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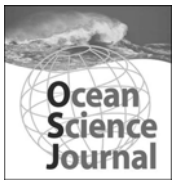

Feeding Selectivity of Calanoid Copepods on Phytoplankton in Jangmok Bay, South Coast of Korea

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Abstract – Grazing impacts of calanoid copepods on size-fractionated phytoplankton biomass [chlorophyll (Chl)-*a*] were measured in Jangmok Bay, Geoje Island, Korea, monthly from November 2004 to October 2005. The ingestion rate of calanoid copepods on total phytoplankton biomass ranged between 1 and 215 ng Chl-*a* copepod^{-1} day^{-1} during bottle incubations. Results indicated that microphytoplankton (> 20 μm) was the primary food source for calanoid copepods in grazing experiments on 3 phytoplankton size categories (< 3 μm, 3-20 μm, and > 20 μm). The ingestion rate on microphytoplankton showed a significant increase ($r = 0.93$, $p < 0.01$) with Chl-*a* concentration. Nanophytoplankton (3-20 μm) showed a negative ingestion rate from June 2005 to October 2005, but the reason is not completely understood. Calanoid copepods were unable to feed efficiently on picophytoplankton (< 3 μm) due to unfavorable size. Calanoid copepods removed between 0.1% and 27.7% (average, 3.6 ± 15.8%) of the phytoplankton biomass daily during grazing experiments. Grazing pressure was high in winter and early spring (January-March: 15.6-27.7%), while low in summer (June-August: -33.1-0.0%) and autumn (September–November: -1.4-5.1%). Results suggest that calanoid copepods play an important role in controlling the biomass and size structure of phytoplankton in winter and early spring.

Key words – calanoid copepods, grazing, Jangmok Bay

1. Introduction

Within the food web of the pelagic ecosystem, copepods are an important element linking energy flow between phytoplankton as a primary producer and nekton such as fish (Frost 1972; Richardson and Shoeman 2004). Studies over the past 20 years have also revealed that copepods function as an energy medium between constituent organisms of the microbial loop (such as heterotrophic flagellates and ciliates) and organisms of upper nutrition (Stoecker and Capuzzo 1990; Turner 2004; Gifford et al. 2007).

In general, most copepods tend to be omnivorous when the dominant phytoplankton are too small (mainly pico size) to be directly consumed. On the other hand, copepods tend to become increasingly herbivorous when phytoplankton are of a convenient, available size (mainly micro size) to copepods (Stoecker and Capuzzo 1990; Gifford 1991; Gifford and Dagg 1991; Froneman 2002a). Thus, phytoplankton size composition alters the feeding type of copepods and plays an important role in determining trophic interactions within food webs (Froneman 2006).

Copepods feed on a wide size range of phytoplankton and are capable of selectively feeding on phytoplankton of specific sizes according to species (Wilson 1973; Cowles 1979). In copepods, this feeding selectivity is a factor of an adjustment mechanism to overcome interspecific competition for food resources (Pagano et al. 2003). Feeding selectivity also works as a direct factor controlling changes in size structure and species composition of phytoplankton (Ryther and Sanders 1980). In addition, copepods indirectly affect structure changes of phytoplankton by feeding on microzooplankton (mainly ciliates) that primarily feed on small-sized (pico and nano size) phytoplankton (Calbet and Landry 1999; Froneman 2002b; Fileman et al. 2007).

Despite the importance of the feeding behavior of copepods,

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research in Korea on copepod feeding habits is absolutely lacking. At this time, there have only been two reported studies (Shin and Choi 1992; Yang et al. 2009) on copepods. One study tested *Calanus sinicus* and *Acartia clausi* (*A. omorii*) in Gyeonggi Bay and the other tested *C. sinicus* and *Neocalanus plumchrus* in Ulleung Basin.

The objective of this study was to understand the role of calanoid copepods in changes of biomass and size composition of phytoplankton in Jangmok Bay on the south coast of Korea. To that end, grazing pressure and size selectivity of calanoid copepods on biomass of size-fractionated phytoplankton (<3 μm, 3-20 μm, >20 μm) was measured by the bottle incubation method using natural seawater as the food medium.

2. Materials and Methods

Monthly grazing experiments of calanoid copepods on phytoplankton were carried out at a research wharf (34°59'37.8"N, 128°40'28.2"E) at the South Sea Research Institute, which is a part of the Korea Ocean Research and Development Institute (KORDI) located on Jangmok Bay, Geoje Island from November 2004 to October 2005 (Fig. 1). Conductivity-temperature-depth probes (Idronaut, Ocean Seven 319) were used to measure water temperature and salinity *in situ*. Calanoid copepod specimens were collected for the experiment by vertically hauling a conical-type net with a mesh size of 200 μm. Specimens were carefully diluted in a 20-L container with surface seawater and moved to the laboratory. Only healthy calanoid copepods were isolated quickly using sterile pipettes under a dissecting microscope (Zeiss Model SV11). The sorted calanoid copepods were placed in seawater filtered through Whatman GF/F filters. The sorting process was conducted in the laboratory under the same temperature conditions as surface water.

For the food medium of calanoid copepods, seawater was collected from the surface layer (0.5 m) using a clean Niskin water sampler. Seawater from the Niskin water sampler was gently drained into a 20-L polycarbonate carboy. During the filling of No. 7 polycarbonate bottles (2.75 L) that had been prewashed with 10% HCL and Milli-Q water, the seawater was then screened through a 200-μm mesh to remove most grazers. The No. 7 polycarbonate bottles consisted of 3 experimental bottles in which isolated calanoid copepods were placed, 3 control bottles filled only with seawater filtered through the 200-μm mesh, and 1 initial bottle to measure Chl-*a* and the abundance of tintinnid ciliates at the initial condition (t_0). Thirty individuals were placed in the 3 experimental bottles based on the

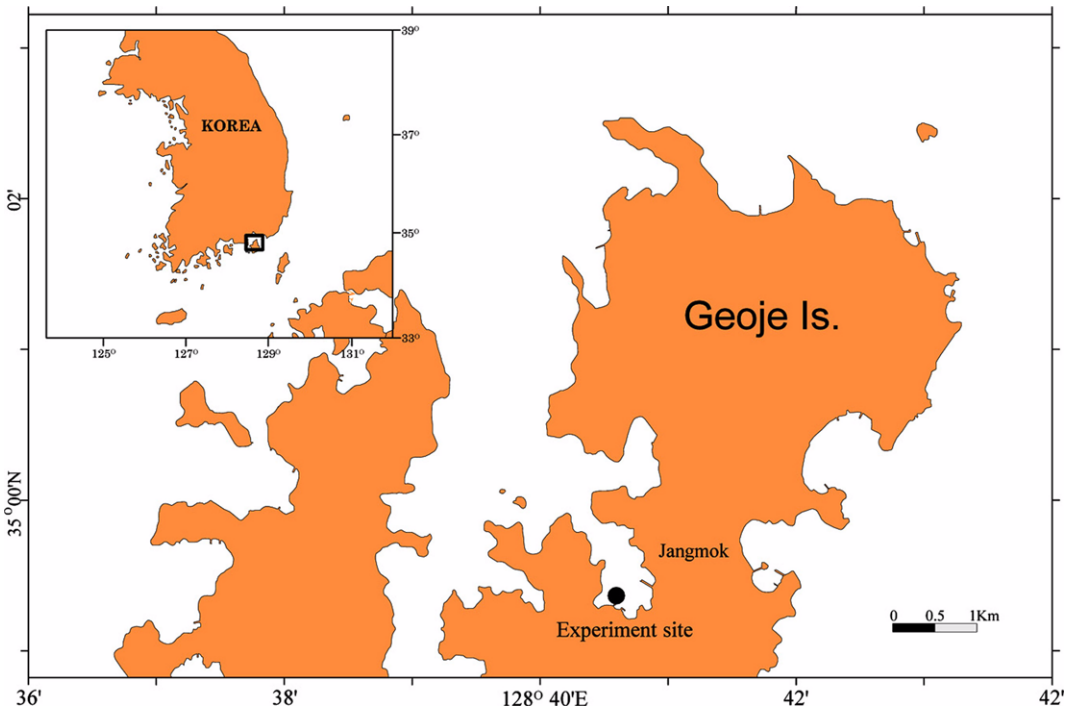

Fig. 1. Map showing experiment site location in Jangmok Bay

proportion that appeared during advance identification of abundance of calanoid copepod species at the experiment site. All the bottles were completely filled to avoid air bubbles. Incubations were carried out for 20-24 h in a large acrylic container with flow-through surface water at *in situ* temperature and the bottles were rotated intermittently by hand.

At the end of the incubation period, water samples were taken from all the bottles for measurement of Chl-*a* and a total count of tintinnid ciliates. Chl-*a* concentration was measured in 3 size categories (< 3 μm, 3-20 μm, > 20 μm), which indicate picophytoplankton, nanophytoplankton, and microphytoplankton, respectively. Nylon mesh (20 μm) and polycarbonate filters (3 μm) were used for size fractionation of the water samples. 500 mL of seawater from each category was filtered through Whatman GF/F filters for Chl-*a* analysis. The filters were placed in 90% acetone for 24 h at -20 ºC and a high performance liquid chromatography (HPLC) with a SCL-10AVP system (Shimazu, Japan) was used to determine the Chl-*a* concentration.

500 mL water samples were preserved with formalin (2% final concentration) and concentrated to 25 mL by sedimentation for at least 24 h to determine the abundance of tintinnid ciliates. Then, 1-5 mL of these concentrated samples were enumerated under a light microscope (Zeiss Model Axioplan 2) using a Sedgwick-Rafter chamber.

Individual ingestion rates of calanoid copepod, *I*, (ng Chl-*a* copepod^{-1} day^{-1} for 3 size categories of Chl-*a* and number$_{tintinnid}$ copepod^{-1} day^{-1} for tintinnid ciliates) were calculated using Frost's formula (Frost 1972).

$$I = F \times C$$

where F is clearance rate (L copepod^{-1}day^{-1}) and C is the average concentration of prey (L^{-1}) during the incubation period.

Clearance rate is calculated by

$$F = [\ln(C_0/C_c) - \ln(C_0/C_e)] \times V/(t \times N)$$

where C_0 is the initial concentration of prey (Chl-*a* and tintinnid ciliates); C_c and C_e are the prey concentrations in the control and experimental bottles at the end of the incubation period, respectively; V is the volume of the incubation bottle (in L); N is number of calanoid copepods added to the incubation bottle and t is the incubation time (h).

The average concentration of prey is calculated by

$$C = C_0[(e^{ke} - 1)/k_e],\ k_e = \ln(C_0/C_e)$$

The calanoid copepod community ingestion rate (mg Chl-*a* m^{-3} day^{-1}) on Chl-*a* was estimated by multiplying the abundance of *in situ* calanoid copepods by the individual ingestion rate. Grazing pressure (%) was calculated as a percentage of initial Chl-*a* concentration consumed by the community ingestion rate.

3. Results

Environmental conditions and population of calanoid copepods

Table 1 and Fig. 1 show the environmental conditions in the water surface layer. Surface water temperature ranged

Table 1. Summary of hydrographic conditions, initial chlorophyll (Chl)-*a* concentrations and percentage of Chl-*a* in three size-fractions during grazing experiments

Experiment number	Date	Temp (ºC)	Sal (psu)	Tintinnid ciliates (indiv. L^{-1})	Initial Chl-*a* (μg L^{-1})				% of Chl-*a*		
					<3 μm	3-20 μm	>20 μm	Total	<3 μm	3-20 μm	>20 μm
1	29 Nov 2004	14.0	32.0	0	4.8	2.7	1.7	9.2	52.4	29.2	18.4
2	20 Dec 2004	12.1	32.6	0	3.2	3.7	1.1	8.0	39.7	46.1	14.2
3	31 Jan 2005	5.0	33.7	0	1.8	0.6	0.1	2.5	70.6	24.8	4.6
4	28 Feb 2005	6.0	33.8	34	1.0	1.1	0.3	2.3	41.9	47.0	11.2
5	30 Mar 2005	10.7	32.9	1	1.0	0.2	0.9	2.1	46.5	10.7	42.8
6	29 Apr 2005	15.7	33.0	0	3.7	0.4	6.5	10.6	34.6	3.9	61.4
7	30 May 2005	18.9	33.3	0	0.5	3.2	0.7	4.4	11.3	72.5	16.1
8	30 Jun 2005	22.4	32.0	498	5.3	5.7	1.0	12.1	44.0	47.6	8.4
9	27 Jul 2005	24.9	32.3	124	2.0	4.3	1.3	7.7	26.0	56.7	17.4
10	30 Aug 2005	24.6	29.3	1	1.6	6.8	2.9	11.3	14.3	60.1	25.7
11	28 Sep 2005	23.9	30.8	10	5.2	8.5	11.8	25.5	20.3	33.4	46.3
12	26 Oct 2005	19.5	31.5	306	2.1	1.9	2.1	6.1	34.5	31.2	34.2

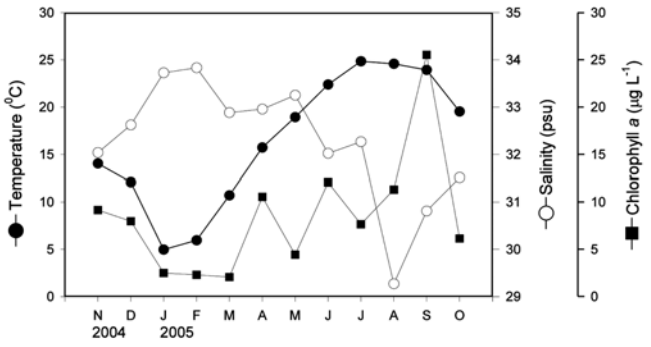

Fig. 2. Variations in temperature, salinity, and total chlorophyll *a* concentrations during grazing experiments

between 5.0 °C and 24.9 °C. Salinity varied between 29.3 psu and 33.8 psu and was relatively low in August. The concentration of total Chl-*a* varied dramatically, ranging from 2.1 to 25.5 μg L^{-1}. In general, high concentrations (14.1 μg L^{-1} on average) appeared with high water temperature (> 20 °C). Conversely, there were low concentrations (2.4 μg L^{-1} on average) observed with low water temperature (< 10 °C). With the exceptions of March 2005 and May 2005, high concentrations (> 5 μg L^{-1}) were recorded in water temperature of > 10 °C in all months of the study. Concentrations of the < 3 μm category, indicating biomass of picophytoplankton, accounted for 11.3-70.6% (average 33.3%) of total Chl-*a* and accounted for a higher percentage of total Chl-*a* in November 2004 and January 2005. Concentrations of the 3-20 μm category, indicating biomass of nanophytoplankton, accounted for 3.9-72.5% (average 39.1%) of total Chl-*a* and accounted for a higher percentage from May-September. Concentrations of the > 20 μm category, indicating biomass

Table 2. Species composition and abundance (indiv.m^{-3}) of calanoid copepods sampled at experiment station during study periods

Date	2004								2005			
Taxon	Nov 29	Dec 20	Jan 31	Feb 28	Mar 30	Apr 29	May 30	Jun 30	Jul 27	Aug 30	Sep 28	Oct 26
Acrocalanus sp.												85
Acartia erythraea											56	231
Acartia omorii	1399	340	1322	1396	835	6		14	626		12	37
Acartia steueri		43	2617	392	334							
Calanus sinicus				35	56							
Centropages abdominalis	11	10	139	692	543	2	5					
Centropages furcatus												8
Eucalanus spp.												21
Eurytemora pacifica			28	12	14	3						
Paracalanus parvus	204	115	153	46	139	1	6	20	906	2136	186	463
Pseudodiaptomus marinus									19	119		6
Temora turbinata	26											
Total	1640	508	4259	2573	1921	12	11	34	1551	2255	254	851

Table 3. Calanoid copepods used during grazing experiments. Number of individuals is per 2.75 L incubation bottle

Date	2004								2005			
Taxon	Nov 29	Dec 20	Jan 31	Feb 28	Mar 30	Apr 29	May 30	Jun 30	Jul 27	Aug 30	Sep 28	Oct 26
Acrocalanus sp.												3
Acartia erythraea											7	8
Acartia omorii	26	19	9	16	14	14		12	12		1	1
Acartia steueri		3	19	5	5							
Calanus sinicus					1							
Centropages abdominalis		1	1	8	8	5	14					
Eucalanus spp.												1
Eurytemora pacifica						8						
Paracalanus parvus	4	7	1	1	2	3	16	18	18	28	22	17
Pseudodiaptomus marinus										2		
Temora turbinata												
Total	30	30	30	30	30	30	30	30	30	30	30	30

of microphytoplankton, accounted for 4.6-61.4% (average 27.6%) of total Chl-*a*.

There were 9 genera and 12 species of calanoid copepods that occurred during the experimental period, including 2 unidentified species (Table 2). The abundance of calanoid copepods varied remarkably, ranging from 11 indiv.m^{-3} to 4259 indiv.m^{-3}. In January, February, and August, the abundance was relatively high (> 2000 indiv.m^{-3}) while it was low (< 40 indiv.m^{-3}) in April, May, and June. *Acartia omorii*, *A. steueri*, and *Centropages abdominalis* occurred predominantly in low water temperature (January-March), whereas *Paracalanus parvus* was predominant in high water temperature (July and August). *Acrocalanus* sp., *Centropages furcatus*, *Eucalanus* sp., and *Temora turbinata* occurred in low abundance (< 100 indiv.m^{-3}) in October and November. The proportion of each species that appeared in each research month at the site (Table 2) was used to determine abundance of calanoid copepods used in the grazing experiments (Table 3). Small species of calanoid copepods, *A. omorii* and *P. parvus*, were primarily used in most of the research months. Another small species, *A. steueri*, and *C. abdominalis*, an intermediate-sized species, were mainly used for experiments from December 2004 to May 2005.

Ingestion rates of calanoid copepods

The daily ingestion rate of individual calanoid copepod versus total phytoplankton biomass during the experiment period was > 100 ng Chl-*a* copepod^{-1} day^{-1} in April and May 2005, which was higher than in other periods (Fig. 3). *A. omorii*, *C. abdominalis*, *P. parvus*, and *Eurytemora pacifica* were used as grazers in experiments during this period. A negative ingestion rate was observed in the measurement process from June to September 2005, which means that abundance by growth of phytoplankton during incubation was greater than that consumed by calanoid copepods. There was low ingestion rate only in February 2005 in biomass in the < 3 μm category. During other periods, a negative ingestion rate appeared. This suggests that phytoplankton was not a preferred food of calanoid copepods. In the 3-20 μm category, there was a positive ingestion rate of < 50 ng Chl-*a* copepod^{-1} day^{-1} from November 2004 to May 2005. During the period of June-October 2005, which was the period of relatively high water temperature, there was a negative ingestion rate that was clearly divided by period. The ingestion rate of calanoid copepods in the > 20 μm category was positive over all the experiment periods, with the highest ingestion rate of > 200

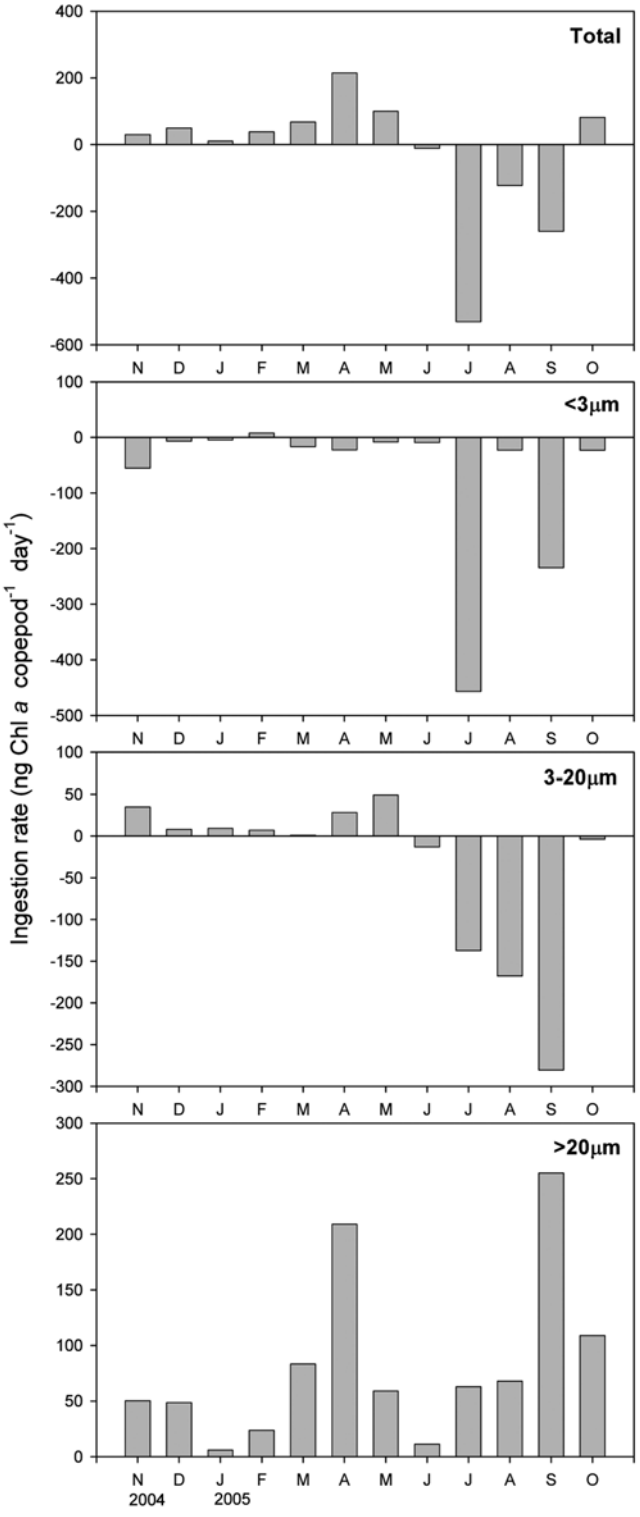

Fig. 3. Variations in ingestion rate of calanoid copepod on total and three size-fractions of phytoplankton biomass

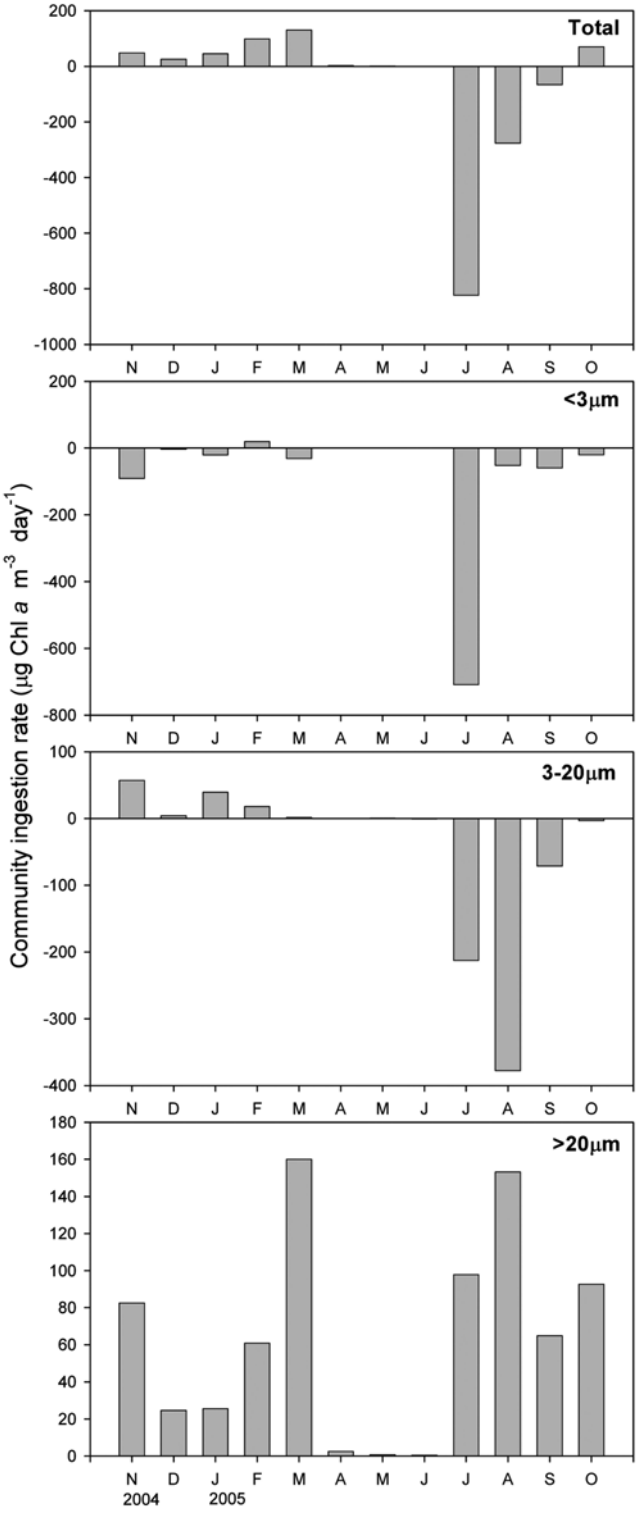

Fig. 4. Variations in community ingestion rate of calanoid copepods on total and three size-fractions of phytoplankton biomass

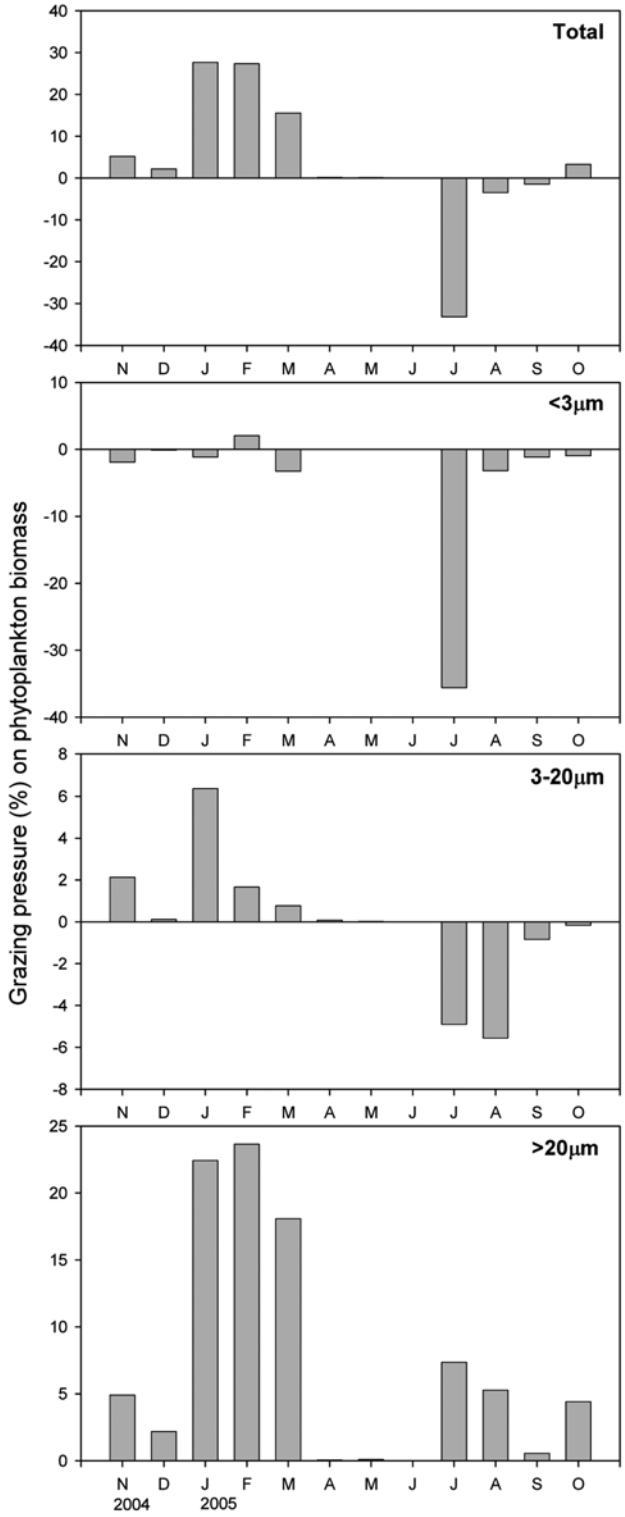

Fig. 5. Variations in grazing pressure of calanoid copepods on total and three size-fractions of phytoplankton biomass

ng Chl-*a* copepod^{-1} day^{-1} in April 2005 and September 2005. Calanoid copepods preferred phytoplankton in the > 20 μm category rather than those in the < 3 μm and 3-20 μm categories based upon analysis of the ingestion rates against

3 size categories of phytoplankton.

Figure 4 shows calanoid copepod community ingestion rates. Overall, the community ingestion rate was higher in the > 20 μm category than the < 3 μm and 3-20 μm categories. The abundance of calanoid copepods greatly influenced changes in the community ingestion rate versus phytoplankton biomass. This aspect was clear in April and May when calanoid copepods emerged at < 15 indiv.m^{-3}. This indicates that, although individual ingestion rates were relatively high in this period, low calanoid copepod abundance led to the very low community ingestion rate of < 3 μg Chl-*a* m^{-3} day^{-1} (sum of the 3-20 μm and > 20 μm categories, but not the < 3 μm category).

Grazing pressure of calanoid copepods

Between < 0.1% and 27.7% of the initial biomass of total phytoplankton was consumed by calanoid copepods during the experimental period (Fig. 5). Grazing pressure was high (> 15%) in January-February 2005, but low (< 5%) in other months. Especially during the period of April-June 2005, grazing pressure was at the lowest level except for negative values (July-September 2005) due to a low abundance of calanoid copepods. Most of the research months showed negative values (except for February 2005) that were unaffected by feeding of calanoid copepods in the < 3 μm category. Grazing pressure ranged from 0.1% to 6.4% only from November 2004 to May 2005 in the 3-20 μm category. However, grazing pressure was negative from June to November 2005. In this category, grazing pressure was < 2% in all research periods except January 2005, when it was 6.4%. Grazing pressure against the > 20 μm category was between < 0.1% and 23.6%. This was the highest grazing pressure among the size categories of phytoplankton.

4. Discussion

The acquisition of reliable data is the most important concern in studying zooplankton feeding. There have been various approaches to feeding studies, but each method has specific problems and none is completely satisfactory (Båmsted et al. 2000). Application of the incubation method in this experiment has methodological problems arising out of so-called bottle effects such as stress of capture, differences in light penetration and turbulence, crowding of grazers, and enhanced growth of algae assemblages because of excrement (Roman and Rublee 1981; Sautour 1994). Incubation has its own strength in enabling direct and convenient measuring of feeding effects of zooplankton on natural prey despite these problems (Gauld 1951; Paffenhöfer 1988). Also, incubation was recently applied in studies on feeding selectivity and ingestion rate experiments against size categories of phytoplankton (Lonsdale et al. 1996; Liu and Dagg 2003; Liu et al. 2005; Olson et al. 2006; Gifford et al. 2007; Campbell et al. 2009). Therefore, incubation is useful as a way to measure feeding effects of zooplankton on various forms and sizes of diverse prey.

It was found that phytoplankton in the > 20 μm category was preferred during all of the experiment periods based upon our analysis of ingestion rates of calanoid copepods against 3 size categories of phytoplankton. In the sense that it is easier to find and capture larger prey, preference of the > 20 μm category is valid (Stoecker and Egloff 1987). *Neocalanus cristatus*, a large species of copepod, and *C. abdominalis*, an intermediate-sized one, selectively fed on larger phytoplankton (> 20 μm) in reports on experiments with diverse mesozooplankton groups (Tsuda and Nemoto 1988; Liu and Dagg 2003; Liu et al. 2005). However, our experiment was only conducted on calanoid copepods, and small-sized species such as those belonging to the *Acartia* genus and *P. parvus*, were primarily used. The ingestion rate of calanoid copepods in the > 20 μm category showed a high correlation with prey density ($r = 0.93$, $p < 0.01$) (Fig. 6). This means that calanoid copepods selectively fed on phytoplankton of > 20 μm. This result also indicates that feeding of calanoid copepods could affect standing crop and species composition of phytoplankton of > 20 μm.

Generally, copepods do not prefer phytoplankton that are < 5 μm as a food source. This has been reported with large as well as small species of copepods (Nival and Nival 1976; Berggreen et al. 1988; Pagano et al. 2003; Fileman et al. 2007). Also, in this experiment, the ingestion rate in the < 3 μm category was negative in all periods except February 2005. This clearly suggests that this phytoplankton was not used as prey by calanoid copepods.

The ingestion rate was negative in the intermediate-sized category (3-20 μm) from June 2005 to October 2005, when water temperature was high. However, it was positive from November 2004 to May 2005, when water temperature was relatively low. This suggests a clear division by period. In terms that small-sized species in copepods effectively feed on large-sized (> 20 μm) and intermediate-sized (3-20 μm) particles (Gismervik et al. 1996; Broglio et al. 2004), it is

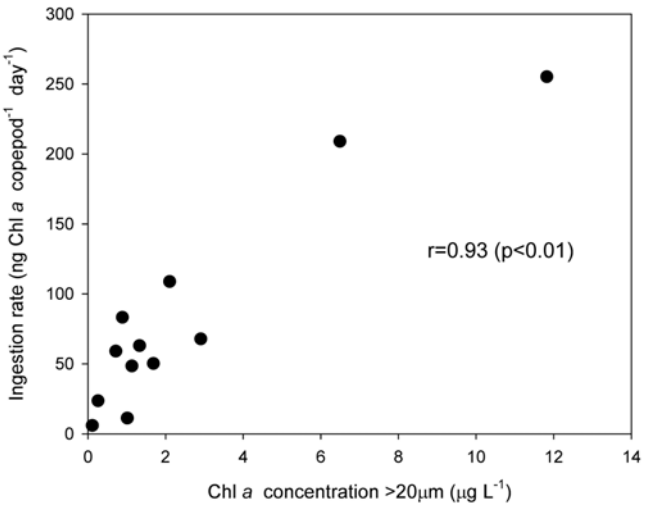

Fig. 6. Relationships between microphytoplankton (>20 μm) biomass (Chl-*a*) and ingestion rate of calanoid copepod

highly probable that the negative ingestion rate in the 3-20 μm category from June 2005 to October 2005 has been underestimated. Nejstgaard et al. (2001) and Liu et al. (2005) reported that such an underestimation might mainly be caused by the incubation process in control bottles without copepods and in experimental bottles with copepods. First, excrement resulting from the feeding of calanoid copepods in experimental bottles promotes growth of subject prey (3-20 μm). Second, during feeding activity of calanoid copepods against microzooplankton (especially ciliates), prey density in the 3-20 μm category was increased in experimental bottles.

In the results of this experiment, we believe that the first factor was not a main cause of underestimation (negative ingestion rate) because small-sized calanoid copepods were used in the experiment. In addition, the experiment took place on the coast where the concentration of nutrients was comparatively high. There was also a consistent negative ingestion rate pattern by period (only in high water temperature, June-October 2005). In fact, the degree of growth promotion of phytoplankton based on excrement of copepods is known to be insignificant in cases of feeding experiments where there is high concentration of nutrients (Liu et al. 2005).

Small-sized copepod species often show a preference for microzooplankton even when suitably-sized phytoplankton are available (Atkinson 1996; Castellani et al. 2005). This behavior was reported to be related to high egg productivity (Ohman and Runge 1994). Species in the *Acartia* genus that were used in all periods except May 2005 and August 2005 had a very strong omnivory tendency. They are also known to have great capacity to feed on ciliates (Gifford and Dagg 1988; Rollwagen-Bollens and Penery 2003). Among ciliates, the preference is for shelled tintinnid ciliates (Gifford et al. 2007). *P. parvus,* used in concentrate between May and October (the period of high water temperature), is capable of feeding on heterotrophic dinoflagellates and ciliates as well as on phytoplankton (Suzuki et al. 1999). Specifically, in terms of quality and quantity, ciliates are reported to be the best food source to increase egg productivity (Fessenden and Cowles 1994; Zeldis et al. 2002). As verified through previous studies, species belonging to the *Centropages* genus have a strong tendency toward omnivory (Calbet et al. 2007). Due to this, it can be understood that *C. abdominalis*, which was used from December 2004 to May 2005 (the period of relatively low water temperature), is also capable of feeding on microzooplankton, including ciliates.

We measured the degree of predation to verify the second factor of underestimation (increase of prey density) in the 3-20 μm category considering that most species of calanoid copepods used in this experiment showed an omnivorous tendency in feeding. Tintinnid ciliates appeared in February 2005 and March 2005 and between June 2005 and October 2005, the period of high water temperature. They showed high density mainly in June, July, and October (Table 1). Based upon the results from the predation measurement of calanoid copepods according to changes of tintinnid ciliate abundance, the minimum and maximum predation rates were < 0.1 and 13.3 $number_{tintinnid}$ $copepod^{-1}$ day^{-1} in August 2005 and October 2005, respectively (Fig. 7). However, in October 2005, although the degree of underestimation in the 3-20 μm category (Fig. 3) was very low (near zero), the density of tintinnid ciliates (Table 1) and the predation rate of calanoid copepods on tintinnid ciliates (Fig. 7) were high. While the density of tintinnid ciliates and the predation rate of calanoid copepods on tintinnid ciliates were low in August and September 2005, the degree of underestimation in the 3-20 μm category was very high. Hence, no evident correlation was found in relation to underestimation among the density of tintinnid ciliates, the predation rate on tintinnid ciliates, and the ingestion rate in the 3-20 μm category. In general, calanoid copepods prefer oligotrich ciliates to tintinnid ciliates (Gifford et al. 2007). In Jangmok Bay, oligotrich ciliates exhibit a very high density compared to tintinnid ciliates, especially between July and October (Kim and

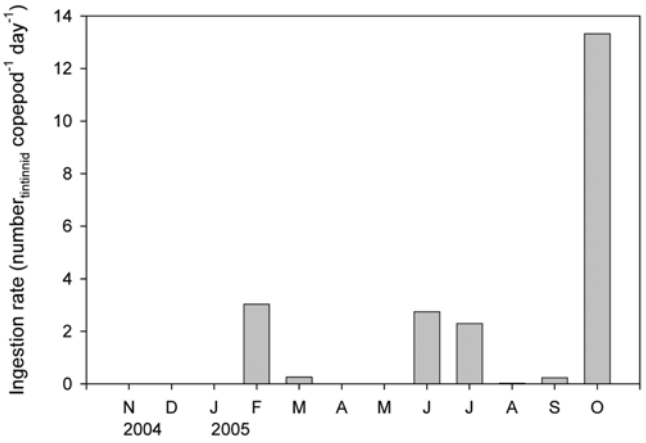

Fig. 7. Variations in predation rate of calanoid copepod on tintinnid ciliates during grazing experiments

Jang 2008). For this reason, the predation rate of calanoid copepods on total ciliates (tintinnids and oligotrichs) between June 2005 and October 2005 was much higher than on tintinnid ciliates alone. However, we failed to measure the predation rate on oligotrich ciliates alone. Thus, only the possibility of the underestimation of the phytoplankton in the 3-20 μm category was checked based on the predation rate measurement on tintinnid ciliates, and the definite cause of underestimation could not be verified. In order to prove the second factor, it will eventually be necessary to conduct experiments on calanoid copepod predation on oligotrich ciliates.

The proportion of each species available on site determined the number of calanoid copepods used for grazing experiments. A shift was discovered in the species composition of the calanoid copepods added to experimental bottles during the experimental period. Specifically, *A. omorii*, *A. steueri*, and *C. abdominalis* were primarily used in the experimental bottles when positive ingestion rates were obtained in the 3-20 μm category between November 2004 and May 2005. *P. parvus* was mainly used between June 2005 and October 2005 when negative ingestion rates were obtained in the same category. Particularly in October 2005 and September 2005, 28 and 22 individuals were used, respectively, when the most negative ingestion rates were obtained. Consequently, it is considered that the shift in the calanoid copepod species composition used in the grazing experiments is one of the major causes of the negative ingestion rate in the 3-20 μm category.

Daily grazing pressure of zooplankton (including copepods) shows changes by region, year, and season, but is generally known to consume < 5% of phytoplankton biomass (Chl-*a*) according to previous studies (Dagg 1993; Dam et al. 1995; Atkinson and Shreeve 1995; Dagg 1995; Barquero et al. 1998). However, other studies have rarely reported that biomass of phytoplankton is mostly or completely consumed to exceed the primary productivity (Bathmann et al. 1990). In this experiment, daily grazing pressure of calanoid copepods against total phytoplankton biomass was 3.6 ± 15.8% on average, including negative values, which is consistent with results from previous studies. From November 2004 to October 2005, grazing pressure ranged from < 0.1% to 27.7% and there was great variation by season. We believe that these differences were based on calanoid copepod abundance at the time of the experiment, the individual ingestion rate, and differences in prey density and form. While the individual ingestion rate was not especially high in January-February 2005 (27.7%), winter grazing pressure was very high (27.4%). This can be explained by the emergence of a high abundance of calanoid copepods (Table 2) during this period. Conversely, very low abundance produced low grazing pressure (< 0.1%) during the period of April-June 2005. During the period of July-September 2005, there was a positive ingestion rate of 0.5-7.4% in the > 20 μm category during the experiment period when high water temperature (around 24 °C) was recorded, but grazing pressure of calanoid copepods against total phytoplankton biomass was negative. This negative ingestion rate is strongly suggestive of calanoid copepod consumption of prey other than phytoplankton outside the > 20 μm category to satisfy their own nutritional requirements (Stoecker and Capuzzo 1990; Fileman et al. 2007). In the size category of > 20 μm, grazing pressure of calanoid copepods against phytoplankton was 7.4% on average. This was much higher compared to grazing pressure in the 3-20 μm and < 3 μm categories. Grazing pressure in the > 20 μm category ranged from < 0.1% to 23.6% and was > 15% in winter (January and February) and early spring (March). This is indicative of changes in the biomass and size structure of phytoplankton in winter and early spring.

In conclusion, calanoid copepods in Jangmok Bay of Geoje Island, Korea directly or indirectly affected changes in phytoplankton size structure through selective feeding on the > 20 μm category. Also, calanoid copepods played an important role to control biomass of phytoplankton in the > 20 μm category in the period of low water temperature

(January-March 2005). Although we found that the feeding form of calanoid copepods changes according to emergence of tintinnid ciliates, we were unable to elucidate the general roles of ciliates in this study. Thus, clearer identification of the feeding relationship between microzooplankton such as ciliates and calanoid copepods is required.

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