Productivity and heterotrophy influences on zooplankton $\delta^{13}\text{C}$ in northern temperate lakes. *Aquat Microb Ecol* 12: 85-93.
- Grey J, Jones RI, Sleep D. 2000. Stable isotope analysis of the origins of zooplankton carbon in lakes of differing trophic state. *Oecologia* 123: 232-240.
- Gu B, Chapman AD, Schelske CL. 2006. Factors controlling seasonal variations in stable isotope composition of particulate organic matter in a soft water eutrophic lake. *Limnol Oceanogr* 51: 2837-2848.
- Gu B, Schell DM, Alexander V. 1994. Stable carbon and nitrogen isotope analysis of the plankton food web in a sub-arctic lake. *Can J Fish Aquat Sci* 51: 1338-1344.
- Hessen DO, Andersen T, Lyche A. 1989. Differential grazing and resource utilization of zooplankton in a humic lake. *Arch Hydrobiol* 114: 321-347.
- Hessen DO. 2008. Efficiency, energy and stoichiometry in pelagic food webs; reciprocal roles of food quality and food quantity. *Freshw Rev* 1: 43-57.
- Hou W, Gu B, Zhang H, Gu J, Han BP. 2013. The relationship between carbon and nitrogen stable isotopes of zooplankton and select environmental variables in low-latitude reservoirs. *Limnology* 14: 97-104.
- Jeppesen E, Jensen JP, Jensen C, Faafeng B, Hessen DO, Sondergaard M, Lauridsen T, Brettum P, Christoffersen K. 2003. The impact of nutrient state and lake depth on top-down control in the pelagic zone of lakes: a study of 466 lakes from the temperate zone to the arctic. *Ecosystems* 6: 313-325.
- Jones RI, Grey J, Sleep D, Arvola L. 1999. Stable isotope analysis of zooplankton carbon nutrition in humic lakes. *Oikos* 86: 97-104.
- Kankaala P, Taipale S, Li L, Jones RI. 2010. Diets of crustacean zooplankton, inferred from stable carbon and nitrogen isotope analyses, in lakes with varying allochthonous dissolved organic carbon content. *Aquat Ecol* 44: 781-795.
- Keough JR, Sierszen ME, Hagley CA. 1996. Analysis of a Lake Superior coastal food web with stable isotope techniques. *Limnol Oceanogr* 41: 136-146.
- Kim B, Choi KS, Lee UH, Kim UH. 2000. Effects of the summer monsoon on the distribution and loading of organic carbon in a deep reservoir, Lake Soyang, Korea. *Water Res* 14: 3495-3504.
- Kim B, Kim JO, Jun MS, Hwang SJ. 1999. Seasonal dynamics of phytoplankton and zooplankton community in Lake Soyang. *Korean J Limnol* 32: 127-134.
- Lee J, Kim J, Jung Y, Kim B. 2010. Isotopic differences among zooplankton taxa and seasonal variation of zooplankton community coexisting with *Microcystis*. *Kor J Ecol Environ* 43: 1-10. (in Korean)
- Lee J, Yoshioka T, Ra K, Owen J, Kim B. 2011. Stable carbon and nitrogen isotope composition of co-existing herbivorous zooplankton species in an oligo-dystrophic lake (Shirakoma-ike, Japan). *N Z J Mar Freshw Res* 45: 29-41.
- Lee JY, Kim JK, Owen JS, Choi Y, Shin K, Jung S, Kim B. 2013. Variation in carbon and nitrogen stable isotopes in POM and zooplankton in a deep reservoir and relationship with hydrological characteristics. *J Freshw Ecol* 28: 47-62.
- Lennon JT, Faiia AM, Feng X, Cottingham KL. 2006. Relative importance of CO_2 recycling and CH_4 pathways in lake food webs along a dissolved organic carbon gradient. *Limnol Oceanogr* 51: 1602-1613.
- Li L. 2007. Variation in zooplankton diets in contrasting small lakes, inferred from stable isotope analyses. MS thesis. University of Jyväskylä, Jyväskylä, Finland.
- Li W, Wu F, Liu C, Fu P, Wang J, Mei Y, Wang L, Guo J. 2008.

- Temporal and spatial distributions of dissolved organic carbon and nitrogen in two small lakes on southwestern China Plateau. *Limnology* 9: 163-171.
- Pace M L, Cole JJ, Carpenter SR, Kitchell JF, Hodgson JR, Van de Bogert MC, Bade DL, Kritzberg ES, Bastviken D. 2004. Whole lake carbon-13 additions reveal terrestrial support of aquatic food webs. *Nature* 427: 240-243.
- Persaud AD, Dillon PJ, Lasenby D, Yan ND. 2009. Stable isotope variability of meso-zooplankton along a gradient of dissolved organic carbon. *Freshwater Biol* 54: 1705-1719.
- Rau G. 1978. Carbon-13 depletion in a Subalpine Lake: carbon flow Implications. *Science* 201: 901-902.
- Rautio M, Vincent WF. 2007. Isotopic analysis of the sources of organic carbon for zooplankton in shallow subarctic and arctic waters. *Ecography* 30: 77-87.
- Rautio M, Mariash H, Forsström L. 2011. Seasonal shifts between autochthonous and allochthonous carbon contributions to zooplankton diets in a subarctic lake. *Limnol Oceanogr* 56: 1513-1524.
- Salonen K, Hammar T. 1986. On the importance of dissolved organic matter in the nutrition of zooplankton in some lake waters. *Oecologia* 68: 246-253.
- Santana ARA, Lansac-Tôha FA, Benedito E. 2009. Variability of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in three zooplankton species from the upper Paraná River floodplain. *Zoologia (Curitiba)* 26: 725-732.
- Schindler DE, Carpenter SR, Cole JJ, Kitchell JF, Pace ML. 1997. Influence of food web structure on carbon exchange between lakes and the atmosphere. *Science* 277: 248-251.
- Tranvik LJ. 1989. Bacterioplankton growth, grazing mortality and quantitative relationship to primary production in a humic and a clearwater lake. *J Plankton Res* 11: 985-1000.
- Vuorio K, Meili M, Sarvala J. 2006. Taxon-specific variation in the stable isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of lake phytoplankton. *Freshwater Biol* 51: 807-822.
- Yoshioka T, Wada E, Hayashi H. 1994. A stable isotope study on seasonal food web dynamics in a eutrophic lake. *Ecology* 75: 835-846.