

Feeding activity of the copepod *Acartia hongii* on phytoplankton and micro-zooplankton in Gyeonggi Bay, Yellow Sea

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ABSTRACT

To improve our understanding of the trophic link between micro-zooplankton and copepods in Gyeonggi Bay, Yellow Sea, the diet composition, ingestion rates, and prey selectivity of *Acartia hongii*, known as the most abundant and widespread copepod species, was estimated by conducting *in situ* bottle incubation throughout the different seasons. The results showed that *A. hongii* preferentially grazed on ciliate and heterotrophic dinoflagellate of a size ranging from 20 to 100 μm rather than phytoplankton. Although micro-zooplankton comprised only an average 13.7% of the total carbon available in the natural prey pool, micro-zooplankton accounted for >70% of the total carbon ration ingested by *A. hongii* throughout the year, except for winter diatom blooming periods when *A. hongii* obtained about 60% of its carbon ration from phytoplankton. Our results demonstrated that *A. hongii* modified their diet composition and feeding rates in response to change in composition and size of prey available to them, and that *A. hongii* preferentially ingested micro-zooplankton over phytoplankton. Feeding activity of *A. hongii* could therefore affect the species composition and size structure of natural plankton communities in this study area, particularly the micro-zooplankton. Strongly selective feeding and high grazing pressure by *A. hongii* on micro-zooplankton shows the role of trophic coupling between copepods and the microbial food web in the pelagic ecosystem of Gyeonggi Bay.

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1. Introduction

Pelagic copepods have been considered as being primarily major grazers on phytoplankton in most marine ecosystems (Dahms and Qian, 2005). In recent years it has become increasingly clear however that micro-zooplankton plays a significant role in not only competing with copepods as grazers of phytoplankton but also as being an important copepod prey (Calbet and Landry, 2004; Gismervik, 2006). This double role of micro-zooplankton may be a critical effect in marine planktonic food webs (Calbet and Landry, 2004). The intermediate trophic position of micro-zooplankton may also explain the uncoupled relationships between copepod production and phytoplankton biomass (Saiz et al., 1999; Vargas et al., 2008). A significant number of studies have highlighted the potential role of micro-zooplankton (Gismervik, 2005), and have reported high grazing rates and preference of pelagic copepods on micro-zooplankton in contrasting trophic situations, ranging from

abundant primary production such as during spring blooms (Leising et al., 2005; Liu et al., 2005; Fileman et al., 2007) to oligotrophic areas (Pérez et al., 1997; Broglio et al., 2004). Copepod feeding selection on both phytoplankton and micro-zooplankton therefore provides a differential grazing impact. It can directly and indirectly affect the plankton community and population structure at lower trophic levels via trophic cascades (Calbet and Saiz, 2005; Leising et al., 2005; Olson et al., 2006; Vargas et al., 2008).

Gyeonggi Bay, considered a temperate eutrophic coastal area, has the potential for high levels of primary productivity because of a large input of nutrients and organic matter from the Han River (Chung and Park, 1988; Youn and Choi, 2008). Phytoplankton blooms therefore periodically occur throughout the year (Yang et al., 2008). The copepod *Acartia hongii* is known to be the most abundant and widespread planktonic copepod species in Gyeonggi Bay, being present throughout the year and accounting for 44% of Gyeonggi Bay's average copepod assemblage (Youn and Choi, 2003). Previous studies have reported that *A. hongii* had a low impact on the standing stock of phytoplankton (0.01–15.8%, according to Seo and Choi, 2008), and that egg production in *A. hongii* is affected by ciliate abundance during the warm season (Youn and Choi, 2007). In

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addition, the carbon requirement of micro-zooplankton in Gyeonggi Bay ranges from 60 to 83% of the daily primary production (Yang et al., 2008). These results imply that heterotrophic food sources (i. e., ciliates and heterotrophic dinoflagellates) may be important for sustaining copepod populations in this study area. No information is however available on the relative importance of micro-zooplankton as a food source for *A. hongii* in Gyeonggi Bay.

We present here a study to improve our understanding of the trophic link between micro-zooplankton and copepods in Gyeonggi Bay. This study was guided by two hypotheses: (i) that micro-zooplankton should be an important component of the diet of *A. hongii* in the productive ecosystem of Gyeonggi Bay, and (ii) that the relative contributions of phytoplankton and micro-zooplankton to *A. hongii* diets should vary according to the trophic situation. In order to evaluate these hypotheses, we analyzed the diet composition, ingestion rate and prey selectivity of *A. hongii* under diverse natural prey assemblages.

2. Materials and methods

2.1. Sampling and grazing experiments

This study was conducted from January 1999 to November 2000 at two sites in Gyeonggi Bay, which is located in the mid-eastern part of the Yellow Sea at the Korean coast (Fig. 1). Station 1 was located in the inner part of Gyeonggi Bay. Station 2, located off the sluice gate of lake Shihwa, was considerably eutrophic because of discharges of polluted water through the gate and from neighboring industrial complexes (Han and Park, 1999).

Water samples were collected from the surface using Niskin bottles and were gently transferred to a 20 L carboy. *Acartia hongii* were collected by oblique tows from depths of 10–20 m to the water surface with a 200 m³ conical net. The copepods were gently diluted, transferred into a cooler that was filled with surface water, and

transported to the laboratory as soon as possible. Adult female *A. hongii* were sorted under a dissecting microscope and transferred to 250 mL bottles containing sea water filtered through 0.45 μm membrane filters. After 2 or 3 h, females were transferred to a 1300 mL polycarbonate bottle with 4–5 individual copepods per bottle, filled with sea water pre-screened by gentle reverse filtration through a 200 μm mesh to remove other copepods and large grazers (Table 1). Each experiment was conducted with three sets of replicate treatment bottles, and initial and control bottles (without copepods). To override nutrient enrichment effects from copepod excretion in grazing bottles, the water used in the experiments was pre-enriched with a nutrient mixture of 5 μM NH₄Cl and 1 μM Na₂HPO₄. Incubation was conducted for 24 h on a slowly rotating (approximately 1 rpm) underwater plankton wheel under 300 μm E m⁻² s⁻¹ on a 14:10 h light: dark cycle at *in situ* temperature (Table 1; Youn and Choi, 2007). At the end of the experiment, no dead copepods could be found. At the beginning and end of each incubation period, we collected sub-samples for the assessment of the plankton abundance and composition and chlorophyll *a* concentrations.

2.2. Sample analysis and calculations

Chlorophyll *a* was fractionated into two size categories: total- and nano-, by passing water samples through a 20 μm nylon mesh. We filtered 300 mL of sea water through Whatman GF/F filters. Chlorophyll *a* concentrations were determined using a spectrophotometer after extraction with 90% acetone (Parsons et al., 1984). To determine the abundance of phytoplankton and micro-zooplankton, 250 mL of water was preserved with acidic Lugol's iodine (5% final concentration) and formalin (2% final concentration), respectively. Lugol's iodine preserved samples were stored in the dark and formalin preserved samples were stored at 4 °C in the dark until analysis. To determine abundances of ciliates and diatom, samples preserved in

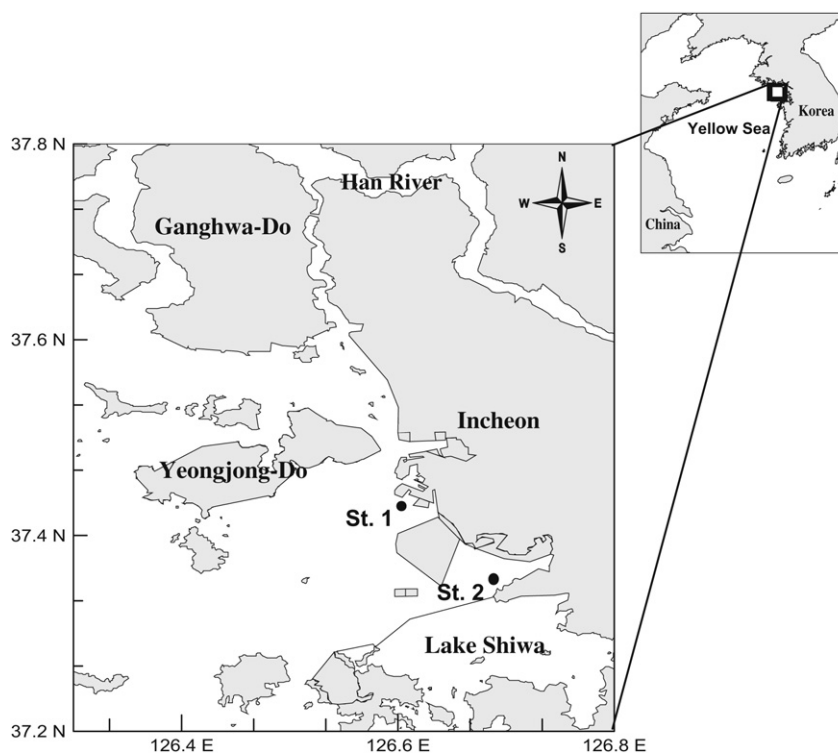


Fig. 1. Map showing the location of sampling stations.

Table 1
Initial conditions, initial chlorophyll *a* concentrations, and dominant species of phytoplankton for all experiments.

Exp. No	Date	Site	Number of per bottle	Temperature (°C)	Chl- <i>a</i> ($\mu\text{g L}^{-1}$)	Net-chl/Total (%)	Dominant species (>15%)
1	Jan., 1999	St.1	5	2.6	14.3	61.5	<i>Paralia sulcata</i> (31%), <i>Nitzschia</i> spp.(24%), <i>Thalassiosira</i> spp. (25%)
2	April, 1999	St.1	5	7.3	5.0	58.0	<i>Asterionella japonica</i> (45%), <i>Detonula</i> sp. (32%)
3	June, 1999	St.1	4	15.9	5.7	19.6	<i>Cryptomonad</i> sp.(70%), <i>Skeletonema costatum</i> (17%)
4	Dec., 1999	St.1	5	4.5	14.0	81.4	<i>Nitzschia</i> spp.(45%), <i>Thalassiosira</i> spp. (42%)
5	April, 2000	St.1	5	10.8	6.2	61.3	<i>Eucampia zodiacus</i> (52%), <i>Chaetoceros</i> spp. (32%)
6	June, 2000	St.1	4	18.2	1.8	44.4	<i>Prorocentrum minimum</i> (62%), <i>Prorocentrum triestinum</i> (24%)
6a	June, 2000	St.2	4	19.2	10.7	25.2	<i>Prorocentrum minimum</i> (72%), <i>Prorocentrum triestinum</i> (20%)
7	July, 2000	St.1	5	22.8	1.1	45.5	<i>Prorocentrum minimum</i> (52%), <i>Navicula</i> spp. (23%)
7a	July, 2000	St.2	5	23.4	3.8	43.6	<i>Prorocentrum minimum</i> (59%), <i>Navicula</i> spp. (21%)
8	Aug., 2000	St.1	5	26.4	6.8	71.9	<i>Eucampia zodiacus</i> (62%), <i>Prorocentrum triestinum</i> (22%)
8a	Aug., 2000	St.2	5	27.4	11.3	64.2	<i>Eucampia zodiacus</i> (68%), <i>Prorocentrum triestinum</i> (24%)
9	Nov., 2000	St.1	4	9.5	1.2	35.0	<i>Paralia sulcata</i> (34%), <i>Thalassiosira</i> spp. (29%)

Lugol's solution were concentrated in sedimentation chambers for ≥ 48 h and were enumerated under an inverted microscope (Olympus IX 70) at 200 \times magnification (Yang et al., 2008). For inspection of the protist cells all ciliates were considered to be heterotrophic, except the autotrophic ciliate *Mesodinium rubrum* (Crawford, 1989). To determine the abundance of heterotrophic dinoflagellates (HDFs) and autotrophic dinoflagellates (ADFs), samples preserved in formalin were concentrated in sedimentation chambers for ≥ 48 h in a refrigerator (4 °C), stained with DAPI (5% final concentration), and then enumerated under an inverted epifluorescence microscope at 200 \times magnification. To estimate the carbon biomass of phytoplankton and micro-zooplankton, cell volume was calculated by measuring cell dimensions with an ocular micrometer on the microscope (Edler, 1979). The conversion factors and equations used to convert cell volume to carbon biomass were: 0.19 $\mu\text{g C } \mu\text{m}^{-3}$ for naked ciliates (Putt and Stoecker, 1989); carbon (pg) = 44.5 + 0.053 \times lorica volume (μm^3) for loricate ciliates (Verity and Langdon, 1984); and carbon (pg) = 0.216 \times [volume, μm^3]^{0.939} for dinoflagellates and diatom (Menden-Deuer and Lessard, 2000). A minimum of 100 cells were counted per sample, identified to genus, and grouped into one of the following major prey categories: diatom, ADFs, loricate ciliates, naked ciliates, athecate HDFs, thecate HDFs. All cells of micro-zooplankton were separated into size classes (<20 μm , 20–50 μm , 50–100 μm , >100 μm). Diatoms, however, could not easily be separated according to their cell size because most dominant diatoms were chain-forming that could be long or large enough to be perceived as large plankton objects by copepods. ADFs were also separated into two classes (<20 μm and >20 μm) because ADFs dominated over 85% being < 20 μm cells during the study periods.

Clearance and ingestion rates by copepods on micro-zooplankton and phytoplankton were calculated by Frost's equation (Frost, 1972), but corrected for reduced micro-zooplankton grazing due to predation by the copepods, according to the formula given by Nejstgaard et al. (2001). The general method proposed by Nejstgaard et al. (2001) was used to correct the bias caused by micro-zooplankton grazing pressure outweighing copepod grazing rates on smaller food items in the incubation bottles. Unfortunately, dilution experiments for micro-zooplankton grazing were not run simultaneously with the bottle incubation at each experiment. In the study different micro-zooplankton grazing coefficient was used: 0.31 for phytoplankton bloom conditions (Experiment 1, 4, 6a and 8a) and 0.36 for non-bloom conditions. These values were estimated through direct measurements in the same region during the previous study (Yang et al., 2008).

In each experiment, the results from all replicates were averaged. Ingestion and clearance rates were calculated only when the difference of prey concentrations between control and experimental bottles was significant (*t*-test, $p < 0.05$). Copepod prey

selectivity was determined using the Chesson's index of selectivity (α) corrected for food depletion (Chesson, 1983; Broglio et al., 2004; Yang et al., 2009). Using these data, we examined whether or not certain size ranges or groups of plankton were preferentially selected by *A. hongii*.

3. Results

3.1. Initial grazing condition, prey biomass, and composition

Chlorophyll *a* concentrations ranged from 1.1 to 14.34 $\mu\text{g L}^{-1}$ (Table 1). Net-fractionated chlorophyll *a* (<20 μm) accounted for 19.6–81.4% (average of 51.1%) of the total chlorophyll *a* concentration with greater contribution of net-fractionated chlorophyll *a* during phytoplankton blooms (i.e., experiments 1, 4, and 8a) and experiments 2, 5, and 8. The initial carbon biomass of phytoplankton ranged from 34.9 to 653.3 $\mu\text{g C L}^{-1}$ (Fig. 2). Phytoplankton blooms occurred during experiments 1, 4, 6a and 8a. During the phytoplankton bloom, the phytoplankton community was dominated by chain-forming diatoms (i.e., *Paralia sulcata*, *Thalassiosira* sp., *Nitzschia* sp., *Eucampia zodiacus*), except experiment 6a in which phytoplankton was dominated by ADF (i.e., *Prorocentrum minimum*). During the study periods, most of the dominant diatoms were chain-formed and their biomass accounted for average 70.3% of total phytoplankton biomass. ADF biomass was more than diatoms' in experiments 3, 6, 6a, 7 and 7a. Particularly, *Cryptomonad* sp. (average 12 μm) was predominant in experiment 3.

The initial carbon biomass of micro-zooplankton ranged from 8.1 to 85.94 $\mu\text{g C L}^{-1}$; values were relatively higher in experiments 6a and 8a than others (Fig. 2). With the exception of experiments 2, 5, 8, and 9, ciliates comprised >50% of the micro-zooplankton biomass. In experiment 5, the high biomass of HDFs occurred. Among the micro-zooplankton, naked ciliates and athecate HDFs were predominant during these experiments. In experiment 8a however, loricate ciliates, specifically *Eutintinnus* sp., and thecate HDFs dominated. Average biomasses of each size-fractionated micro-zooplankton (<20, 20–50, 50–100, and >100 μm) were 8.5%, 37.2%, 37.1%, and 24.2% of total micro-zooplankton biomass, respectively. Among them, ciliate and HDF were dominant in size group of 20–50 μm and 50–100 μm , respectively. Micro-zooplankton thus represented a small portion (less than 15% without a few occasion) of the total available prey resources (i.e., phytoplankton + micro-zooplankton; Table 2).

3.2. Copepod ingestion rates

Clearance and ingestion rates by *A. hongii* on phytoplankton and micro-zooplankton differed depending on prey type and size (Figs.

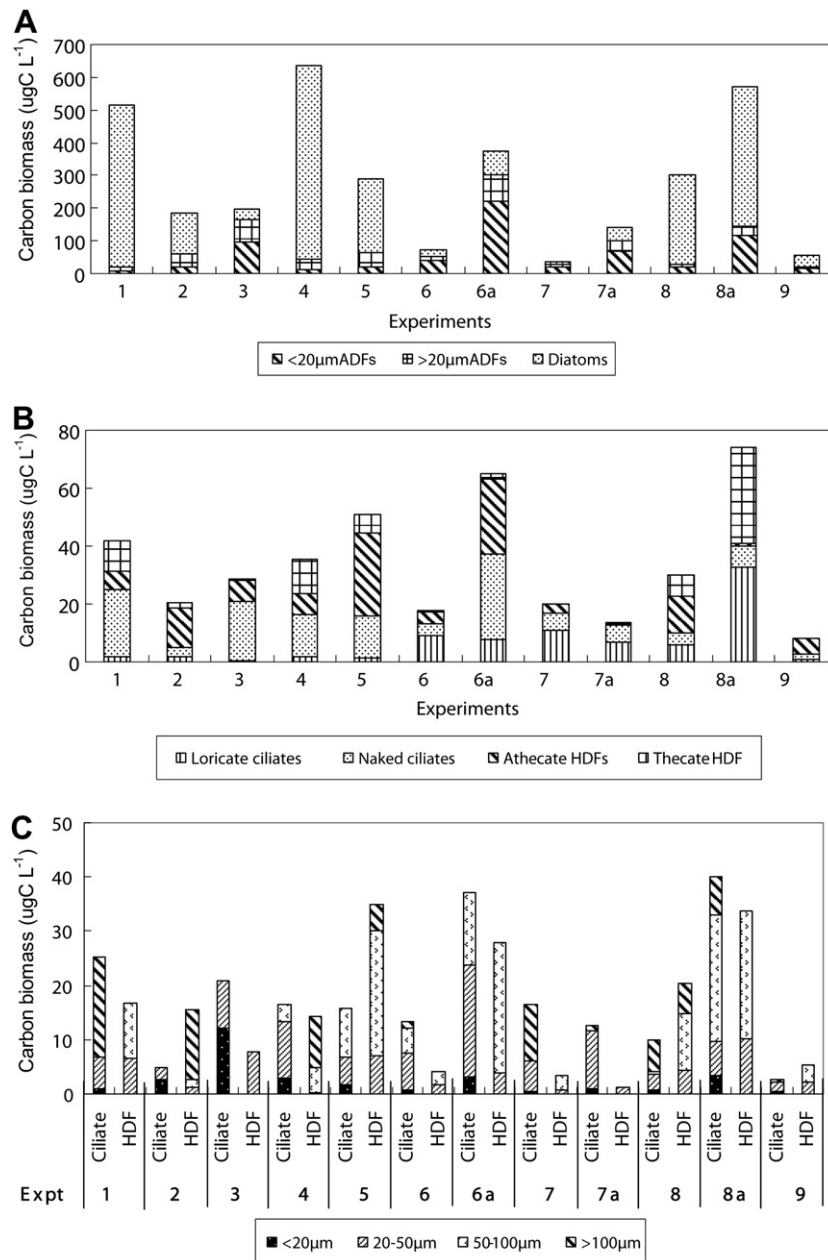


Fig. 2. Initial carbon biomass of micro-zooplankton as a function of composition and size. ADF and HDF are autotrophic dinoflagellates and heterotrophic dinoflagellates, respectively.

3 and 4). Clearance rates for phytoplankton ranged between 16.4 and 69.2 ml copepod⁻¹ d⁻¹, with higher rates during winter diatom blooms (i.e., experiment 1 and 4). Clearance rates for micro-zooplankton ranged between 89.4 and 289.1 ml copepod⁻¹ d⁻¹, with higher rates occurring during summer diatom blooms (i.e., experiment 8a). It appeared that micro-zooplankton was cleared at a higher rate than phytoplankton by *A. hongii*.

The ingestion rate patterns for *A. hongii* consuming phytoplankton and micro-zooplankton were similar to the clearance rate patterns (Fig. 4). Phytoplankton and micro-zooplankton were ingested at rates of 0.2–1.6 $\mu\text{g C copepod}^{-1} \text{d}^{-1}$ and 1.0–5.1 $\mu\text{g C copepod}^{-1} \text{d}^{-1}$, respectively. Diatom accounted for 66.1% of the total phytoplankton carbon ingested by *A. hongii*. The diatom *Thalassiosira* spp. contributed the most to the carbon ration of *A. hongii* diet during winter blooms (Fig. 4). Ingestion rates by *A. hongii* on

ADFs were the highest in experiment 6a, in which ADFs contributed most of total prey biomass. Despite a very high concentration of *Cryptomonad* sp. in experiment 3, negative ingestion rate on *Cryptomonad* sp. was occurred because *A. hongii* mainly fed on diatom *Skeletonema costatum* (Fig. 4). *A. hongii* ingested micro-zooplankton at higher rates than phytoplankton, except during winter diatom blooms. Maximum ingestion rates by *A. hongii* on micro-zooplankton occurred during the summer diatom bloom when the diatom *E. zodiacus* represented 63% of the available prey. Among the micro-zooplankton, ciliates were ingested at higher rates and accounted for 65.1% of the micro-zooplankton carbon ingested by *A. hongii*. Naked ciliates contributed the largest portion to the carbon ration of *A. hongii* consuming micro-zooplankton (average 34.6%). Ingestion rates on loricate ciliates were relatively low compared to naked ciliates; the highest ingestion rate of this

Table 2
Individual taxa of total prey consumed by *Acartia hongii*. Available prey is % of total prey concentrations available during incubation; Eaten is % of total prey concentrations consumed during incubation. MZP is microzooplankton.

	1	2	3	4	5	6	6a	7	7a	8	8a	9
(A) Available prey												
Ciliates	4.5	2.3	9.3	2.4	4.7	14.7	8.5	30.3	8.1	3.0	6.2	4.4
HDFs	3.0	7.5	3.5	2.9	10.3	4.8	6.4	6.1	0.8	6.1	5.3	8.6
Diatoms	89.0	60.6	13.9	87.9	66.0	22.3	16.5	13.4	25.3	82.9	66.0	55.4
ADFs	3.4	29.6	73.4	6.8	19.1	58.2	68.7	50.3	65.8	8.0	22.5	31.7
Size												
MZP <20um	0.2	1.3	5.4	0.4	0.5	0.9	0.7	0.7	0.6	0.3	0.5	0.6
MZP 20–50um	2.2	1.7	7.3	1.6	3.5	9.4	5.8	11.6	7.7	2.2	2.6	6.4
MZP 50–100um	1.8	0.7	0.0	1.6	9.5	7.7	12.1	4.9	0.0	3.3	7.3	5.0
MZP <100um	3.3	6.2	0.0	1.7	1.4	1.3	0.0	19.1	0.6	3.4	1.1	1.0
Phyto. <20um	1.6	10.7	43.6	1.8	6.5	45.6	47.8	38.3	43.7	6.1	17.9	23.7
Phyto. >20um	90.9	79.5	43.7	92.9	78.6	35.0	33.5	25.4	47.3	84.8	70.7	63.3
(B) Eaten												
Ciliates	24.2	34.1	63.9	16.0	18.9	54.2	25.5	76.0	41.7	33.3	60.6	39.0
HDFs	17.6	27.6	20.8	22.3	55.6	23.7	45.7	14.5	23.2	48.9	24.4	34.9
Diatoms	54.7	30.1	14.5	51.9	21.1	10.5	6.7	2.4	11.3	9.6	8.8	18.0
ADFs	3.6	8.2	0.8	9.8	4.3	11.5	22.1	7.1	23.8	8.2	6.3	8.0
	41.8	61.7	84.7	38.3	74.5	78.0	71.2	90.5	64.9	82.2	84.9	73.9
Size												
MZP <20um	0.0	2.6	29.2	3.6	1.9	0.4	4.1	1.7	1.6	0.7	1.8	0.0
MZP 20–50um	16.0	42.4	39.5	19.6	38.5	60.8	12.4	27.2	36.8	33.6	33.3	44.2
MZP 50–100um	14.5	3.6	10.4	8.4	28.2	9.1	55.9	30.9	10.6	44.3	46.8	1.9
MZP <100um	6.7	4.5	0.0	2.3	3.4	1.8	0.0	25.3	6.9	3.4	4.2	10.3
Phyto. <20um	3.2	5.6	0.0	5.8	1.3	7.6	18.6	9.5	22.8	6.7	5.0	5.6
Phyto. >20um	59.6	41.4	29.2	60.2	26.6	20.3	9.1	5.5	21.4	11.4	8.9	37.9

taxon was $3.26 \mu\text{g C copepod}^{-1} \text{d}^{-1}$ in experiment 8a (result not shown). In all experiments, thecate HDFs were a minor contributor for the micro-zooplankton component of *A. hongii* diets, except in experiment 4 and 8.

Even though ciliates provided 8.8% of total available plankton carbon and 40.6% of the total carbon ratio ingested by *A. hongii* (Table 2). Ciliates 20–50 μm and HDFs 50–100 μm were most commonly consumed by *A. hongii* throughout all the experiments

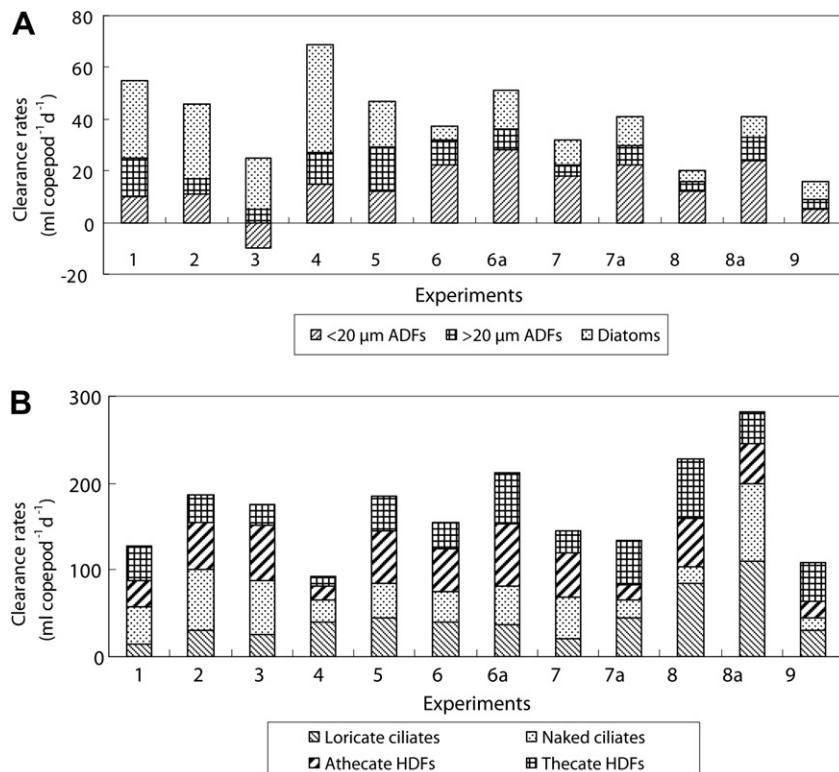


Fig. 3. Mean clearance rates of the copepod *Acartia hongii* on phytoplankton (A) and micro-zooplankton (B). Clearance rates differ significantly between control and experimental prey concentrations (t -test, $p < 0.05$).

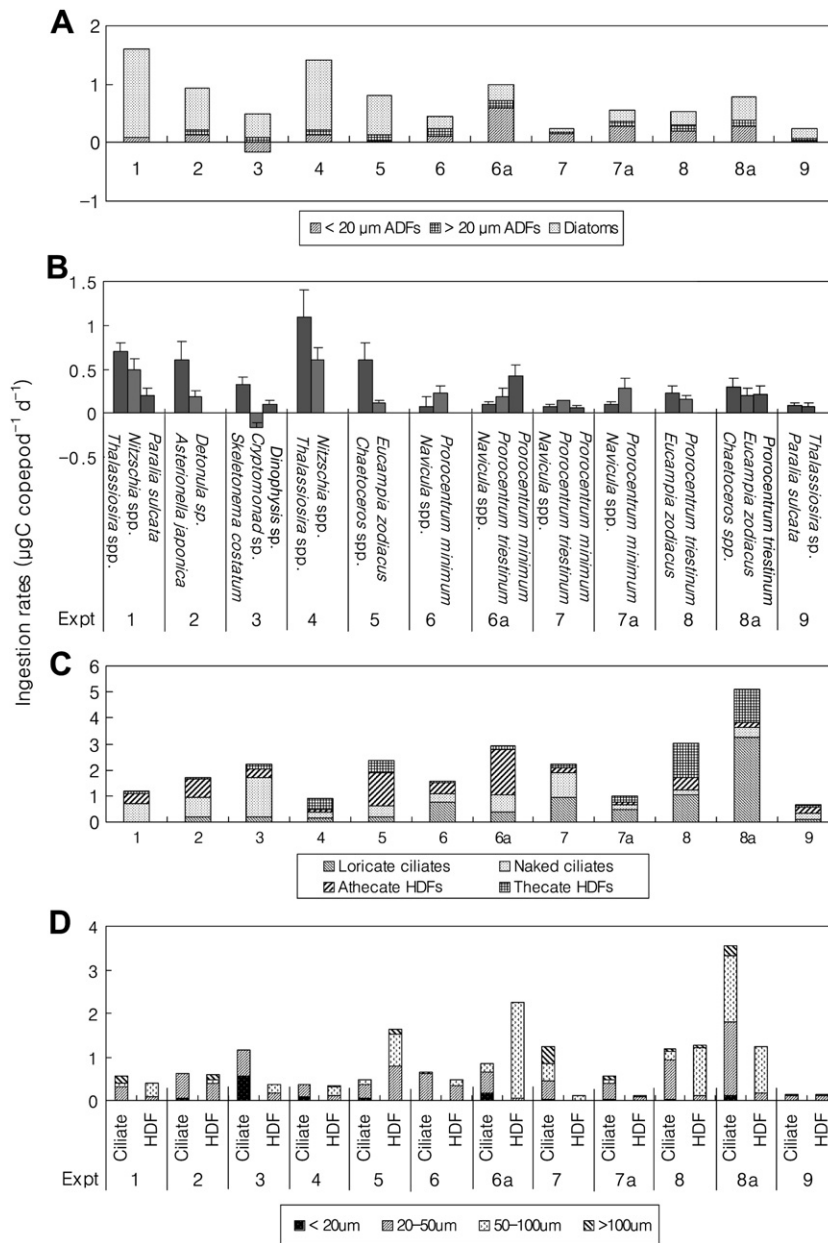


Fig. 4. Mean ingestion rates of the copepod *Acartia hongii* on phytoplankton (A and B) and micro-zooplankton (C and D). Ingestion rates differ significantly between control and experimental prey concentration (*t*-test, $p < 0.05$).

(Fig. 4). Ciliates $< 20 \mu\text{m}$ and HDFs $> 100 \mu\text{m}$ which were ingested by *A. hongii* were however undetected or at low rates. As for the total plankton consumption, micro-zooplankton made up 38.3–90.5% of the total ingested carbon ration of *A. hongii*, although they accounted for an average of 13.7% of the available total prey carbon (Fig. 4; Table 2). Ingestion rates by *A. hongii* were positively correlated with the initial concentrations of phytoplankton and micro-zooplankton (Fig. 5).

3.3. Prey selectivity

The selectivity index showed obvious differences between micro-zooplankton and phytoplankton assemblages; size-dependent patterns of prey selection were also evident (Figs. 6 and 7). Feeding by *A. hongii* showed positive selection for ciliates and HDFs

in all experiments (i.e., most values were above the 1:1 line). *Acartia hongii* showed a strong prey preference on micro-zooplankton over phytoplankton. Size-dependent selective feeding by *A. hongii* showed positive selection for micro-zooplankton with cell sizes that were 20–50 μm and/or 50–100 μm . Ciliates $< 20 \mu\text{m}$ were positively selected in experiment 3, 4, 5, 6a, and 7, whereas phytoplankton $< 20 \mu\text{m}$ were negatively selected in all experiments.

4. Discussion

Our results demonstrated that *A. hongii* modified their diet composition and feeding rates in response to differences in the composition and size of prey available to them, and that *A. hongii* preferentially ingested micro-zooplankton over phytoplankton and positively selected the micro-zooplankton in the productive coastal area studied here.

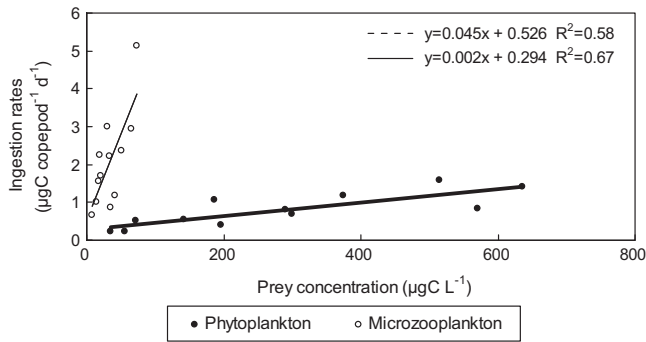


Fig. 5. Relationship between ingestion rates and initial concentration of phytoplankton and micro-zooplankton.

During our experiments, phytoplankton biomass largely exceeded that of micro-zooplankton, nevertheless *A. hongii* ingested micro-zooplankton at considerably higher rates (38.3–90.5% of the total ingested carbon ration) than phytoplankton (Fig. 4; Table 2). The relative contribution of micro-zooplankton to the *A. hongii* diet was relatively low during the winter diatom blooms, when chain-forming diatoms (i.e., *Thalassiosira* spp.) consisted of more than 50% of the *A. hongii* diet. Maximum ingestion rates by *A. hongii* on micro-zooplankton were recorded during the summer diatom bloom, dominated by a large chain-forming diatom (i.e. *E. zodiacus*). The similar findings were also reported that *Acartia* spp. consumed heterotrophic nano-plankton and ciliates at considerably higher rates than diatoms during spring diatom bloom in San Pablo Bay (Rollwagen Bollens and Penry, 2003) and clearance rates of *Acartia hudsonica* on *E. zodiacus* were significantly lower than those on other diatom species (Teegarden et al., 2001). Support for these findings is given by the findings from other studies: (1) *E. zodiacus*

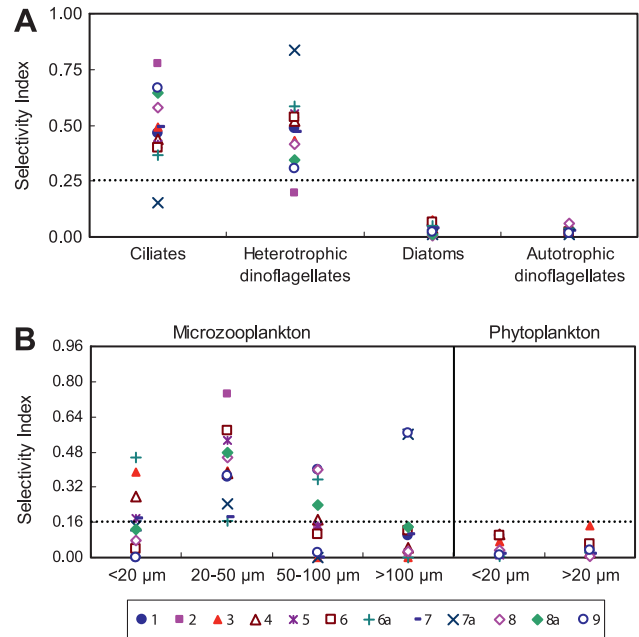


Fig. 7. Chesson's index values calculated for selectivity patterns of *Acartia hongii* with respect to prey composition (A) and size class of prey (B). Values above 0.25 (=1/n classes, $n = 4$, n is number of prey classes) for prey groups and 0.16 ($n = 6$) for size of prey indicate positive prey selection for the particular prey, while values below 0.25 and 0.16 indicate negative prey selection.

may have been avoided as a food item, since its colonies are considerably larger than those of other chain-forming diatoms. Therefore, *E. zodiacus* could be too large to feed by passive filter-feeding copepods (i.e., *Acartia* spp.) (Vargas et al., 2008), (2) despite the dominance of large phytoplankton, the preferential prey selection and the high ingestion rate on micro-zooplankton (i.e. loricate ciliates, *Eutimninus* sp.) may be due to their optimal cell size as prey, nutritional benefit, and high encounter rates (search time) of this prey (Turner and Anderson, 1983; Levinsen et al., 2000; Rollwagen Bollens and Penry, 2003; Castellani et al., 2005; Liu et al., 2005), and (3) the ingestion rates of copepods could be directly related to their initial prey concentrations (as indicated in Fig. 5; Levinsen et al., 2000; Castellani et al., 2008). Our results therefore indicate that diatoms are generally the most abundant food source in Gyeonggi Bay, but their species-specific cell and/or chain size and palatability may prevent *A. hongii* from consuming diatoms at certain conditions.

Although ADFs contributed more than 50% of total prey biomass during the summer (experiments 3, 6, 6a, 7 and 7a), ADFs, dominated by *P. minimum* (<20 µm), were ingested at a lower rate than micro-zooplankton. This negligible ingestion rate on ADFs indicated that *A. hongii* avoid this prey item. The lack of feeding on this species by *A. hongii* may be due to the smaller cell size that is accompanied by relative low nutritional value (Dam and Colin, 2005) or the inability to capture such small items (Wu et al., 2010). The reduced clearance of prey size < 20 µm agrees well with results for *Acartia* spp. from other field studies (Rollwagen Bollens and Penry, 2003; Olson et al., 2006; Dutz and Peters, 2008).

One of the potential biases during the bottle incubation being used in this study was the trophic cascade (Nejstgaard et al., 2001). Trophic cascade could have affected the ingestion rates of copepods we estimated because micro-zooplankton grazing artifacts can be apparent in experiments provided natural plankton assemblages as food. When copepods selectively ingest micro-zooplankton grazers as observed here, different micro-zooplankton grazing pressure on

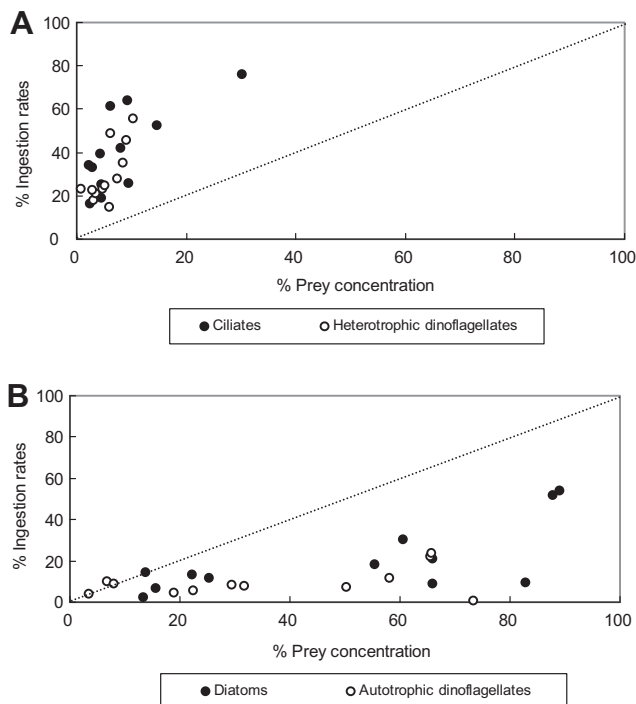


Fig. 6. Relative presence of total prey concentration in the diet of *Acartia hongii* as a function of its relative concentration in the water. Data above the 1:1 line indicate positive grazing selection for that particular prey. (A) ciliates and heterotrophic dinoflagellates, (B) diatoms and autotrophic dinoflagellates.

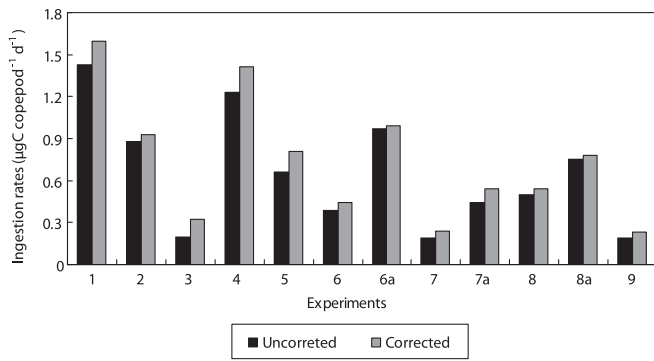


Fig. 8. Uncorrected and corrected ingestion rates of *Acartia hongii* on phytoplankton. Uncorrected and corrected values are calculated according to Frost (1972) and Nejstgaard et al. (2001), respectively.

phytoplankton can be resulted in the underestimation of copepod ingestion rate on phytoplankton, particularly smaller phytoplankton, during the incubation. In this study, negative feeding rate on prey *Cryptomoad* sp. also appeared in experiment 3. This is theoretically impossible and could be an artifact due to the trophic cascade. In order to reduce this artifact we corrected our estimates using the formula given by Nejstgaard et al. (2001). The corrected values resulted in higher than uncorrected values of our grazing estimation on phytoplankton (Fig. 8). This error represented from 1.8% to 37.5% (average 13.1%) of the total phytoplankton ingestion by *A. hongii*. Although we used literature values as micro-zooplankton grazing coefficients, artifacts by the trophic cascade have been partially corrected in our grazing rate estimates on phytoplankton prey. Nevertheless, the microbial food web is complex and most components have multiple trophic effects and feed across more than one trophic level (Liu et al., 2005). For example, ciliate and heterotrophic nano-flagellates feed on picoplankton, and HDFs can feed on from bacteria to nauplii, including chain-forming diatoms (Lessard, 1991). This complexity might have dampened trophic cascades in productive coastal areas as this present study. During our bottle incubation, *A. hongii* was feeding on large particles, both phytoplankton and micro-zooplankton, and most of the micro-zooplankton consumed are possibly omnivores as well. It is difficult therefore to predict detailed outcomes of food web changes that could be caused by *A. hongii* according to the bottle incubations.

Among phytoplankton and micro-zooplankton assemblages, ciliates were identified as an important dietary item of the Calanoid

copepod *A. hongii*. Although ciliate biomass was significantly less than phytoplankton biomass, ciliates accounted for 40.7% of the total carbon ration ingested by *A. hongii* (Table 2). Moreover, *A. hongii* showed a strong selective preference for micro-zooplankton compared to phytoplankton, and a specific preference for ciliates. Despite the low abundance of ciliates under natural conditions, the high consumption rates and strong selection for ciliates by copepods have been discussed previously (Gismervik, 2005, 2006). The high nutritional quality of ciliates, their optimal cell size as prey, and their high encounter rates (i.e. low search time) have been proposed as the most likely reasons for high ciliate consumption by copepods (Levinsen et al., 2000; Castellani et al., 2005; Liu et al., 2005).

In particular, feeding activity of *A. hongii* had a pronounced effect on the 20–100 µm ciliates and HDFs biomass and phytoplankton, but not on the plankton of smaller size classes (<20 µm) (Fig. 7). These results are also supported by a previous study on *Acartia* spp. in San Francisco Bay that found a preference grazing on the plankton >15 µm in size, although planktons < 15 µm were by far abundant (Rollwagen Bollens and Penry, 2003). Li et al. (2008) also reported that *Acartia bifilosa* females tended to ingest larger cells (>20 µm) that were explained by the size selective mechanism of filter-feeding copepods. In this study, *A. hongii* also might indiscriminately ingested abundant particles with any sizes, but preferred larger cells. Under natural prey conditions, the prey selectivity of *A. hongii* followed a similar pattern in all experiments, showing a strong preference for micro-zooplankton 20–50 µm (Fig. 7). However, *A. hongii* showed negative selection towards phytoplankton, both <20 µm and >20 µm, which accounted for the largest fraction of the total prey pool. Selectivity by *A. hongii* for larger prey can be explained by enhanced abilities of detection and better capture abilities compared to smaller prey (Wu et al., 2010). This may hold particularly for environmental situations where particles of large size ranges are abundant (Runge, 1980). Accordingly may *A. hongii* diversify its diet depending on the surrounding environmental conditions, with higher selectivity for larger sized ciliates or HDFs even diatom or small ADFs are dominant. Therefore, selective feeding behavior by *A. hongii*, both negative and positive, may affect the size structure and diversity of plankton communities in this study area, particularly regarding the micro-zooplankton. Given the dominance of *A. hongii* in the study area, this might even provide a major controlling effect, suggesting *A. hongii* as a key species in the pelagic system of the area studied.

Comparable field studies of *Acartia* spp. feeding in coastal areas are limited. Clearance rates of *A. hongii* on phytoplankton and

Table 3

Comparisons of clearance rates and ingestion rates of *Acartia* species on phytoplankton and micro-zooplankton. Values in parentheses are SD.

Copepod species	Clearance rates (ml copepod ⁻¹ day ⁻¹)		Ingestion rates (µgC copepod ⁻¹ day ⁻¹)		Region	Reference
	Phytoplankton	Microzooplankton	Phytoplankton	Microzooplankton		
<i>Acartia tonsa</i>	–	–	3.2(2.8)	0.7(0.5)	Chesapeake Bay	White and Roman, 1992
<i>Acartia tonsa</i>	3.6(1.6)	25.2(1.7)	2.8(2.6)	1.1(1.4)	Terrebonne Bay, Louisiana	Gifford and Dagg, 1991
<i>Acartia tonsa</i>	6.4(4.9)	76.0(55.5)	4.0(1.9)	0.7(0.53)	Terrebonne Bay, Louisiana	Gifford and Dagg, 1988
<i>Acartia tonsa</i>	147.5(201.5)	127.5(180.3)	3.9(0.8)	1.5(0.7)	Mejillones Bay, Chile	Vargas and González, 2004
<i>Acartia longiremis</i>	41.2(41.3)	33.1(16.6)	–	–	Washington coastal waters	Olson et al., 2006 *
<i>Acartia clausi</i>	45.6(27.6)	12.0(4.8)	<0.001	0.4(0.018)	German Bight, North sea	Dutz and Peters, 2008 †
<i>Acartia</i> spp.	19.7(15.4)	21.8(11.8)	1.3(2.0)	0.06(0.03)	South Bay, San Francisco	Rollwagen Bollens and Penry, 2003 *
<i>Acartia</i> spp. (<i>A. hudsonica</i> & <i>A. tonsa</i>)	14.4(2.4)	20.6(9.6)	0.04(0.07)	0.4(1.0)	San Pablo Bay, San Francisco	
<i>Acartia</i> spp. (<i>A. hudsonica</i> & <i>A. tonsa</i>)	18.5(48.1)	108.7(89.0)	5.9(11.4)	2.3(5.3)	Long Island Bay	Lonsdale et al., 1996 ‡
<i>Acartia hongii</i>	39.2(15.6)	128.1(54.7)	0.7(0.4)	2.1(1.2)	Gyeonggi Bay, Yellow sea	This study

* Values scanned from figure.

† Only diatom and ciliates considered.

‡ Clearance rates scanned from figure, and micro-zooplankton considered only ciliates.

micro-zooplankton in this study are within the range reported for various coastal areas (Table 3). Interestingly, our estimates of ingestion rate on micro-zooplankton appeared to be higher than other *Acartia* species, whereas those on phytoplankton were lower than other species. Therefore, the relative contribution of micro-zooplankton in *A. hongii* diets might be large in comparison to other *Acartia* species. These results imply that feeding behavior of genus *Acartia* might differ with the conspecific, and possibly vary with environmental conditions.

In conclusion, our results indicate that the contribution of micro-zooplankton to *A. hongii* diets vary widely and this appears to depend not only on the trophic status but also on the differential availability of prey biomass, composition, and size. A previous study reported that micro-zooplankton removed 60–83% of the daily primary production in this study area, and it may greatly affect trophic interrelations by regulating phytoplankton biomass and diversity (Yang et al., 2008). Although *A. hongii* does not represent the entire copepod assemblage in Gyeonggi Bay, *A. hongii* would significantly affect the micro-zooplankton and phytoplankton assemblage by selective predation and trophic cascade rather than by direct grazing on phytoplankton. This confirms the importance role of micro-zooplankton as a trophic coupling between copepods and the microbial food web in pelagic systems such as Gyeonggi Bay, Korea.

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References

- Broglio, E., Saiz, E., Calbet, A., Trepast, I., Alcaraz, M., 2004. Trophic impact and prey selection by crustacean zooplankton on the microbial communities of an oligotrophic coastal area (NW Mediterranean Sea). *Aquatic Microbial Ecology* 35, 65–78.
- Calbet, A., Landry, M.R., 2004. Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnology and Oceanography* 49, 51–57.
- Calbet, A., Saiz, E., 2005. The ciliate-copepod link in marine ecosystems. *Aquatic Microbial Ecology* 38, 157–167.
- Castellani, C., Irigoien, X., Harris, R.P., Lampitt, R.S., 2005. Feeding and egg production of *Oithona similis* in the North Atlantic. *Marine Ecology Progress Series* 288, 173–182.
- Castellani, C., Irigoien, X., Mayor, D.J., Harris, R.P., Wilson, D., 2008. Feeding of *Calanus finmarchicus* and *Oithona similis* on the microplankton assemblage in the Irminger Sea, North Atlantic. *Journal of Plankton Research* 30, 1095–1116.
- Chesson, J., 1983. The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64, 1297–1304.
- Chung, K.H., Park, Y.C., 1988. Primary production and nitrogenous regeneration by zooplankton in the Kyeonggi Bay, Yellow Sea. *Journal of the Korean Society of Oceanography* 23, 194–206.
- Crawford, D.W., 1989. *Mesodinium rubrum*: the phytoplankton that wasn't. *Marine Ecology Progress Series* 58, 161–174.
- Dahms, H.-U., Qian, P.Y., 2005. Exposure of biofilms to meiofaunal copepods affects the larval settlement of *Hydroides elegans* (Polychaeta). *Marine Ecology Progress Series* 297, 203–214.
- Dam, H.G., Colin, S.P., 2005. *Prorocentrum minimum* (Clone Exuv) is nutritionally insufficient, but not toxic to the copepod *Acartia tonsa*. *Harmful Algae* 4, 575–584.
- Dutz, J., Peters, J., 2008. Importance and nutritional value of large ciliates for the reproduction of *Acartia clausi* during the post spring-bloom period in the North Sea. *Aquatic Microbial Ecology* 50, 261–277.
- Edler, L., 1979. Phytoplankton and chlorophyll recommendations for biological studies in the Baltic Sea. *Baltic Marine Biologists Publications* 5, 1–38.
- Fileman, E., Smith, T., Harris, R., 2007. Grazing by *Calanus helgolandicus* and *Parapseudocalanus* spp. on phytoplankton and protozooplankton during spring bloom in the Celtic Sea. *Journal of Experimental Marine Biology and Ecology* 348, 70–84.
- Frost, B.W., 1972. Effects of size and concentration of food particles on feeding behavior of the marine planktonic copepod *Calanus pacificus*. *Limnology and Oceanography* 17, 805–815.
- Gifford, D.J., Dagg, M.J., 1988. Feeding of the estuarine copepod *Acartia tonsa* Dana: carnivory vs. herbivory in natural microplankton assemblages. *Bulletin of Marine Science* 43, 458–468.
- Gifford, D.J., Dagg, M.J., 1991. The microzooplankton-mesozooplankton link; consumption of planktonic protozoa by the calanoid copepods *Acartia tonsa* Dana and *Neocalanus plumchrus* Murukawa. *Marine Microbial Food Webs* 5, 161–177.
- Gismervik, I., 2005. Numerical and functional responses of choreo- and oligotrich planktonic ciliates. *Aquatic Microbial Ecology* 40, 163–173.
- Gismervik, I., 2006. Top-down impact by copepods on ciliate numbers and persistence depends on copepod and ciliate species composition. *Journal of Plankton Research* 28, 499–507.
- Han, M.W., Park, Y.C., 1999. The development of anoxia in the artificial Lake Shihwa, Korea, as a consequence of intertidal reclamation. *Marine Pollution Bulletin* 38, 1194–1199.
- Leising, A.W., Pierson, J.P., Halsband-Lenk, C., Horner, R., Postel, J.R., 2005. Copepod grazing during spring blooms: can *Pseudocalanus newmani* induce trophic cascades? *Progress in Oceanography* 67, 406–421.
- Lessard, E.J., 1991. The trophic role of heterotrophic dinoflagellates in diverse marine environments. *Marine Microbial Food Webs* 5, 49–58.
- Levinsen, H., Turner, J.T., Nielsen, T.G., Hansen, B.W., 2000. On the trophic coupling between protists and copepods in arctic marine ecosystems. *Marine Ecology Progress Series* 204, 65–77.
- Li, J., Sun, S., Li, C., Zhang, Z., Pu, X., 2008. Effects of different diets on the reproduction and naupliar development of the copepod *Acartia biflosa*. *Journal of Experimental Marine Biology and Ecology* 355, 95–102.
- Liu, H., Dagg, M.J., Strom, S., 2005. Grazing by the calanoid copepod *Neocalanus cristatus* on the microbial food web in the coastal Gulf of Alaska. *Journal of Plankton Research* 27, 647–662.
- Lonsdale, D.J., Cospser, E.M., Kim, W.S., Doall, M., Divadeenam, A., Jonasdottir, S.H., 1996. Food web interactions in the plankton of Long Island bay, with preliminary observations on brown tide effects. *Marine Ecology Progress Series* 134, 247–263.
- Menden-Deuer, S., Lessard, E.J., 2000. Carbon to volume relationships for dinoflagellates, diatoms and other protist plankton. *Limnology and Oceanography* 45, 569–579.
- Nejstgaard, J.C., Naustvoll, L.J., Sazhin, A., 2001. Correcting for underestimation of microzooplankton grazing in bottle incubation experiments with mesozooplankton. *Marine Ecology Progress Series* 221, 59–75.
- Olson, M.B., Lessard, E.J., Wong, C.H.J., Bernhardt, M.J., 2006. Copepod feeding selectivity on microplankton, including the toxicigenic diatom *Pseudo-nitzschia* spp., in the coastal Pacific Northwest. *Marine Ecology Progress Series* 326, 207–220.
- Parsons, T.R., Maita, Y., Lalli, C.M., 1984. *A Manual of Chemical and Biological Methods for Seawater Analysis*. Pergamon Press, Oxford, 173 pp.
- Pérez, M.T., Dolan, J.R., Fukai, E., 1997. Planktonic oligotrich ciliates in the NW Mediterranean: growth rates and consumption by copepods. *Marine Ecology Progress Series* 155, 89–101.
- Putt, M., Stoecker, D.K., 1989. An experimentally determined carbon: volume ratio for marine "oligotrichous" ciliates from estuarine and coastal waters. *Limnology and Oceanography* 34, 1097–1103.
- Rollwagen Bollens, G.C., Penry, D.L., 2003. Feeding dynamics of *Acartia* spp. copepods in a large, temperature estuary (San Francisco Bay, CA). *Marine Ecology Progress Series* 257, 139–158.
- Runge, J.A., 1980. Effects of hunger and season on the feeding behavior of *Calanus pacificus*. *Limnology and Oceanography* 25, 134–145.
- Saiz, E., Calbet, A., Irigoien, X., Alcaraz, M., 1999. Copepod egg production in the western Mediterranean: response to food availability in oligotrophic environments. *Marine Ecology Progress Series* 187, 179–189.
- Seo, J.H., Choi, J.K., 2008. In situ grazing pressure of *Acartia hongii* female (Copepoda: Calanoida) on phytoplankton in Gyeonggi Bay, Korea. *The Journal of International Society of Yellow Sea Research* 9, 32–39.
- Teegarden, G.J., Campbell, R.G., Durbin, E.G., 2001. Zooplankton feeding behavior and particle selection in natural plankton assemblages containing toxic *Alexandrium* spp. *Marine Ecology Progress Series* 218, 213–226.
- Turner, J.T., Anderson, D.M., 1983. Zooplankton grazing during dinoflagellate blooms in a Cape Cod embayment, with observations of predation upon Tintinnids by Copepods. *Marine Ecology* 4, 359–374.
- Vargas, C.A., González, H.E., 2004. Plankton community structure and carbon cycling in a coastal upwelling system. I. Bacteria, microprotozoans and phytoplankton in the diet of copepods and appendicularians. *Aquatic Microbial Ecology* 34, 151–164.
- Vargas, C.A., Martínez, R.A., González, H.E., Silva, N., 2008. Contrasting trophic interactions of microbial and copepod communities in a fjord ecosystem, Chilean Patagonia. *Aquatic Microbial Ecology* 53, 227–242.
- Verity, P.G., Langdon, C., 1984. Relationships between Loric volume, carbon, nitrogen and ATP content of tintinnids in Narragansett Bay. *Journal of Plankton Research* 6, 859–868.

- White, J.R., Roman, M.R., 1992. Egg production by the calanoid copepod *Acartia tonsa* in the mesohaline Chesapeake Bay: the importance of food resources and temperature. *Marine Ecology Progress Series* 86, 239–249.
- Wu, C.-H., Dahms, H.-U., Buskey, E.J., Strickler, J.R., Hwang, J.-S., 2010. Behavioral interactions of the copepod *Temora turbinata* with potential ciliate prey. *Zoological Studies* 49, 157–168.
- Yang, E.J., Choi, J.K., Hyun, J.H., 2008. Seasonal variation in the community and size structure of nano-and microzooplankton in Gyeonggi Bay, Yellow Sea. *Estuarine, Coastal and Shelf Science* 77, 320–330.
- Yang, E.J., Kang, H.G., Yoo, S., Hyun, J.H., 2009. Contribution of auto- and heterotrophic protozoa to the diet of copepods in the Ulleung Basin, East Sea/Japan sea. *Journal of Plankton Research* 31, 647–659.
- Youn, S.H., Choi, J.K., 2003. Seasonal change in zooplankton community in the coastal waters off Incheon. *Journal of the Korean Society of Oceanography* 38, 111–121.
- Youn, S.H., Choi, J.K., 2007. Egg production of the copepod *Acartia hongii* in Gyeonggi Bay, Korea. *Journal of Marine Systems* 67, 217–224.
- Youn, S.H., Choi, J.K., 2008. Distribution pattern of zooplankton in the Han River estuary with respect to tidal cycles. *Ocean Science Journal* 43, 135–146.