한국해양환경공학회지
Journal of the Korean Society
for Marine Environmental Engineering
Vol. 9, No. 2. pp. 109-119, May 2006

인위적인 동물플랑크톤 첨가에 따른 중형 폐쇄생태계 내 플랑크톤 변동

강정훈[1†] · 김웅서[2]
[1]한국해양연구원 남해특성연구본부
[2]한국해양연구원 해양자원연구본부

The Effect of Enhanced Zooplankton on the Temporal Variation of Plankton in a Mesocosm

Jung-Hoon Kang[1†] and Woong-Seo Kim[2]

[1]Southern Coastal Environment Research Division, South Sea Institute, KORDI, 391, Changmokmyun Koje-shi, Kyungnam, 656-830, Korea
[2]Marine Resources Research Department, KORDI, Ansan P.O. Box 29, Seoul 425-600, Korea

요 약

2001년 가을철 대발생 시기에 인위적으로 상승 첨가된 동물플랑크톤이 식물플랑크톤에 미치는 영향을 파악하기 위해 중형폐쇄생태계를 이용한 연구가 남해안의 장목만에서 연구되었다. 2500리터 용량의 폴리에틸렌 백 4개에 현장 해수를 채운 후, 현장에서 플랑크톤 네트(망목: 300 μm)로 수직 예인하여 얻은 동물플랑크톤 시료를 이용하여 실험구가 대조구보다 6배 높도록 조성하였다. 연구기간동안 대조구와 실험구 폐쇄생태계 간의 식물플랑크톤 군집에서는 유의한 차이가 없었다(one-way ANOVA, $p>0.05$). 대조구와 실험구에서 배양 초기 높은 값을 나타낸 식물플랑크톤의 현존량 및 엽록소-*a*는 실험 종료시까지 급속히 감소하였다. 식물플랑크톤 군집을 대표한 우점 분류군은 규조류로서 *Skeletonema costatum*, *Pseudo-nitzschia seriata*, *Chaetoceros curvisetus*, *Ch. debilis*, *Cerataulina pelagica*, *Thalassiosira pacifica*, *Cylindrotheca closterium*과 *Leptocylindrus danicus*로 구성되었다. 배양 10일째에 대조구와 실험구에서 최대를 나타낸 야광충은 중형동물플랑크톤 총 개체수 변화를 주도한 최 우점종 이었고, 다음으로 우점한 분류군으로 배양 7일째에 최대를 나타낸 요각류였다. 배양초기에는 인위적 첨가로 인해 실험구안의 요각류 개체수가 대조구에 비해 높았으나, 이후에는 실험 종료 시까지 뚜렷한 차이가 없었다. 이는 젤라틴성 동물플랑크톤의 조절에 의한 것으로 여겨지며, 실험구내의 유즐동물과 메듀사의 개체수와 길이분포가 대조구에 비해 높았던 점이 이를 뒷받침한다. 그런데 초식자인 요각류의 개체수가 상위포식자에 의해 감소한 후 식물플랑크톤 현존량이 다시 증가하는 연쇄효과가 나타나지 않았다. 이는 주요 초식자인 요각류*Acartia erythraea*가 식물플랑크톤을 효과적으로 조절하지 못하고 있음을 의미하며, 그 이유로 *A. erythraea*의 낮은 초식률, 식물플랑크톤의 빠른 침강으로 인한 조우기회 감소, 그리고 질소결핍 환경으로의 변화에 의한 것으로 판단된다.

Abstract – This study investigated the effect of artificially enhanced mesozooplankton on the phytoplankton dynamics during fall blooming period using a mesocosm in Jangmok bay located in the Southern Sea of Korea in 2001. The four bags with 2,500 liter seawater containment were directly filled with the ambient water. And then, abundances of mesozooplankton in two experimental bags were treated 6 times higher than those in control bags by towing with net (300 μm) through the ambient water. Phytoplankton community between control and experimental bags were not significantly different in terms of chlorophyll-*a* (chl-*a*) concentration and standing crop (one-way ANOVA, $p>0.05$) during the study period. Initial high standing crop and chl-*a* concentration of phytoplankton drastically decreased and remained low until the end of the experiment in all bags. Diatoms, accounting for most of the phytoplankton community, consisted of *Skeletonema costatum*, *Pseudo-nitzschia seriata*, *Chaetoceros curvisetus*, *Ch. debilis*, *Cerataulina pelagica*, *Thalassiosira pacifica*, *Cylindrotheca closterium*, and *Leptocylindrus danicus*. *Noctiluca scintillans* dominated the temporal variation of mesozooplank-

†Corresponding author: jhkang@kordi.re.kr

ton abundances, which peaked on Day 10 in the control and experimental bags, while the next dominant copepods showed their peak on Day 7. Shortly after mesozooplankton addition, copepod abundance in the experimental bags was obviously higher than that in the control bags on Day 1, however, it became similar to that in the control bags during the remnant period. It was supported by the higher abundance and length of both ctenophores and hydromedusae in experimental bags relative to the control bags. However, the cascading trophic effect, commonly leading to re-increase of phytoplankton abundance, was not found in the experimental bags, indicating that copepods were not able to control the phytoplankton in the bags based on the low grazing rate of *Acartia erythraea*. Besides that, rapidly sunken diatoms in the absence of natural turbulence as well as N-limited condition likely contributed the no occurrence of re-increased phytoplankton in the experimental bags.

Keywords: Copepods(요각류), diatoms(규조류), gelatinous plankton(젤라틴성 플랑크톤), cascade effect(연쇄효과), Mesocosm(중형폐쇄생태계)

1. INTRODUCTION

The two hypotheses, "Top-down control" and "Bottom-up regulation", are still under consideration in planktonic ecosystem (Fraser and Keddy [1997]; Kim [2001]; Granéli and Turner [2002]). Multitrophic interactions from physico-chemical parameters via phytoplankton to mesozooplankton have been intensively studied by using a mesocosm in the marine environment (Jacobsen *et al.* [1995]; Escaravage *et al.* [1996]; Carlsson and Granéli [1999]; Escaravage *et al.* [1999]). Yet, researches in relation to the role of herbivorous zooplankton controlling the dynamics of phytoplankton community are limited (Turner *et al.* [1999]). Instead, effects of gelatinous zooplankton on the herbivorous zooplankton have been emphasized as a regulator to affect the size and species composition of phytoplankton community (Olsson *et al.* [1992]; Turner and Granéli [1992]; Kim *et al.* [1992]; Granéli and Turner [2002]). Generally, enhanced abundance of zooplankton has been found around the area where availability of nutrients and light irradiance by phytoplankton is maximal as well as different characteristics of water masses meet such as frontal area (Pakhomov and Perissinotto [1997]; Liu *et al.* [2003]). However, zooplankton biomass prior to enhancement of phytoplankton has been mostly low, resulting in the considerable mismatch between the growth of phytoplankton and grazing pressure from copepods (Maar *et al.* [2002]). Considering that the most important grazers of the enhanced phytoplankton are mesozooplankton, the information how the increased mesozooplankton affect the bloomed phytoplankton dynamics remains scarce. For the verifying the process, artificial concentration of zooplankton through biomanipulation is inevitable and continuous sampling is required from the water mass with identical plankton community.

Mesocosm permits a portion of aquatic environment to be contained and sampled in replicate over a fairly long period. And it can be used as a tool for studying ecosystems, how they work, and how organisms respond to toxic materials due to the possibility of manipulation (Kim [2001]). The main role of mesocosm is to act as a bridge between theory and nature, thus the output from the mesocosms can increase our understanding of natural process by simplifying the complexities of natural environment (Fraser and Keddy [1997]). Suspended bags have often been employed in marine environment to study natural plankton ecosystem.

Present study was originally designed to understand the effect of artificially enhanced mesozooplankton on the phytoplankton bloom using enclosed bags during the fall bloom period in Jangmok bay. However, after repetitive netting through the water column in the ambient water, unintended input of gelatinous zooplankton into the experimental bags turned attention on the original hypothesis into different way. This study described the way how the phytoplankton and mesozooplankton affected each other, resulting from unexpectedly enhanced gelatinous zooplankton.

2. METHODS AND MATERIALS

2.1 Experimental design

Four impermeable polyethylene bags (2,500 liter) consisted of two control and two experimental treatments (mesozooplankton addition) in September-October 2001. Enclosure bags were cylinder type (1.0 m diameter×3.2 m deep) with acrylic round roof which could prevent contamination from precipitation (Fig. 1). The bags were installed at the mesocosm raft, which is fixed and suspended near the Jangmok bay. By suspending the enclosure in the ocean, natural characteristics of ambient light, temperature and a little bit of the water's turbulence is available to maintain the condition inside the bag similar to the surrounding water.

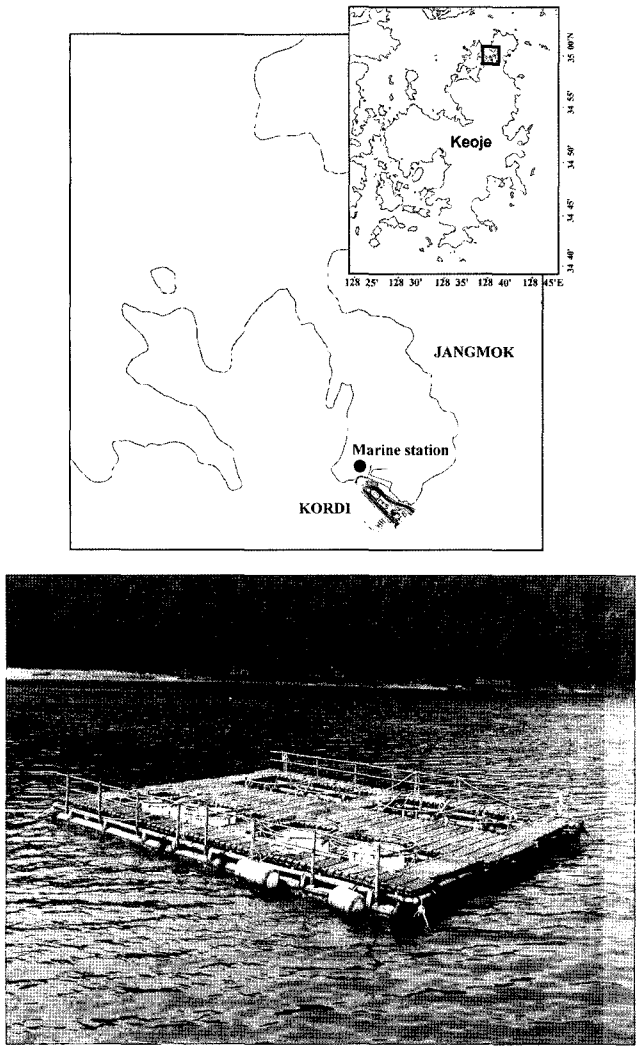

Fig. 1. Enclosed bags suspended to mesocosm raft which is located in Jangmok bay of South Sea.

Addition of six times mesozooplankton natural assemblage in the ambient seawater into two experimental bags was carried out by tender net towing through the ambient water column, mainly considering herbivorous copepods as a major grazer. Shortly after the treatment of mesozooplankton addition, incubation in the bags immediately started on 17 September 2001 and ended on 11 October 2001. Each enclosure was sampled once every 3 days until 27 September and then once a week until the end of the experimental period. Physical parameters such as temperature and salinity, and standing crop and chlorophyll-*a* (hereafter chl-*a*) concentration of phytoplankton, and mesozooplankton abundance, were determined. For comparative analysis with phytoplankton variation, N/P ratio was cited from the report (KORDI, 2003), which included concurrently experimented results with present study.

2.2 Analysis in laboratory and *in situ*

Water temperature (°C) and salinity (psu) were measured using ISTEK conductivity meter (model 43C) directly from seawater collected from a depth of 3 m using the Niskin sampler in the four bags. Seawater for analysis of chl-*a* was filtered through 47 mm Whatman GF/F glass-fiber filters from 1-seawater sub-sampled from the four bags in September-October 2001. Filtered GF/F papers were immersed and extracted overnightly in 90% acetone in the refrigerator (4°C) and analyzed with a fluorometer (Model 10AU, Turner-designs). Seawater for phytoplankton quantification was duplicately filled into 500 ml polyethylene bottles and preserved with Lugol's iodine solution. Subsample of 1 ml from settled and concentrated sample was placed into a Sedgwick-Rafter counting chamber and enumerated using a light microscope (Microscope BHS, Olympus, Japan).

Mesozooplankton samples, which was casted with the Niskin sampler (5-liter) from the 3 m depth in the four bags, were concentrated through a 200 μm mesh net and rinsed down into polyethylene bottle. And the samples were preserved with formalin (final concentration of 5%) and identified into genus or species level for copepods and to class level for the non-copepods under the stereomicroscope (Stemi-2000C). Actively swimming ctenophores were observed throughout the all bags on the last day of experiment. After the incubation terminated, most water inside the bags was poured into through 200 μm mesh net and preserved with formalin in an attempt to determine the abundance and diameter of ctenophores.

2.3 Grazing rate

The balance method was used to acquire the grazing rate according to the difference of added zooplankton in control and experimental bags. Live copepods were sampled by vertical towing with the Norpac type net (300 μm in mesh size and 45cm in mouth diameter)and transferred into the jar filled with pre-filtered seawater through 0.7 μm filter paper. After isolated copepods were acclimated in the filtered seawater for 3 or 4 hours, female copepods (*Acartia erythraea*) were sorted out into the experimental polycarbonate bottles (2*l*). The initial chl-*a* (t=0) was filtered and determined with seawater casted from each bag (Control 1, Control 2, Experiment 1 and Experiment 2). Control (natural assemblage) and experimental polycarbonate bottles (copepod enhancement relative to natural assemblage) were filled with 300 μm mesh filtered seawater. To meet with the condition of 6 times difference between control and experimental bags, 5 copepods were put into the

two control bottles and 30 copepods were into two experimental bottles, respectively. After copepod treatment was finished, all bottles were shielded by aluminum foil to avoid the exposure to light and then suspended at the 3m depth from the raft. Incubation time was fixed from 6 P.M. to 6 A.M. to avoid the growth of phytoplankton by sunlight. After incubation ended, seawater in bottles was filtered through GF/F filter paper and stored in a deep-freezer (<20°C). Extracted samples in 90% acetone were measured with a fluorometer (Field Fluorometer 10AU, Turner-Designs, USA). Assuming that there was no growth of phytoplankton, grazing rate of copepods was calculated from the difference of chl-*a* concentration between initial and end time of incubation.

By dividing the amount of phytoplankton pigment removed by experimental copepods (μg l^{-1}) by the concentration of phytoplankton in the seawater (μg l^{-1}), the volume of water that the copepods have filtered can be calculated (Boyd *et al.* [1980]). Effects of zooplankton enhancement on the dynamics of plankton community were tested with an analysis of variance (ANOVA) (Zar [1999]).

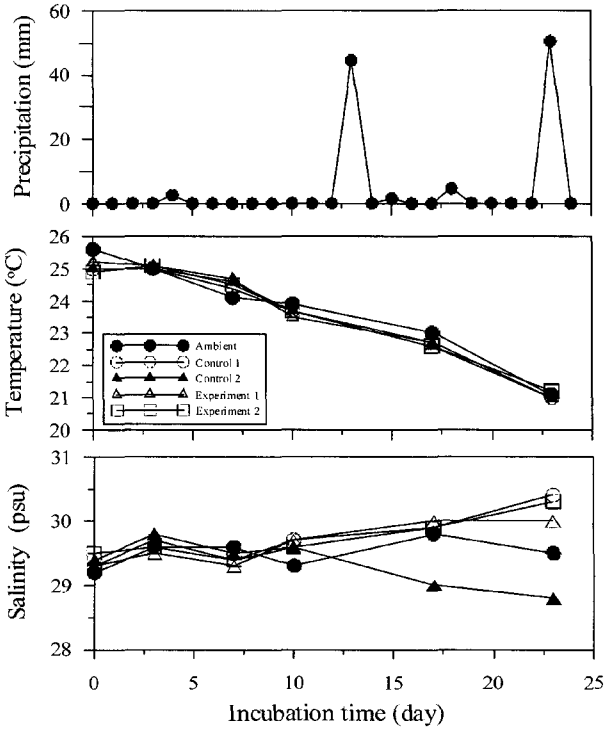

Fig. 2. Temporal variations of precipitation, temperature and salinity in control, experimental (mesozooplankton addition) bags and ambient water in September-October 2001.

3. RESULTS

3.1 Precipitation, temperature and salinity

From the onset to the end of the experiment, sea water temperature gradually decreased in the range of from 21.0~21.2°C to 24.9~25.6°C (Fig. 2). The decreasing pattern of temperature in the surrounding water was similar with that in the enclosed bags during the study period. By contrast, salinity varied in the range of from 29.3~30.4 psu to 29.2~29.8 psu in all bags and the surrounding water, respectively. Exceptionally, salinity in the bag (control 2) decreased by 0.6psu compared to the initial salinity, resulting from the leakage of precipitation due to the broken cover (Fig. 2). Generally, there was no distinct difference between surrounding water and all enclosed bags in terms of temperature and salinity during the study period. Temperature (F_{ratio}=0.0019, p=0.999) and salinity (F_{ratio}=1.485, p=0.248) were not significantly different between control and experimental bags.

3.2 Standing crop and chlorophyll-*a* of phytoplankton

Initial chl-*a* concentration was very high in the ambient water and bags, ranging from 11.4 to 12.7 μg l^{-1} by the fall bloom of phytoplankton (Fig. 3). The chl-*a* decreased within the range of 0.7 and 11.4 μg l^{-1} in the control bags, and 0.6 and

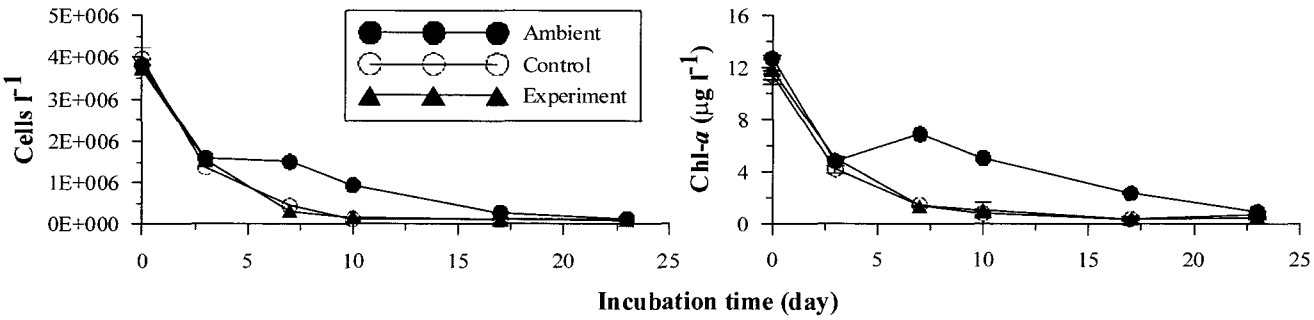

Fig. 3. Temporal variations of chl-*a* concentration and standing crop of phytoplankton in control, experimental bags and ambient water in September-October 2001.

11.8 μg l^{-1} in the experimental bags, respectively (Fig. 3). Chl-*a* concentration in the ambient water showed similar pattern to that of bags within the range of between 0.97 and 12.7 μg l^{-1}. But another peak in the ambient water on Day 7 was not observed in the control and experimental bags (Fig. 3). Phytoplankton standing crop also varied with the chl-*a* concentration in the bags and ambient water. The average standing crop of phytoplankton gradually decreased in the range of 111~3,968×10^3 cells l^{-1} in the control bags, 91~3,725×10^3 cells l^{-1} in the experimental bags during the study period (Fig. 3). The phytoplankton standing crop in the ambient water also decreased in the range of 135~3,819×10^3 cells l^{-1} in accordance with the variation of phytoplankton in the bags.

Diatoms, accounting for 83.1~91.7% of phytoplankton community, explained most of entire phytoplankton variation in the ambient water and all enclosed bags during the study period (Fig. 4). And then, cryptomonads were next abundant group with the relative abundance of 4.6~7.9%, next by unidentified micro-autoflagellates with 2.0~5.9%, and dinoflagellates with 1.1~2.4% (Fig. 4). Standing crop of diatoms lied in the range of 3,256~3,548×10^3 cells l^{-1} during the initial period and decreased into the range of 46~58×10^3 cells l^{-1} (Fig. 4). Standing crop of cryptomonads ranged from 5~54×10^3 cells l^{-1} to 196~449×10^3 cells l^{-1}, unidentified autoflagellates ranging from 20~30×10^3 cells l^{-1} to 31~46×10^3 cells l^{-1}, and dinoflagellates varied from the range of 3~8×10^3 cells l^{-1} to 29~48×10^3 cells l^{-1} (Fig. 4). Diatoms and cryptomonads between ambient water and the bags varied similarly, while micro-autoflagellates and dinoflagellates showed different variation between ambient water and enclosed bags from the initial period to the Day 7. Autoflagellates and dinoflagellates re-increased on Day 7 and immediately decreased from the Day 10 in the bags.

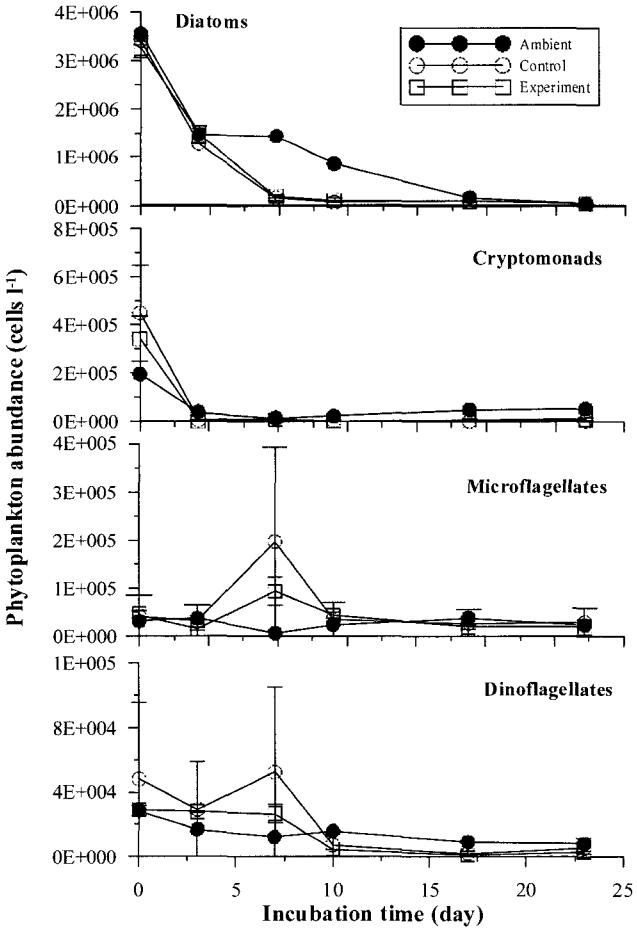

Fig. 4. Temporal variations of dominant groups in the phytoplankton community in control, experimental bags and ambient water in September-October 2001.

The most dominant diatoms consisted of *Skeletonema costatum* (21.5%), *Pseudo-nitzschia seriata* (15.5%), *Chaetoceros curvisetus* (12.3%) and *Cerataulina pelagica* (11.0%) in the ambient water (Fig. 5). *S. costatum* (30.3%), *P. seriata* (12.3%) and *Ch. Curvisetus* (12.0%) were dominant in the control bags and *S. costatum* (35.0%), *Ch. Curvisetus* (11.6%) and *P. seriata* (11.0%) were in the experimental bags (Fig. 5). In the ambient water, standing crops of most dominant phytoplankton peaked on Day 1, and then gradually decreased, whereas *C. pelagica*, *Chaetoceros* spl. and *Cylindrotheca closterium* re-increased on Day 7 and Day 10 and then decreased. In the bags (control and experiment), *Chaetoceros* spp. and *C. closterium* re-increased on Day 10 or Day 17 (Fig. 5). Phytoplankton community showed no significant differences [ANOVA, F_{ratio}= 0.0070, p=0.999 (chl-*a*); F_{ratio}=0.00365, p=0.999 (standing crop)] between control and experiments in September-October 2001.

3.3 Mesozooplankton

Average abundances of mesozooplankton ranged from 6,000~9,400 inds. m^{-3} in the ambient water, 3,300~218,200 inds. m^{-3} in the control bags, and 2,100~238,100 inds. m^{-3} in the experimental bags during the study period (Fig. 6). The highest abundances of mesozooplankton on Day 7 and Day 10 were caused by rapidly increased *Noctiluca scintillans*, which accounted for 91.7% and 89.0% of entire zooplankton community in the control and experimental bags during the study period. However, the relative abundance of *N. scintillans* remained as 39.1% in the ambient water during the study period. Average abundance of *N. scintillans* ranged from 1,600 to 4,400 inds. m^{-3} in the ambient water, from 500 to 212,500 inds.m^{-3} in the control bags, from 300 to 230,700 inds. m^{-3} in the experimental bags (Fig. 6).

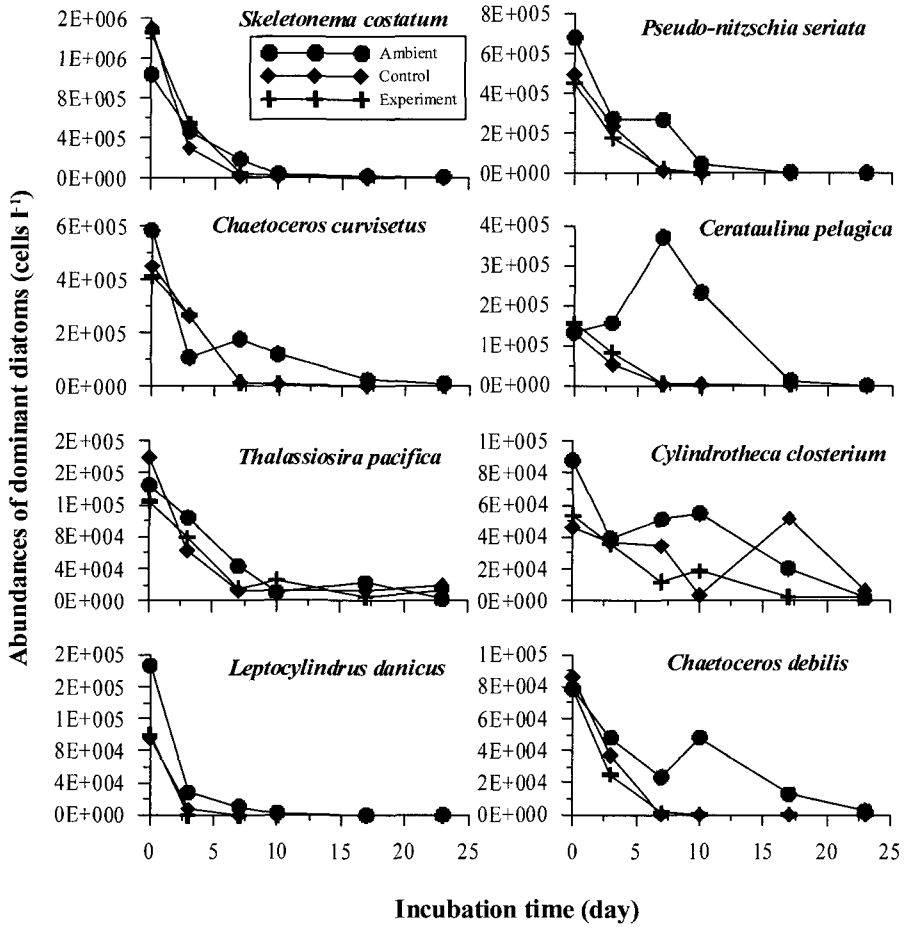

Fig. 5. Temporal variations of dominant diatoms in the phytoplankton community in the control, experimental bags and ambient water in September-October 2001.

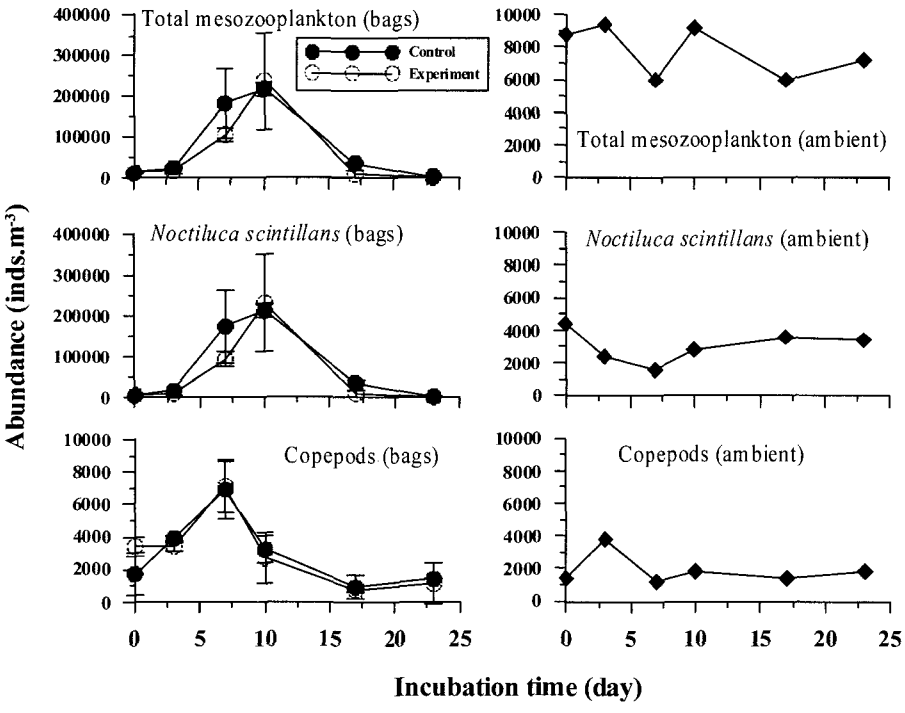

Fig. 6. Temporal variations of total mesozooplankton, copepods and *Noctiluca scintillans* in the control, experimental bags and ambient water in September-October 2001.

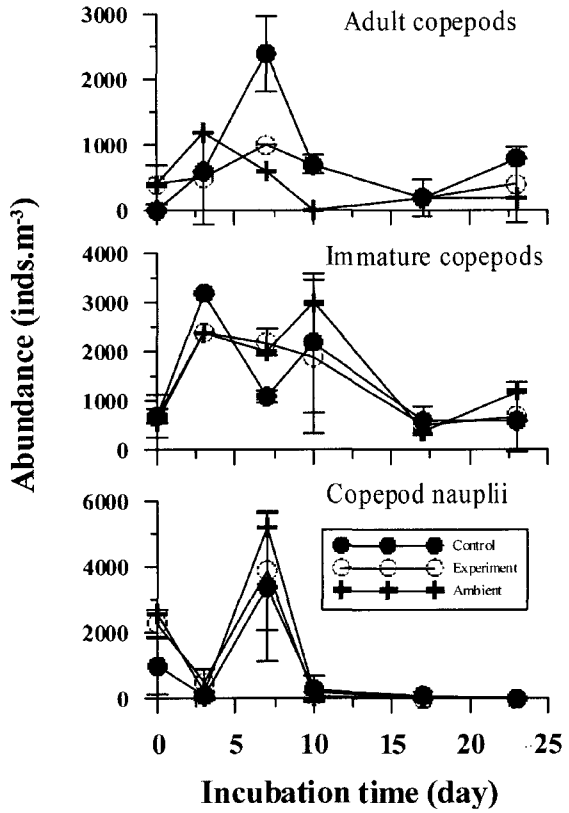

Fig. 7. Temporal variations in copepod nauplii, immature and adult copepods in all bags and ambient water in September-October 2001.

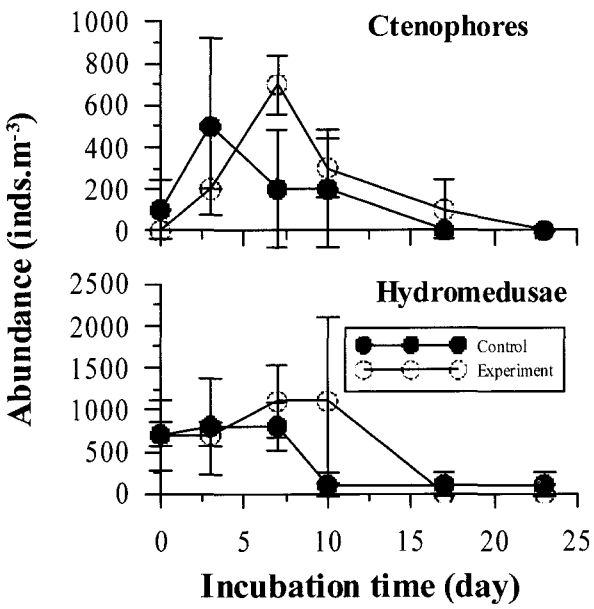

Fig. 8. Temporal variations of gelatinous zooplankton in control and experimental bags in September-October 2001.

Average abundances of copepods, which included adults, immature copepods and nauplii, varied between 900 and 6,900 inds. m^{-3} in the control bags, 700 and 7,100 inds. m^{-3} in the experimental bags, 1,200 and 3,800 inds. m^{-3} in the ambient water during the study period (Fig. 6).

Abundances of adult copepods in the control bags were lower than those in the experimental bags on Day 1 and 3, whereas the pattern changed into opposite way from Day 3 until the end of the incubation (Fig. 7). However, immature copepods and nauplii were not different between control and experimental bags. The abundances of adult copepods, consisting mainly of *Acartia erythraea*, *Corycaeus affinis* and *Oithona brevicornis*, varied within the range of 0~1,200 inds. m^{-3} in the ambient water, 0~2,400 inds. m^{-3} in the control bags and 200~1,000 inds. m^{-3} in the experimental bags (Fig. 7). The immature copepods ranged from 200 to 1,600 inds. m^{-3} in the ambient water, from 600 to 3,200 inds. m^{-3} in the control bags and from 500 to 2,400 inds. m^{-3} in the experimental bags (Fig. 7). The numbers of copepod nauplii varied in the range of 200~1,000 number m^{-3} in the ambient water, 0~3,400 number m^{-3} in the control and 0~3,900 number m^{-3} in the experimental bags (Fig. 7).

Average abundances of ctenophores as top predator in the bags lied in the range of 0~200 inds. m^{-3} in the ambient water, 0~500 inds. m^{-3} in the control bags and 0~700 inds. m^{-3} in the experimental bags (Fig. 8). The hydromedusae varied in the range of 0~600 inds. m^{-3} in the ambient water, 100~800 inds. m^{-3} in the control bags and 0~1,100 inds. m^{-3} in the experimental bags (Fig. 8). Average lengths and abundance of hydromedusae in experimental bags were longer and higher than those in control bags. Moreover, the size distribution of ctenophores in the experimental bags was more diverse than that in the control bags (Fig. 9).

Mesozooplankton community showed no significant differences [ANOVA, F_{ratio}=0.033, p=0.86 (total abundance)] between control and experiment in September-October 2001.

3.4 Grazing rates

Grazing rates ranged from not determined (hereafter N.D.) to 0.00048 μg chl-*a*·copepod^{-1}·hr^{-1} in control and from N.D. to 0.00041 μg chl-*a*·copepod^{-1}·hr^{-1} in experimental bottles (Table 1). In 25th September, the difference between experiments was observed, yet other experiments showed no clear pattern of grazing rate (Table 1). Especially, the grazing rates of all treatments (control and experiment) showed negative values in 27th September (data not shown). These results suggest that the growth rate of phytoplankton was possibly greater than the grazing pressure of herbivorous grazers or grazing pressure of

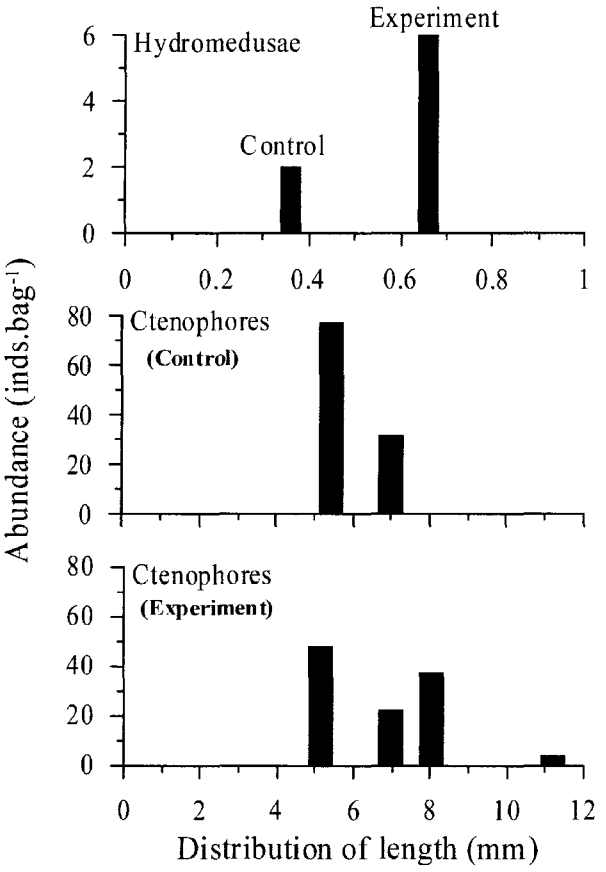

Fig. 9. Size distribution of collected gelatinous zooplankton from control and experimental bags after incubation experiment finished.

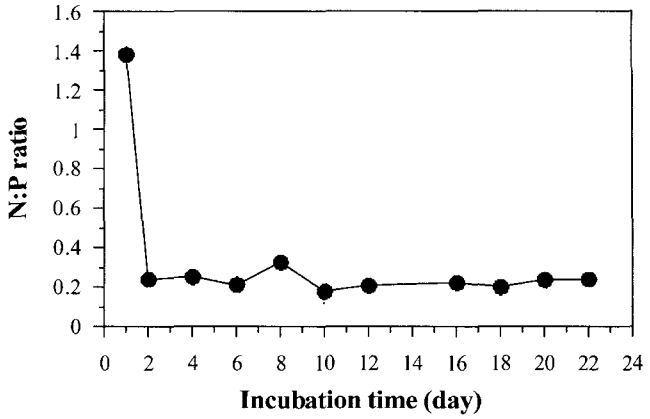

Fig. 10. Variation of N/P ratio in the bags in September-October 2001 (cited from KORDI, 2003).

grazers is minimal during the study period.

4. DISCUSSION

Contrary to our expectation, significant grazing impact in the experimental bags with zooplankton addition (×6) was not observed, resulting in no difference in chl-*a* concentration and standing crop of phytoplankton between treatments (control and experiment). Besides, initial high abundance of mesozooplankton, mainly copepods, in experimental bags decreased and became similar to that in control bags in the last phase of the experiment. They indicated that grazing pressure of herbivores was minimal and "cascade effect" by strong predation of gelatinous zooplankton on the copepods proceeded (Atkinson [1996]; Nejstgaard *et al.* [2001]). The minimal grazing rate of herbivorous copepods may stem from several possible factors such as drastic change of environment and the related succession of prey composition, variation of contact rate between prey and grazer, insidious effects of diatoms on copepods, and negative grazing as result of prey selectivity (Lehman [1980]; Miralto *et al.* [1999]; Liu *et al.* [2003]; Leising *et al.* [2005]).

Under no additional enhancement of nutrient, it was expected that the environment inside bags changed into N-limited condition with time, considering the initial high concentration of chl-*a* from fall blooming period (Fig. 10). On the basis of incorporated nutrient result (Fig. 10), the markedly reduced chl-*a* concentration and standing crop of phytoplankton in all bags are likely primarily related to the changes of N/P ratio rather than grazing pressure of copepods. The phytoplankton variation in control and experimental bags was coincident with the variation of N/P ratio less than 1.5 (Figs. 3 and 11). *Chaetoceros curvisetus*, *Skeletonema costatum* and *Pseudo-nitzschia seriata*, which were dominant species in the phytoplankton community, showed very high standing crop in the first period with relatively high ratio of N/P. However, the dominant species composition changed into *Cylindrotheca closterium*, autotrophic microflagellates and cryptomonads under the condition less

Table 1. Hourly grazing rates of herbivorous copepod, *Acartia erythraea*, in the control and experimental bags in September-October 2001.

Treatment	Grazing rate (μg chl-*a* . copepod^{-1}. hour^{-1})			
	25th Sept.	27th Sept.	5th Oct.	10th Oct.
Cont.1	-0.00059	-0.00066	0.00003	0.00020
Cont.2	-0.00117	-0.00213	0.00048	-0.00171
Exp.1	0.00024	-0.00024	-0.00012	0.00011
Exp.2	0.00010	-0.00006	0.00041	0.00006

than 0.3 of N/P ratio in the last period. This pattern is supported by Harrison and Turpin (1982). They reported that centric diatoms such as *Chaetoceros* spp., *Skeletonema* spp. and *Thalssiosira* were dominant in the first phase of mesocosm experiment with relatively high specific nutrient supply, yet *Cylindrotheca* spp. and *Nitzschia* spp. were dominant with flagellates in the condition that nutrients were mostly demanded. Even though the grazing rates showed minimal values, those of herbivorous *Acartia erythraea* showed decreasing trends in the experimental bags as the composition of dominant species and chl-*a* concentration of phytoplankton changed throughout the study period, except the highest grazing rates in 5 October. Moreover, in 25 September, difference of 6 times enhancement between treatments was clearly observed, whereas it was not found in other period. This pattern implied that grazing rates of the copepod decreased in relation to temporal variations of chl-*a* concentration and species composition of phytoplankton during the study period. The generally low grazing rates of *A. erythraea* in the present study were very similar to those of *A. omorii* in the spring bloom period (KORDI [2003]). Present result is also consistent with Cottingham *et al.*[1997], who reported that blooming of large, chain-forming grazing-resistant phytoplankton weakens coupling with zooplankton. Copepod feeding generally has a relatively low impact on phytoplankton spring blooms which could be mainly attributed to the time lag in the growth of copepod populations, when compared to the faster growth of phytoplankton (Barquero *et al.* [1998]). This may be explained by another viewpoint such as insidious effects of diatoms on the reproductive process of copepods (Miralto *et al.* [1999]; Irigoien *et al.* [2000]). Thus, copepods may simply avoid eating deleterious diatoms when they are present. Present grazing rates were calculated from bulk chl-*a* concentration disappearance using bottle incubation method. If the target copepod is unable to eat the prey mainly consisting of the diatoms, negative or low grazing rates were unavoidable. Besides, if the prey selectivity of copepod is mainly heading for the microzooplankton, release the prey of microzooplankton from grazing pressure can lead the phytoplankton into increasing trend with the nutrient input of sloppy feeding, so called, "trophic cascade" (Lehman [1980]). However, the sloppy-related nutrient input did not occur in the bottle and mesocosm experiments on the basis of low N/P ratio and no re-increased phytoplankton. Therefore, negative or low grazing rates in the present study are likely caused by avoidance of copepods to deleterious diatoms and prey selectivity of copepods in the bottle experiments during the study period. In the same context, no difference of phytoplankton between control and experimental bags was likely related with the negative or low grazing rates, despite the abrupt decrease in standing crop and chl-*a* concentration of phytoplankton.

However, the reason that the initial high copepods in experimental bags relative to control bags did not maintain, was not clearly clarified during the experiment period. This pattern is most likely explained by the cascade effects by gelatinous zooplankton such as ctenophore and hydromedusae. The size distribution and abundance of gelatinous plankton in the experimental bags were diverse and high compared with those in the control bags, coincident with no difference of copepod abundances between bags (Fig. 9).

The elevated predation of gelatinous plankton on copepods led to an undesired blooming of dinoflagellates such as *Gyrodinium aureolum* (Lindahl and Hernroth [1983]; Kim *et al.* [1992]) as well as diatoms such as *Skeletonema costatum* and *Thalassiosira weisflogii* (Olsson *et al.* [1992]). In these cases, grazing pressure of copepods can control the phytoplankton biomass, however, this kind of cascading trophic effect was not found in the present study with being low grazing rate of herbivorous copepod, *A. erythraea*. Commonly, *Acartia* sp. is known to graze actively *Skeletonema costatum*, *Thalassiosira* sp. and cryptomonads (Deason [1980]), but the abrupt decrease of *S. costatum* including other diatoms in this study could not be fully explained in terms of only grazing pressure of *A. erythraea* in the bags. Moreover, *A. erythraea* did not likely prefer the diatoms occurring in this period as a food source, considering the low or negative grazing rates of it. Rather, sinking process of diatoms could be persuasive reason to the rapid decrease of phytoplankton in the bags under no natural turbulence (Kang *et al.* [2005]).

On the basis of the grazing rate of *A. erythraea* and its abundance, the theoretical time to filter out the whole seawater inside the bags ranged from 473~8,221 days in September-October 2001. But it ranged from 36~1,045 days in *A. omorii*, from 46~175 days in *Calanus sinicus* in March-April 2002 (Table 2). The incubation time in the present study was less than 30 days, thus the phytoplankton biomass could not be controlled by *A. erythraea* in September-October 2001, while *A. omorii* and *C. sinicus* showed relatively active filtration rate as compared to that of *A. erythraea*. Thus, the reason that the copepod could not control the phytoplankton biomass in the study period likely stemmed from the reduced contact rate between grazer and diatoms by sinking process (Kang *et al.* [2005]) as well as low grazing pressure and insufficient time to

Table 2. Filtration rates for herbivorous copepods in each mesocosm calculated based on the maximum average abundance of main herbivores. Filtration rates were converted to daily values (ml d^{-1}) and used to calculate the theoretical time required to filter an entire 2,500 liter mesocosm.

Herbivore	Season	Filtration rate		Filtration rate of maximum population in a day	Theoretical time took to filter out a entire mesocosm	Source
		(m*l* h^{-1})	(m*l* d^{-1})	m*l*	day	
Acartia erythraea	Autumn	0.04-0.73	1.0-17.6	304-5,287	473-8,221	This study
Acartia omorii	Spring	0.03-1.0	0.8-24.1	2,393-69,755	36-1,045	(KORDI [2003])
Calanus sinicus	Spring	0.57-2.14	13.6-51.4	14,268-54,022	46-175	"

control phytoplankton.

Besides, the initial addition of six times copepods the ambient concentration, in this case mainly *A. erythraea*, was not consistent in the experimental bags throughout the study period. The diverse size distribution of ctenophore in the experimental bags relative to that in the control bags suggested that the inconsistent enhancement of copepods was related to the predation of the gelatinous plankton such as hydromedusae and ctenophore (Fig. 9). Unlike previous studies, the strong predation of gelatinous plankton on the copepods did not lead to the unexpected increase of phytoplankton in the present study. It may be caused by the N-limited condition, sinking process and inefficient grazing pressure as abovementioned in this study.

In summary, the differences in standing-crop and chl-*a* concentration of phytoplankton were not significantly observed between control and experimental (6 times addition of copepods the ambient concentration) bags in September-October 2001 (one-way ANOVA, $p>0.05$). This may be resulted from minimal or negative grazing rate of copepods, mainly *A. erythraea*, N-limited condition, reduced contact rate by sinking process between phytoplankton and *A. erythraea*, and elevated predation of gelatinous zooplankton on copepods in the experimental bags. Especially, the significant predation of gelatinous zooplankton on copepods was supported by no difference of copepod abundance between bags throughout the study period as well as diverse size distribution and higher abundance of gelatinous plankton in experimental bags relative to control bags after incubation finished. Subsequently, cascading trophic effect, leading to re-increased abundance of phytoplankton, was not found in the experimental bags. This result indicated that *A. erythraea* could not control effectively the fall bloom consisting of mainly diatoms in the bags during the study period.

REFERENCES

[1] Atkinson, A., 1996, "Subantarctic copepods in an oceanic, low chlorophyll environment: ciliate predation, food selectivity and impact on prey population", Mar.Ecol.Prog.Ser., Vol.130, 85-96.

[2] Barquero, S., Cabal, J.A., Anadon, R., Fernandez, E., Varela, M. and Bode, A., 1998, "Ingestion rates of phytoplankton by copepod size fractions on a bloom associated with an off-shelf front off NW Spain", J. Plankton Res., Vol.20, No.5, 957-972.

[3] Boyd, C.M., Smith, S.L. and Cowles, T.J., 1980, "Grazing patterns of copepods in the upwelling system off Peru", Limnol. Oceanogr., Vol.25, No.4, 583-596.

[4] Carlsson, P. and Granéli, E., 1999, "Effects of N:P:Si ratios and zooplankton grazing on phytoplankton communities in the northern Adriatic Sea. II. Phytoplankton species composition", Aquat. Microb. Ecol., Vol.18, 55-65.

[5] Cottingham, K.L., Knight, S.E., Carpenter, S.R., Cole, J.J., Pace, M.L. and Wagner, A.E., 1997, "Response of phytoplankton and bacteria to nutrients and zooplankton: a mesocosm experiment", J. Plankton Res., Vol.19, No.8, 995-1010.

[6] Deason, E.E., 1980, "Grazing of *Acartia hudsonica* (*A. clausi*) on *Skeletonema costatum* in Narragansett Bay (USA): Influence of food concentration and temperature", Mar. Biol., Vol.60, No. 2/3, 101-113.

[7] Escaravage, V., Prins, T.C., Smaal, A.C. and Peeters, J.C.H., 1996, "The response of phytoplankton communities to phosphorus input reduction in mesocosm experiments", J. Exp. Mar. Biol. Ecol., Vol.198, 55-79.

[8] Escaravage, V., Prins, T.C. Nijdam, C. Smaal, A.C. and Peeters, J.C.H., 1999, "Response of phytoplankton communities to nitrogen input reduction in mesocosm experiments", Mar. Ecol. Prog. Ser., Vol.179, 187-199.

[9] Fraser, L.H. and Keddy, P., 1997, "The role of experimental microcosms in ecological research", TREE, Vol.12, No.12, 478-481.

[10] Granéli, E. and Turner, J.T., 2002, "Top-down regulation in ctenophore-copepod-ciliate-diatom-phytoflagellate communities in coastal waters: a mesocosm study", Mar. Ecol. Prog. Ser., Vol.239, 57-68.

[11] Harrison, P.J. and Turpin, D.H., 1982, "The manipulation of physical, chemical, and biological factors to select species from natural phytoplankton communities", In: Grice, GD., Reeve, M.R. (eds) Marine Mesocosms: biological and chemical research in experimental ecosystems. Springer-Verlag, New York, 275-289.

[12] Irigoien, X., Harris, R.P., Head, R.N., and Harbour, D., 2000, "The influence of diatom abundance on the egg production rate

of *Calanus helgolandicus* in the English channel", Limnol. Oceanogr., Vol.45, No.6, 1433-1439.

[13] Jacobsen, A., Egge, J.K. and Heimdal, B.R., 1995, "Effects of increased concentration of nitrate and phosphate during a springbloom experiment in mesocosm", J. Exp. Mar. Biol. Ecol., Vol.187, 239-251.

[14] Kang, J.H., Kim, W.-S., Shin, K., Chang, M. and Hwang, K.C., 2005, "The effect of enhanced nitrate input on the temporal variation of the plankton community in a mesocosm", Ocean and Polar Res., Vol.27, No.3, 341-349.

[15] Kim, W.-S., 2001, "Application of enclosed experimental ecosystem to the study on marine ecosystem", Kor. J. Environ. Biol., Vol.19, No.3, 183-194.

[16] Kim, W.-S., Chang, M. and Shim, J.H., 1992, "Multitrophic interactions as a trigger of the *Gyrodinium aureolum* Bloom in Reeves Bay, New York", J. Oceanol.Soc. Kor., Vol.27, No.4, 268-276.

[17] KORDI, 2003, "Land-ocean interactions in the coastal zone", BSPE 827-01-1493-4, Korea Ocean Research & Development Institute, Ansan, Korea. 505 pp.

[18] Lehman, J.T., 1980, "Release and cycling of nutrients between planktonic algae and herbivores", Limnol.Oceanogr., Vol.25, No.4, 620-632.

[19] Leising, A.W., Pierson, J.J., Halsband-Lenk, C., Horner, R. and Postel, J., 2005, "Copepod grazing during spring blooms: Does *Calanus pacificus* avoid harmful diatoms?", Prog. Oceanogr., Vol.67, 384-405.

[20] Lindahl, O. and Hernroth, L., 1983, "Phytoplankton-Zooplankton community in coastal waters of western Sweden-an ecosystem off balance?", Mar. Ecol. Prog. Ser., Vol.10, 119-126.

[21] Liu, G.M., Sun, S., Wang, H., Zhang, Y., Yang, B. and Ji, P., 2003, "Abundance of *Calanus sinicus* across the tidal front in the Yellow Sea, China", Fish. Oceanogr., Vol.12, No.4/5, 291-298.

[22] Maar, M, Nielsen, T.G., Richardson, K., Christaki, U., Hansen, O.S., Zervoudaki, S. and Christou, E.D., 2002, "Spatial and temporal variability of food web structure during the spring bloom in the Skagerrak", Mar. Ecol. Prog. Ser., Vol.239, 11-29.

[23] Miralto, A., Barone, G., Romano, G., Poulet, S.A., Ianora, A., Russo, G.L. et al., 1999, "The insidious effects of diatoms on copepod reproduction", Nature, Vol.402, 173-176.

[24] Nejstgaard, J.C., Naustvoll, L.J. and Sazhin, A., 2001, "Correcting for underestimation of microzooplankton grazing in bottle incubation experiments with mesozooplankton", Mar. Ecol. Prog. Ser., Vol.221, 59-75.

[25] Olsson, P., E. Granéli, P. Carlsson and P. Abreu. 1992. "Structuring of a postspring phytoplankton community by manipulation of trophic interactions", J. Exp. Mar. Biol. Ecol., Vol.158, 249-266.

[26] Pakhomov, E.A. and Perissinotto, R., 1997, "Mesozooplankton community structure and grazing impact in the region of the Subtropical Convergence south of Africa", J. Plankton Res., Vol.19, No.6, 675-691.

[27] Turner, J.T. and Granéli, E., 1992, "Zooplankton feeding ecology: grazing during enclosure studies of phytoplankton blooms from the west coast of Sweden", J. Exp. Mar. Biol. Ecol., Vol.157, 19-31.

[28] Turner, J.T., Tester, P.A., Lincoln, J.A., Carlsson, P. and Graneli, E., 1999, "Effects of N:P:Si ratios and zooplankton grazing phytoplankton communities in the northern Adriatic Sea. III. Zooplankton populations and grazing", Aquat.Microb.Ecol., Vol.18, 67-75.

[29] Zar, J.H., 1999, Biostatistical analysis, Prentice Hall International, London, 177-207.

2006년 3월 8일 원고접수
2006년 5월 7일 수정본 채택