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ORIGINAL PAPER

Ecological implications and seasonal variability of grazing by marine copepods on phytoplankton: comparison between *Acartia omorii* and *A. steueri* in Jangmok Bay, Korea

Seo Yeol Choi[1] · **Eun Hye Lee**[2] · **Min-Chul Jang**[3] · **Min Ho Seo**[4] · **Ho Young Soh**[2,5]

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Abstract

The grazing impacts of two *Acartia* species (*Acartia omorii* and *A. steueri*) on size-fractionated phytoplankton biomass were measured in Jangmok Bay, Korea (34°59′37.8" N, 128°40′28.2" E) from January to May 2015. Total chlorophyll (Chl-*a*) concentrations ranged from 0.66 to 5.18 μg L^{-1}, and micro-phytoplankton (> 20 μm) comprised up to 66% (range, 10.5–65.6%) of the total pigment. The total abundance of *Acartia* species ranged from 267 to 5931 ind. m^{-3}, and these copepods accounted for 20.8 to 88.0% of the total copepod abundance. The ingestion rates of *A. steueri* ($r^2=0.904$, $P=0.013$) and *A. omorii* ($r^2=0.239$, $P=0.046$) showed a high correlation with micro-phytoplankton. The average grazing impact of *Acartia* species on phytoplankton biomass was approximately 6.8 ± 11.8% (range, 0.1–69.0%). Temperature–salinity (T–S) diagram analysis revealed distinct environmental preferences for each species; *A. omorii* preferred a broader temperature range of 6.2 to 17.1 °C and a salinity range of 31.8 to 33.5, whereas *A. steueri* was more restricted, preferring temperatures between 6.5 and 12.8 °C and a salinity range of 32.2 to 33.5. These findings not only contribute to our understanding of the ecological roles of these copepod species in marine ecosystems but also highlight the importance of continuous research regarding the mechanisms driving their coexistence and interaction with the coastal food web.

Keywords Feeding selectivity · Coastal ecosystems · Competition · Food sources · Copepoda

Introduction

The role of food selectivity in controlling zooplankton communities in pelagic ecosystems has been well documented (Frost 1972; Dahms and Qian 2005). Selectivity in feeding plays a crucial role in interspecies competition for food resources and influences adaptive strategies, making it an important trophic pathway for the transfer of energy and material from lower to higher trophic levels (Mauchline 1998; Bamstedt et al. 2000).

The impact of herbivorous zooplankton grazing on phytoplankton abundance and structure on has been a focus of research (Sterner 1989). Copepoda, in general, feed on phytoplankton of varying sizes and show selectivity in their feeding habits (Wilson 1973; Cowles 1979). These organisms differentiate prey based on factors, such as size, quality, and chemical cues of the prey (Frost 1972; Huntley et al. 1986; Cowles et al. 1988) on their own life cycle stages. Phytoplankton biomass and species composition are altered by their selective feeding (Bautista and Harris 1992; Edgar and Green 1994), which is a key mechanism related to the interspecies competition for food resources in pelagic food webs (Katechakis et al. 2004). The relationship between phytoplankton size and copepod feeding has been reported, with some studies suggesting a direct correlation between copepod body size and grazing effects (Harris 1982; Morales et al. 1991). However, the degree of selectivity that copepods

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✉ Ho Young Soh
hysoh@chonnam.ac.kr

[1] Oceanic Climate and Ecology Research Division, National Institute of Fisheries Science, Busan, Republic of Korea

[2] Fishery Resource Management Research Institute based on ICT, Chonnam National University, Yeosu, Republic of Korea

[3] Ballast Water Center, Korea Institute of Ocean Science and Technology, Geoje, Republic of Korea

[4] Department of Marine Ecology, Marine Ecology Research Center, Yeosu, Republic of Korea

[5] Department of Ocean Integrated Science, Chonnam National University, Yeosu, Republic of Korea

display in their natural environment with respect to the types, sizes, and qualities of available food is not yet fully understood (Huntley 1981; Jang et al. 2010).

High abundances of the planktonic Acartiidae are commonly found in coastal and estuarine areas in Korea, China, and Japan (Kang and Kang 1998; Park et al. 2015). *Acartia omorii* and *A. steueri* are particularly abundant in the Jangmok Bay of Korea during the spring and winter seasons (Hwang et al. 2011). *A. omorii* adults prefer water temperatures below 23 °C, and predominated from January to early July. However, *A. steueri* adults are mainly found during the relatively cooler months of January to May and November to December, with the population rising notably in December when water temperatures are below 10 °C. *Acartia* species are omnivores and also feed on phytoplankton of various sizes and species, with adults generally associated with phytoplankton of a specific size (Rollwagen-Bollens and Penry 2003; Liu et al. 2010). Their seasonal abundance in coastal and estuarine areas can be attributed to niche separation for food (Ueda 1987; Choi et al. 2021).

The objective of this study was to investigate the feeding selectivity of two species of the genus *Acartia*, which would elucidate the mechanisms that promote coexistence and diversity in marine ecosystems. Hence, the role of these species in relation to changes in phytoplankton biomass and size composition was examined, and the grazing effect was calculated by combining the estimated biomass of phytoplankton in different size fractions (micro, nano, and pico).

Materials and methods

The study was conducted between January and May 2015 in Jangmok Bay (34°59′37.8" N, 128°40′28.2" E) located in the northern part of the Geoje Island, South Sea of Korea. Sampling was conducted every 5 to 12 days at the research wharf (average depth, 8.5 m; maximum tidal range, 2.2 m) of the South Sea Research Institute of the Korea Institute of Ocean Science and Technology (KIOST) (Fig. 1).

The physical and biological features of the surface water were investigated. The water temperature (℃) and salinity were measured in situ using a YSI multimeter (model 63; Xylem Inc., Yellow Springs, OH, USA). *Acartia* species were collected by vertical hauling using a conical net (mesh size, 200 µm; mouth diameter, 45 cm). Specimens (*Acartia omorii* and *A. steueri*) were transferred to 20-L containers filled with surface water in a cooler and brought to the laboratory promptly. Except for March 30 and April 7, when we found a few other *Acartia* species, *A. omorii* and *A. steueri* made up almost all of the *Acartia* population. The other *Acartia* species we found on those two days were less than 3% of the total *Acartia* population. Healthy copepods were

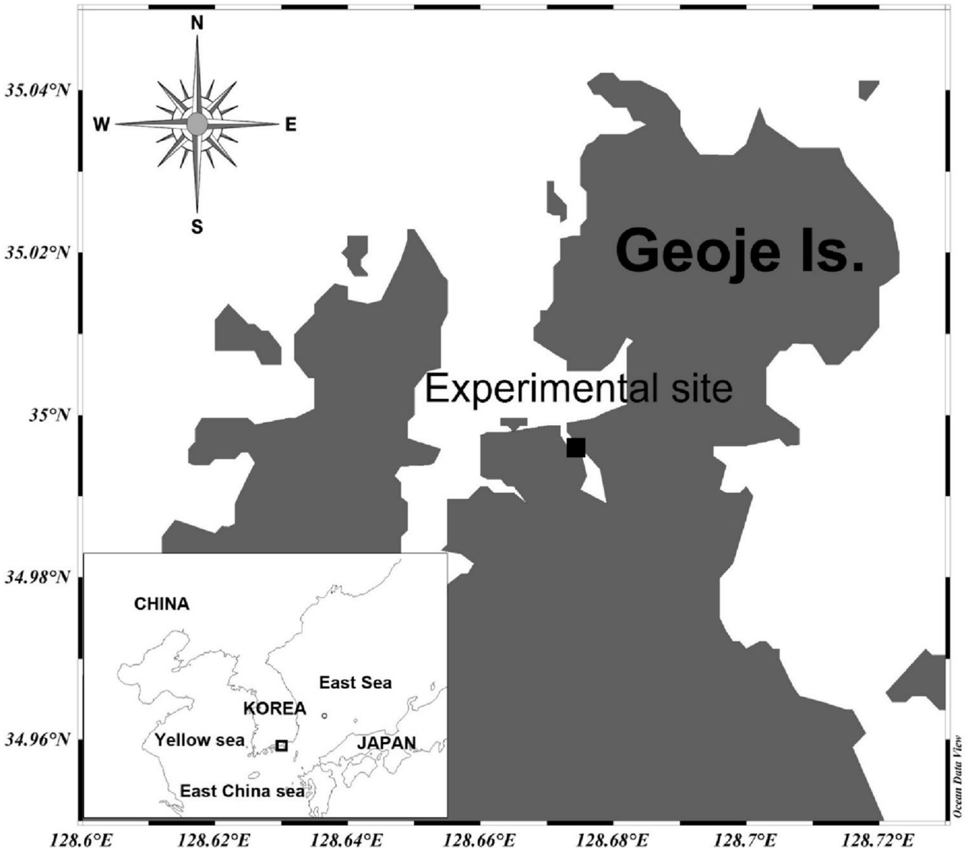


Fig. 1 Location of the experimental site in Jangmok Bay, Korea

immediately isolated using a pipette with a wide opening by observing under a dissecting microscope (Zeiss Stemi SV11, Jena, Germany). Adult male and female copepods were sorted under a dissecting microscope and transferred to a 500-mL bottle containing seawater filtered through Whatman GF/F filters. Seven polycarbonate bottles (2.75 L) were filled with seawater filtered through a 200-µm mesh to remove other copepods and large grazers (Fig. 2). Each experiment was conducted using three experimental bottles, each populated with a set number of copepods (Table 1), alongside three control bottles containing only seawater filtered through a 200-µm mesh to exclude copepods. An additional bottle was set aside to establish initial conditions for measurement of chlorophyll (Chl-*a*) concentration. When specimens of both *A. omorii* and *A. steueri* were present simultaneously, 10 polycarbonate bottles were used. Details regarding variations in the specific *Acartia* species and number of individuals during the study period are provided in Table 1. In addition, the mean prosome length (PL) of adult females was measured for 10 individuals from each species. This incubation setup was housed in a custom-designed rotating incubation chamber, which ensured uniform conditions by simulating natural water movement, thereby maintaining the ecological validity of the study.

Seven polycarbonate bottles were filled to eliminate air bubbles. The incubation process was conducted over a 24-h period, during which surface water was continuously pumped from sizable acrylic tanks, and the bottles containing the specimens were rotated to ensure consistent conditions throughout the incubation period. After 24 h, water samples were collected from the polycarbonate bottles to measure Chl-*a* concentration and divided into three size categories (micro, nano, and pico) by size fractionation using 20-µm nylon mesh and 2-µm polycarbonate filter. To measure Chl-*a* concentration, 500-mL seawater from each bottle was filtered through a 47-mm Whatman GF/F filter. The filters were extracted with 90% acetone for 24 h at − 20 ℃ and subsequently analyzed by fluorometry (10 AU Fluorometer, Turner Designs, CA, USA) (Parsons et al. 1984).

The individual ingestion rates for the three size categories of Chl-*a* in *Acartia* species were calculated as follows using Frost's equation (Frost 1972):

$$I = F \times C \tag{1}$$

where F is the clearance rate (mL copepod^{-1} day^{-1}), and C is the mean concentration of prey (mL^{-1}) during the 24-h incubation period.

The clearance rate was calculated as follows:

$$F\left(L\ \text{copepod}^{-1}\text{day}^{-1}\right) = [\ln\left(C_0/C_c\right) \text{ - } \ln\left(C_0/C_e\right)] \times V/Zt \tag{2}$$

where V is the volume (mL) of the incubation bottle, Z is the number of *Acartia* individuals added to the incubation bottle, t is the incubation time, C_0 is the initial concentration of Chl-*a*, and C_c and C_e are the concentrations of prey in the experimental bottles at the end of the incubation period.

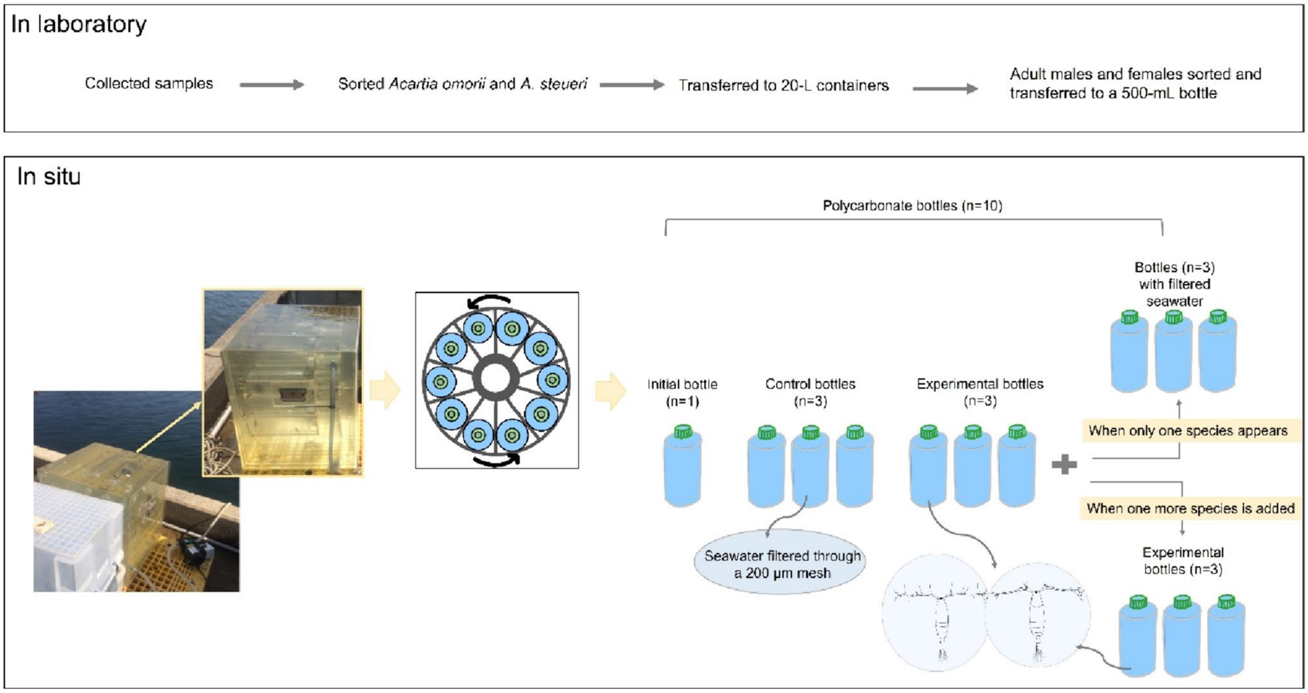


Fig. 2 Setup of incubation bottles for *Acartia* species grazing experiments

Table 1 Number of individuals of *Acartia* species per incubation bottle used in grazing experiments

Date		*Acartia steueri*		*A. omorii*	
		Female	Male	Female	Male
Jan 06, 2015	Bottle 1	5	10	23	7
	Bottle 2	5	10	24	6
	Bottle 3	7	8	22	8
Jan 13, 2015	Bottle 1			27	3
	Bottle 2			26	4
	Bottle 3			28	2
Jan 21, 2015	Bottle 1			23	7
	Bottle 2			22	8
	Bottle 3			26	4
Jan 29, 2015	Bottle 1			21	9
	Bottle 2			18	12
	Bottle 3			18	12
Feb 05, 2015	Bottle 1	1	15	13	7
	Bottle 2	2	14	13	7
	Bottle 3		16	16	4
Feb 16, 2015	Bottle 1			29	6
	Bottle 2			29	6
	Bottle 3			29	6
Feb 23, 2015	Bottle 1			23	7
	Bottle 2			23	7
	Bottle 3			16	14
Mar 02, 2015	Bottle 1	3	27	21	9
	Bottle 2	7	13	15	15
	Bottle 3	8	12	16	14
Mar 09, 2015	Bottle 1			19	11
	Bottle 2			19	11
	Bottle 3			18	12
Mar 16, 2015	Bottle 1			17	13
	Bottle 2			19	11
	Bottle 3			22	8
Mar 24, 2015	Bottle 1	7	23		
	Bottle 2	4	26		
	Bottle 3	7	23		
Mar 30, 2015	Bottle 1			26	4
	Bottle 2			26	4
	Bottle 3			15	15
Apr 07, 2015	Bottle 1			20	10
	Bottle 2			15	15
	Bottle 3			9	21
Apr 14, 2015	Bottle 1	6	6	15	15
	Bottle 2	5	7	12	10
	Bottle 3	5	7	16	14
Apr 20, 2015	Bottle 1			17	13
	Bottle 2			20	10
	Bottle 3			20	10
Apr 30, 2015	Bottle 1			6	24
	Bottle 2			7	23
	Bottle 3			8	22
May 06, 2015	Bottle 1			18	12
	Bottle 2			18	12
	Bottle 3			15	15
May 18, 2015	Bottle 1			15	15
	Bottle 2			11	19
	Bottle 3			15	15
May 28, 2015	Bottle 1			18	12
	Bottle 2			16	14
	Bottle 3			15	15

The mean concentration of prey (L^{-1}) was calculated using the following formula:

$$C = C_0\left(e^{kt} - 1/k_t\right) \tag{3}$$

Grazing impact (%) was calculated as the percentage of the initial concentration of Chl-*a* consumed by *Acartia* species.

Linear regression was calculated to determine the relationship between ingestion rates in copepods and phytoplankton concentrations. All the statistical analyses were performed using the IBM SPSS Statistics for Windows, version 20 (IBM Corp., Armonk, NY, USA). The significance level was set at $P < 0.05$.

Results

Environmental conditions

The water temperature in Jangmok Bay was 6.2–17.1 °C, with higher values in May (Table 2). The salinity of the water was 31.8–33.5, with the lowest values observed in May (Table 2). The total Chl-*a* concentration varied from 0.66 to 5.18 µg L^{-1}, with the highest concentration in May and the lowest in March (Table 2). Micro-phytoplankton (> 20 µm) made up an average of 38.5 ± 16.5% of total Chl-*a* (range, 10.5–65.6%). Nano-phytoplankton (2–20 µm) accounted for an average of 34.1 ± 8.7% of total Chl-*a* (range, 15.6%–45.8%), with the highest percentage observed during March–April. The average contribution of pico-phytoplankton (< 2 µm) was 27.5 ± 14.8% of total Chl-*a* (range, 6.8% to 57.3%), with the highest concentration observed in April.

Occurrence of *A. omorii* and *A. steueri*

Acartiidae accounted for 20.8–88.0% of the total copepod population (Fig. 3A) with adults belonging to the species *Acartia omorii* and *A. steueri*. The abundance of

Table 2 Short-term variations of environmental variables and Chl-*a* concentrations in Jangmok Bay from January to May 2015

Date	Water temperature (°C)	Salinity	Chl-*a* (µg L^{-1}) (% of Chl-*a*)			
			Total	> 20 µm	2–20 µm	< 2 µm
Jan 06, 2015	7.6	33.1	2.99	1.96 (65.6)	0.47 (15.6)	0.57 (18.9)
Jan 13, 2015	7.1	33.2	4.25	2.63 (61.7)	1.13 (26.6)	0.50 (11.7)
Jan 21, 2015	6.2	32.9	1.22	0.49 (40.2)	0.31 (25.0)	0.43 (34.8)
Jan 29, 2015	7.4	33.1	1.19	0.36 (30.4)	0.38 (31.8)	0.45 (37.9)
Feb 05, 2015	6.5	33.3	1.20	0.34 (28.3)	0.53 (44.1)	0.33 (27.6)
Feb 16, 2015	6.6	33.4	1.29	0.14 (10.5)	0.58 (45.2)	0.57 (44.2)
Feb 23, 2015	7.2	33.4	0.91	0.43 (47.4)	0.21 (23.0)	0.27 (29.6)
Mar 02, 2015	7.0	33.5	0.66	0.31 (46.5)	0.16 (24.2)	0.19 (29.3)
Mar 09, 2015	7.8	33.2	1.04	0.45 (42.8)	0.40 (38.7)	0.19 (18.5)
Mar 16, 2015	9.2	33.4	0.98	0.39 (39.5)	0.40 (40.6)	0.20 (20.0)
Mar 24, 2015	9.7	33.3	1.80	0.85 (47.4)	0.82 (45.8)	0.12 (6.8)
Mar 30, 2015	11.6	33.3	1.03	0.49 (47.2)	0.37 (35.8)	0.17 (16.9)
Apr 07, 2015	11.1	32.8	1.97	0.21 (10.5)	0.64 (32.4)	1.12 (57.1)
Apr 14, 2015	12.8	32.2	2.76	0.36 (12.9)	0.82 (29.8)	1.58 (57.3)
Apr 20, 2015	12.6	32.8	3.18	1.38 (43.4)	1.02 (32.2)	0.77 (24.4)
Apr 30, 2015	16.4	32.5	2.85	1.27 (44.7)	1.13 (39.8)	0.44 (15.4)
May 06, 2015	15.2	32.6	5.18	2.87 (55.4)	1.63 (31.5)	0.68 (13.1)
May 18, 2015	17.1	31.8	4.45	1.85 (41.6)	1.91 (43.0)	0.68 (15.4)
May 28, 2015	16.9	32.6	1.96	0.29 (14.6)	0.83 (42.3)	0.85 (43.1)

Values in parentheses are percentages of Chl-*a* in three size fractions

Chl chlorophyll

Acartiidae was relatively high from January to February, contributing to more than an average of 60% of the total zooplankton, and it was low during mid-March to mid-April, accounting for an average of 26.6 ± 4.6% of the total zooplankton. The abundance of Acartiidae exhibited significant variability, ranging from 267 to 5931 ind. m^{-3}. High abundance of more than 5000 ind. m^{-3} was recorded on January 21 (5931 ind. m^{-3}), February 23 (5931 ind. m^{-3}), and March 2 (5033 ind. m^{-3}). The abundance of *A. omorii* adults ranged from 0 to 5931 ind. m^{-3} (mean: 2374 ± 1667 ind. m^{-3}), with maximum abundance recorded in January and February (Fig. 3B). Except for a single occurrence at the end of March, *A. omorii* adults was consistently present throughout the study period. Conversely, the abundance of *A. steueri* adults ranged from 0 to 3733 ind. m^{-3} (mean: 463 ± 1027 ind. m^{-3}), with a maximum abundance recorded for *A. omorii* adults, which appeared at its highest at the end of March. The temperature-salinity (T-S) diagram analysis indicated that *A. omorii* adults exhibit a broader tolerance range for both temperature and salinity (Fig. 4). In contrast, *A. steueri* adults demonstrated a more restricted pattern of occurrence, with higher abundances occurring particularly at lower temperatures (below 10 °C). Furthermore, *A. steueri* adults showed a preference for salinity levels between 32.2 and 33.5.

Ingestion and clearance rates

The maximum ingestion rate for total Chl-*a* was higher in *A. steueri* (396 ng Chl-*a* ind.$^{-1}$ day^{-1}) than that in *A. omorii* (170 ng Chl-*a* ind.$^{-1}$ day^{-1}) (Fig. 5). During the experiment, negative ingestion rates were observed once in *A. steueri* and three times in *A. omorii* during the measurement process. *A. steueri* showed positive ingestion rates of micro-phytoplankton (> 20 µm) throughout the experimental period, with the highest rate recorded in January 2015 (231 ng Chl-*a* ind.$^{-1}$ day^{-1}). The daily ingestion rate of *A. omorii* for micro-phytoplankton was greater than − 40 ng Chl-*a* ind.$^{-1}$ day^{-1} in April, which was higher than the negative ingestion rate in other periods. The ingestion rate of nano-phytoplankton (2–20 µm) and pico-phytoplankton (< 2 µm) biomass was negative for *A. steueri* in all the experiments, except for that of those in January and April. This was lower than that of the total and micro-size phytoplankton. The ingestion rate for nano-phytoplankton (2–20 µm) and pico-phytoplankton (< 2 µm) biomass was more negative for *A. omorii* than for *A. steueri*.

A. omorii and *A. steueri* displayed higher clearance rates for total and micro-phytoplankton (> 20 µm) than those for nano-phytoplankton (2–20 µm) and pico-phytoplankton (< 2 µm) (Fig. 6). The clearance rate of total Chl-*a* concentration biomass ranged between − 0.64 and 3.21 mL

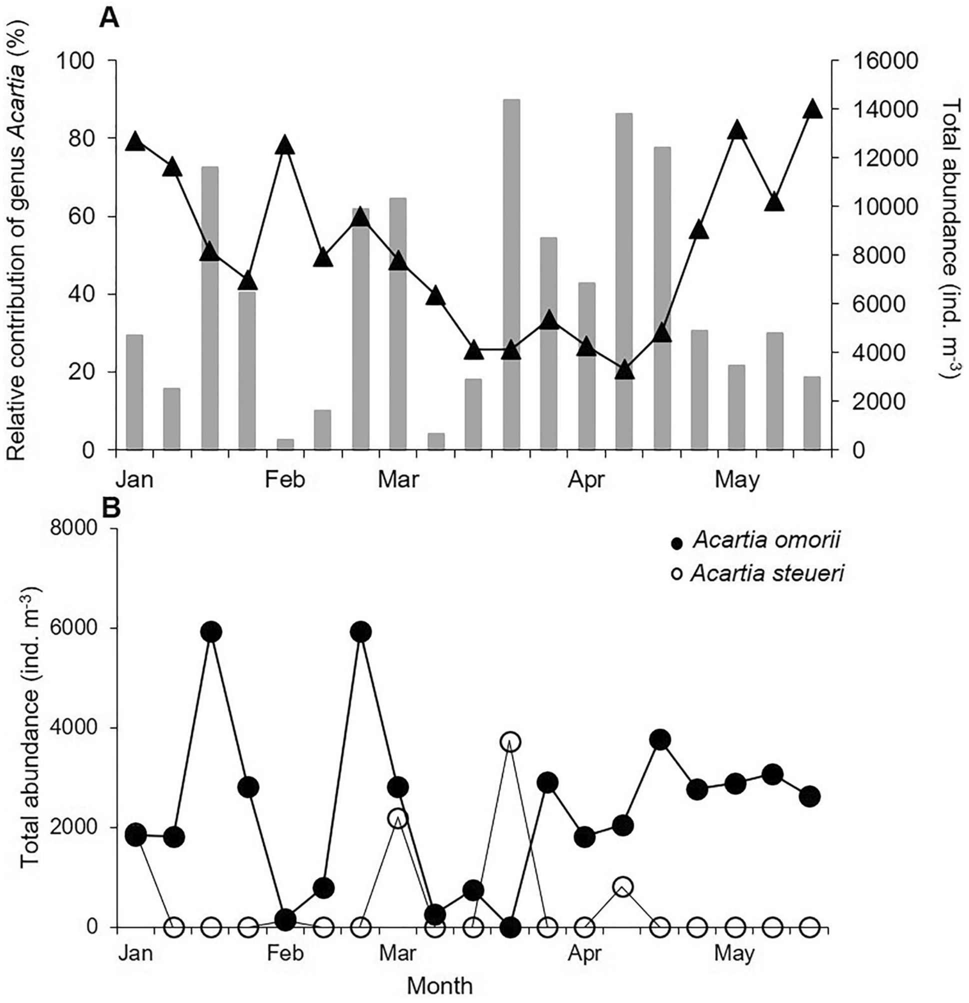


Fig. 3 Relative contribution of Acartiidae (*Acartia omorii* and *A. steueri*) and total abundance of Copepoda Calanoida observed in the experimental station during the study period (triangle shape, relative contribution; bar graph, total abundance) (**A**) and Acartiidae total abundance (**B**)

ind.$^{-1}$ day^{-1} for *A. omorii* and between – 0.06 and 8.42 mL ind.$^{-1}$ day^{-1} for *A. steueri* (Fig. 6). *A. steueri* had positive micro-phytoplankton clearance rates throughout the experiment, with the highest rate (10.88 mL ind.$^{-1}$ day^{-1}) observed in April 2015. *A. omorii* had its highest micro-phytoplankton clearance rate (> 10 mL ind.$^{-1}$ day^{-1}) in March. *A. steueri* showed the highest nano- and pico-phytoplankton clearance rates in January, i.e., 10.93 mL ind.$^{-1}$ day^{-1} and 6.46 mL ind.$^{-1}$ day^{-1}, respectively. However, overall, these rates were lower than the total and micro-phytoplankton clearance rates. The nano- and pico-phytoplankton clearance rates of *A. omorii* showed a similar pattern to the ingestion rate and were more negative than those of *A. steueri*.

Grazing impacts of *Acartia* species

The grazing impacts of *Acartia* species on phytoplankton varied seasonally. In some months, the grazing impact was low, while in others it was high, with consumption of < 0.1–50.5% of the initial biomass of total phytoplankton (Fig. 7). The grazing impact of *A. omorii* on micro-phytoplankton was 0.1–57.3%, with the highest impact in March. The grazing impact of *A. steueri* on micro-phytoplankton was 19.5–53.5%, with the highest impact in April. The grazing impact of both species on nano-phytoplankton (2–20 μm) and pico-phytoplankton (< 2 μm) was mostly negative, except in January and April. *A. steueri* had the highest impact on nano-phytoplankton (79.5%) in January.

Fig. 4 Temperature-salinity diagram showing preferences of *Acartia omorii* and *A. steueri*

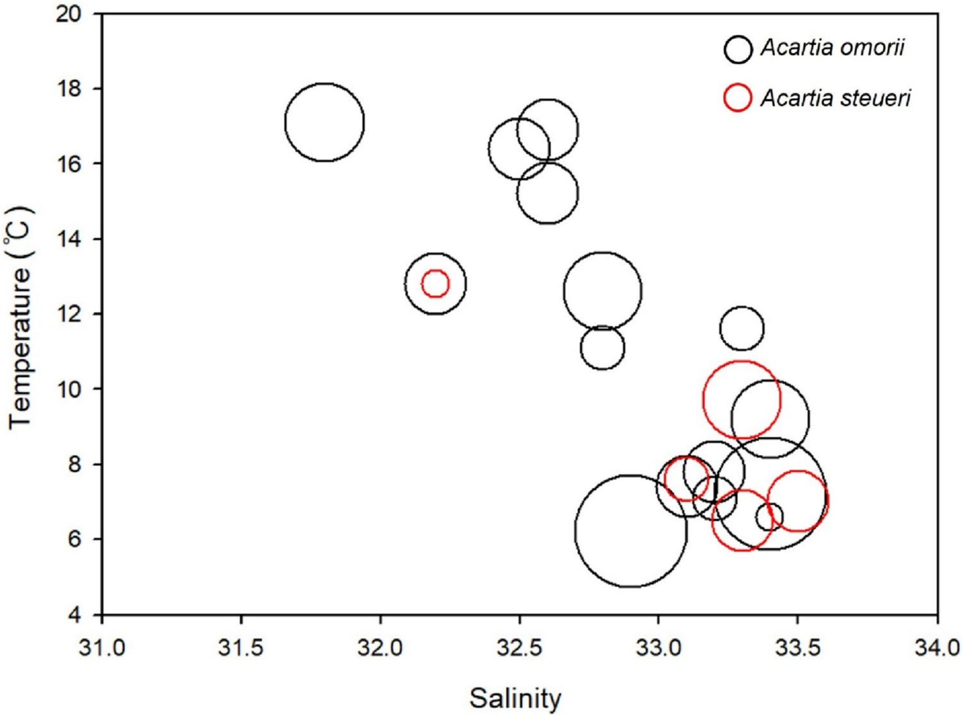
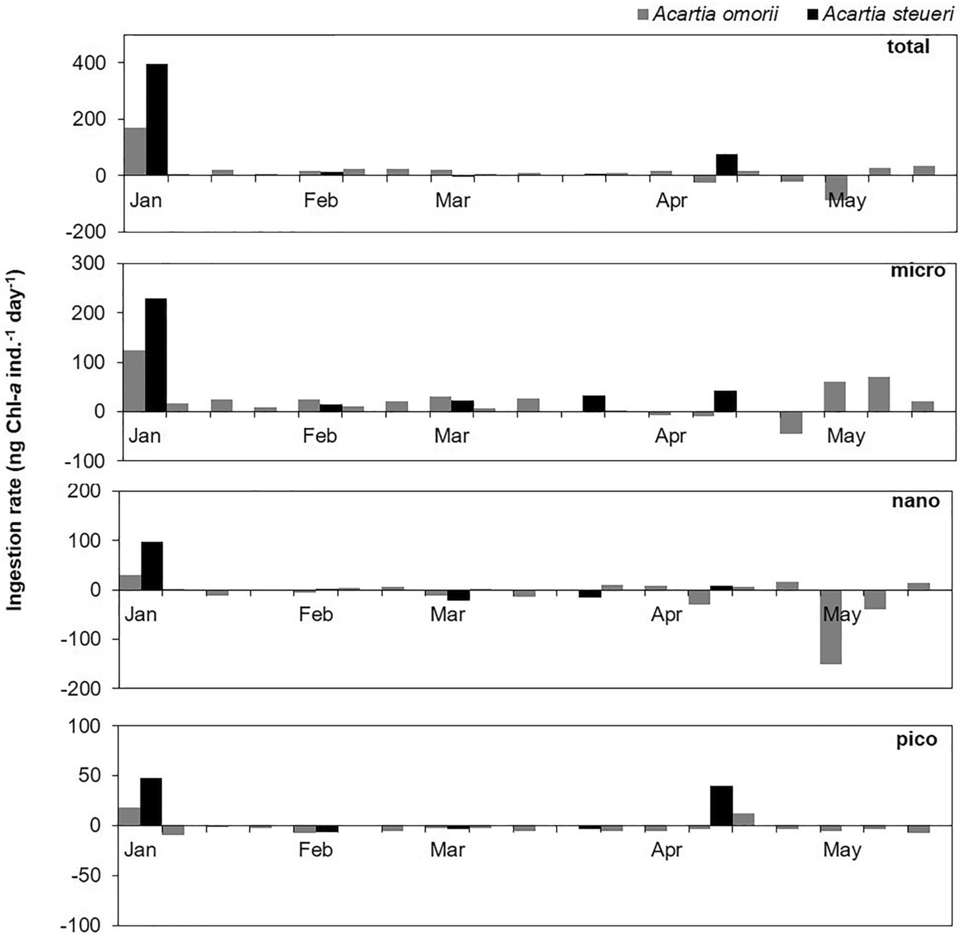


Fig. 5 Variations in rates of ingestion of various sized phytoplankton by *Acartia* species (*Acartia omorii* and *A. steueri*)



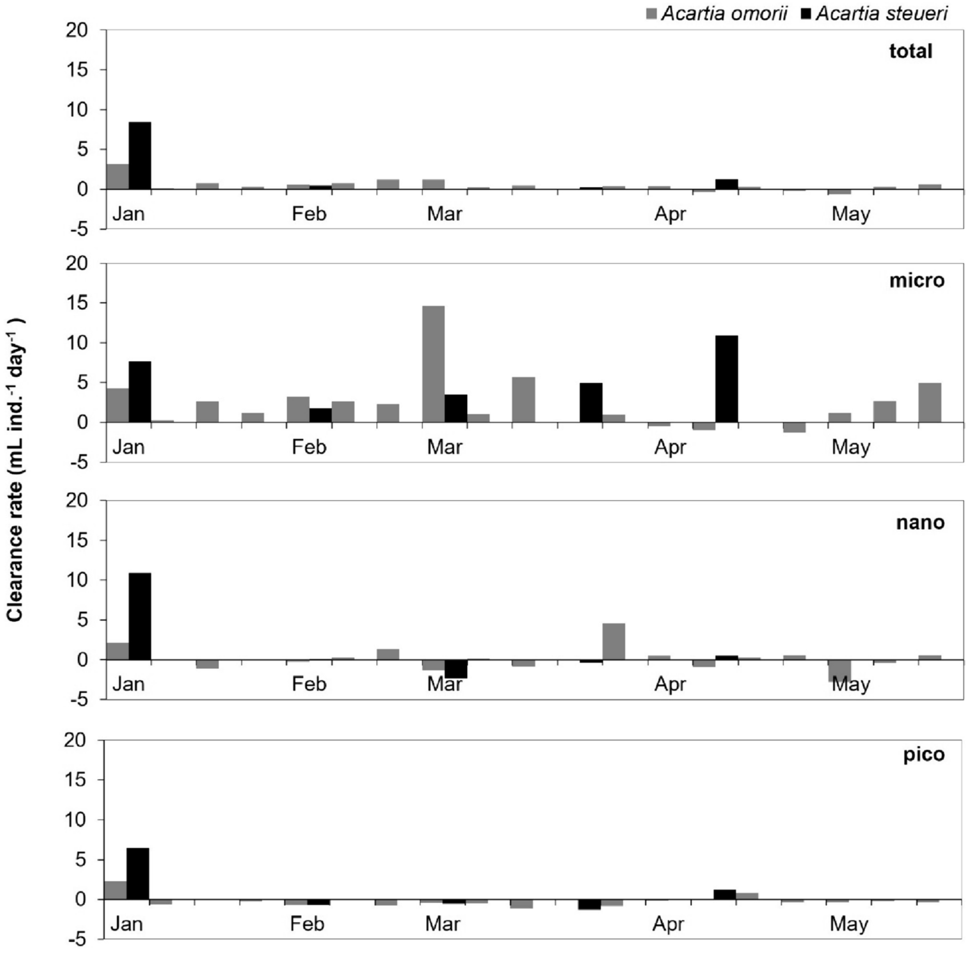


Fig. 6 Variations in rates of clearance of various sized phytoplankton by *Acartia* species (*Acartia omorii* and *A. steueri*)

Prosome length of *Acartia* species

The prosome length (PL) of *Acartia omorii* females ranged from 806.6 to 963.2 µm, with a mean of 873.2 ± 45.6 µm, while *A. steueri* females exhibited PL ranged from 865.1 to 1132.1 µm, with a mean of 1031.4 ± 72.7 µm (Fig. 8).

Discussion

The presence of congener species in overlapping ecological niches can lead to competition for resources, such as habitat, life cycle, and food. This study analyzed the feeding selectivity of adult females of two *Acartia* species based on the size of their phytoplankton prey. Our results revealed that micro-phytoplankton (> 20 µm) was a significant food source for both *A. omorii* and *A. steueri*, yet their ingestion rates and grazing impacts differed markedly.

Furthermore, the distinct feeding preferences of *A. omorii* and *A. steueri* observed in our study highlight the broader dietary patterns within the *Acartia* genus. In Ilkwang Bay, *A. omorii* adopts a herbivorous diet, mainly feeding on phytoplankton, as evidenced by the correlation between its production rate and Chl-*a* (Kang et al. 2007). However, this predominantly herbivorous tendency may not be a fixed trait for *A. omorii* across different environments. *Acartia* species, including *A. steueri* found in offshore waters, exhibit varied dietary behaviors in different ecological settings, ranging from omnivorous to carnivorous feeding patterns and also due to their developmental stages (Ara 2001; Kang and Kang 2005). This adaptability is crucial, particularly during periods of food scarcity, when *Acartia* species are known to alter their feeding strategies. Studies have indicated that *Acartia* species show preferences for a variety of prey, often driven by prey availability and environmental conditions. For instance, the diet of *A. tonsa* is diverse and comprises diatoms, dinoflagellates, heterotrophic protists, and nanoplankton, none of which is dominant prey (Kleppel and Hazzard 2000; Rollwagen-Bollens and Penry 2003). Not only when phytoplankton are scarce, *Acartia* species have been known to shift their diet to alternative prey, such as nauplii, ciliates, other calanoid stages, and heterotrophic dinoflagellates (Tackx and Polk 1982; Atkinson 1996; Levinsen et al.

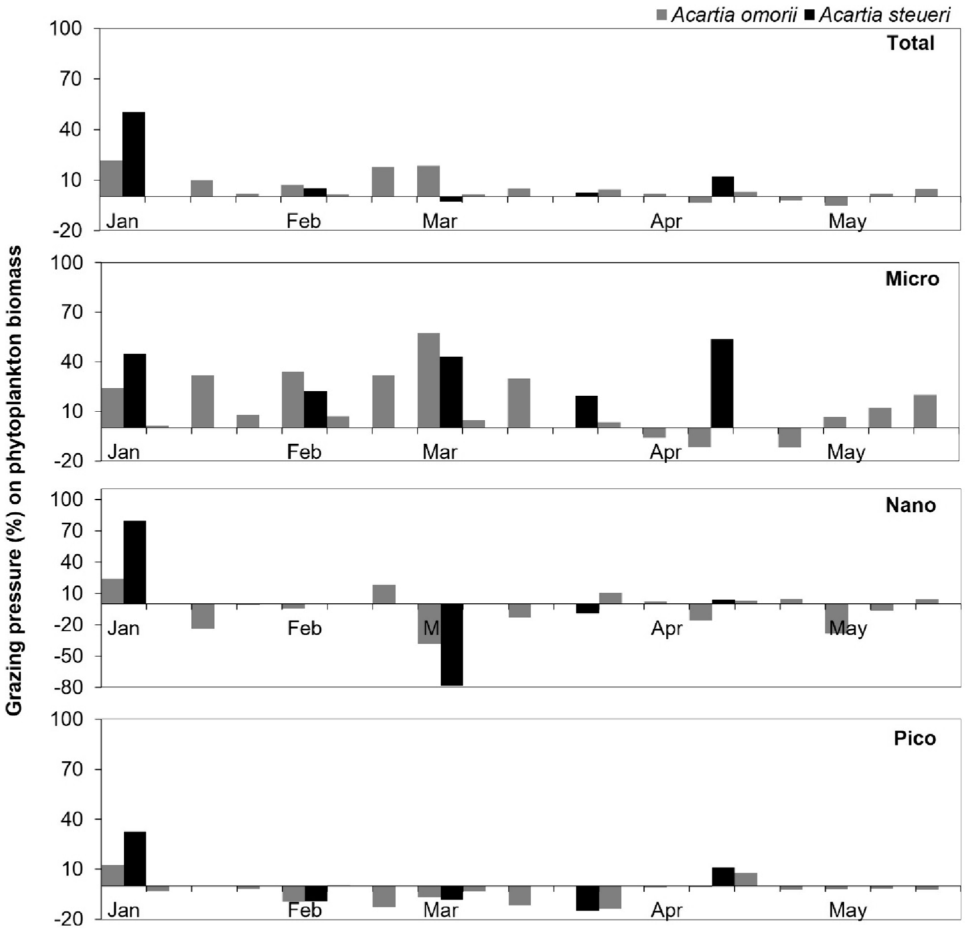


Fig. 7 Variations in grazing pressure on various sized phytoplankton due to *Acartia* species (*Acartia omorii* and *A. steueri*)

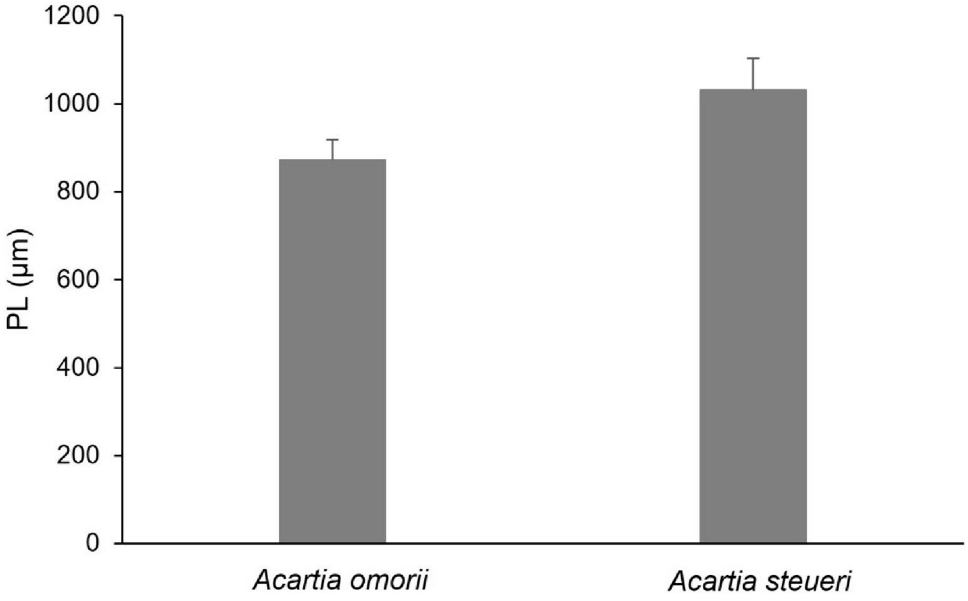


Fig. 8 Mean values of prosome length (PL), for adult females of *Acartia* species (*Acartia omorii* and *A. steueri*). Data are presented as mean ± standard deviation

2000; Calbet et al. 2007), or even to detritus derived from the macrophyte (Roman 1984). This flexibility in diet suggests that *Acartia* species, including *A. omorii* and *A. steueri*, might adjust their feeding preferences based on environmental conditions and prey availability, which is crucial for their survival, especially in areas where food sources are variable.

In our experimental design, the use of in situ temperatures was important in reflecting the natural conditions experienced by *A. omorii* and *A. steueri* in Jangmok Bay, thus ensuring the ecological validity of our findings. The difference in temperature preferences between *Acartia* species could significantly influence their feeding rates and behaviors (Durbin and Durbin 1992; Wlodarczyk et al. 1992). For instance, the metabolic and feeding efficiencies of *A. omorii*, which is dominant in cooler months, may differ from those of *A. steueri*, which thrives in relatively warmer conditions (Hwang et al. 2011). Previous studies showed that *A. steueri* appears throughout the year and reaches peak of abundance when water temperatures are above 20 °C in Ilkwang Bay, South Korea, and Sagami Bay, Japan (Jung et al. 2004; Kang and Kang 2005; Onoue et al. 2006). However, Hwang et al. (2011) found that in Jangmok Bay, *A. steueri* exhibits maximum densities at water temperatures below 10 °C and is absent when water temperatures exceed 20 °C. This divergence could affect their prey selection, grazing pressure, and ultimately, their roles in the marine food web, suggesting a complex interplay between local environmental conditions and species-specific adaptive strategies. Recognizing the crucial role of temperature in influencing the biological processes of these species, we also acknowledge that a comprehensive ecological assessment necessitates considering a wider array of environmental variables. Beyond water temperature, factors such as salinity, light availability, and nutrient levels are essential in fully capturing the ecological dynamics experienced by these copepods.

The accurate measurement of zooplankton feeding and grazing rates is essential. Numerous methods have been developed to measure these rates, but none has been fully effective, and their uncritical use can lead to misinterpretation of results (Peters 1984; Mauchline 1998). The incubation method used in this study has several limitations (crowding of grazers, algae growth due to excrement, and differences in turbulence) because of bottle effects (Roman and Rublee 1981; Sautour 1994). Nevertheless, it is a direct, convenient method to measure the impact of zooplankton feeding on various phytoplankton size categories (Paffenhöfer 1988; Liu et al. 2005; Olson et al. 2006). Kiørboe and Møhlenberg (1985) showed that culture methods can reliably help estimate natural feeding rates despite potential bottle effects, which can impact the in situ feeding rates of planktonic copepods. Thus, these methods are valuable for measuring the feeding impact of zooplankton on natural prey.

Ingestion and clearance rates of *Acartia* species fall within the range showed in Table 3. These rates were calculated as ng Chl-*a* ind.$^{-1}$ day^{-1} and mL ind.$^{-1}$ day^{-1}, respectively. Although direct comparison with our study's methodology is not possible, the original units used in each study are included in the legend of the table because different units

Table 3 Comparison of ingestion rates and clearance rates of *Acartia* species between the present study and previous reports

Species	Clearance rate (mL ind. $^{-1}$ day^{-1})	Ingestion rate (ng Chl-*a* ind. $^{-1}$ day^{-1})	Developmental stage (sex)	References
Acartia hudsonica		19.0–145.7	Adult (female)	Wlodarczyk et al. (1992)
A. natalensis		6.2–23.5	Adult (none)	Kibirige and Perisinotto (2003)
A. tonsa		24–109.9	Adult (female)	Kiørboe and Tiselius (1987)
A. tonsa	1–106	16–476[a]	Adult (both sexes)	Stoecker and Egloff (1987)
A. hongi	3–62	2.2–29.0	Adult (female)	Lee et al. (2012)
A. hongi	16.4–289.1		Adult (female)	Yang et al. (2010)
A. pacifica	19	2.2–32.6	Adult (female)	Lee et al. (2012)
A. clausi		0.4–1.3	Adult and Copepodite V (CV) stages (both sexes)	Pagano et al. (2003)
A. clausi	6.6–74		Adult (female)	Broglio et al. (2001)
A. clausi	3.5–24	1400–60,500[a]	Adult (female)	Ayukai (1987)
A. clausi	27.7–52.5		Adult (female)	Tiselius (1989)
A. steueri	20.3–77.0	17.7–309[a]	Adult (female)	Yamada et al. (2020)
A. grani	34–39		Adult (female)	Isari et al. (2015)
A. grani	0.071–0.49	0.0015–0.030[b]	Nauplii (none)	Henriksen et al. (2007)
A. omorii	0.1–14.6	0.4–196.6	Adult (both sexes)	Present study
A. steueri	0.25–26	0.0059–0.94[b]	Nauplii (none)	Natori and Toda (2018)
A. steueri	0.1–10.9	0.6–395.7	Adult (both sexes)	Present study

Units measured by the authors

[a] cells ind. $^{-1}$ d^{-1}

[b] µg C ind. $^{-1}$ d^{-1}

were used depending on the study. It is important to note that ingestion rates are influenced by various factors, including temperature, food size and density, body size and activity, and experimental methods (Meyer-Harms et al. 1999; Levinsen et al. 2000; Henriksen et al. 2007).

The present study showed that adults of *A. omorii* and *A. steueri* prefer phytoplankton larger than 20 µm, which is in line with other studies that have found similar food-size preferences in copepod species (Batten et al. 2001; Rollwagen-Bollens and Penry 2003; Gifford et al. 2007; Campbell et al. 2009; Fileman et al. 2010). Copepods generally feed selectively based on food size when food is abundant (Cowles 1979). Particles sized lesser than 5 µm are too small to serve as a food source and thus not preferred by some copepod species (Landry 1981; Pagano et al. 2003; Campbell et al. 2009). The present study demonstrated the limited utilization of nano- and pico-phytoplankton by *Acartia* adults as food sources, which was indicated by consistently negative ingestion rates for these sizes, except in January. The prey selectivity of *A. steueri* was decreased for nano-phytoplankton and that of both species was particularly poor for pico-phytoplankton. In addition, the negative ingestion rate of *A. omorii* for micro-phytoplankton (> 20 µm) suggests that *Acartia* species may require different diets to maintain populations in Jangmok Bay. This aligns with the concept that copepod feeding preferences and strategies are not solely influenced by prey size but also a combination of factors, including prey density, nutritional quality, and behavior. Studies have shown that copepods, including *Acartia* species, can adapt their diets based on environmental conditions, often switching to alternative prey, such as ciliates and other microzooplankton when phytoplankton is scarce (Calbet and Saiz 2005; Castellani et al. 2008). Yang et al. (2010) reported that *A. hongi* favors motile ciliates over similar-sized diatoms, indicating a preference for prey with active motility. This suggests that factors beyond prey size, such as motility and nutritional content, influence copepod feeding choices. In addition, experiments, wherein mixed diets of similar-sized *Tintinnopsis angustior* and *Thalassiosira* sp. were provided, the high filtration rate and selective feeding on certain ciliates by *A. hongi* could not be solely explained by prey size but rather by a selective feeding mechanism favoring quality or motile prey. Therefore, particle size alone may not fully explain selective feeding by copepods.

It is important to note that the grazing effect of copepods, including *Acartia* species, can vary based on region, year, and season and plays a role in controlling the composition and dynamics of phytoplankton communities in marine ecosystems (Gifford and Dagg 1988; Yang et al. 2010). The grazing pressure of the *Acartia* adults on total phytoplankton biomass in the present study was found to be 6.8 ± 11.8%, which is similar to that calculated in previous studies. This grazing pressure can equal or even exceed daily primary productivity, highlighting the significant role of *Acartia* species in marine food webs. Their selective feeding on larger phytoplankton could have important implications for the structure and dynamics of plankton communities, potentially influencing energy transfer and nutrient cycling in coastal ecosystems.

The present study demonstrated the preference of *A. omorii* and *A. steueri* for phytoplankton larger than 20 µm, which is consistent with other studies that showed similar food-size preferences in copepod species (Liu and Dagg 2003; Jang et al. 2010; Yoshida et al. 2012). *A. steueri* had significantly higher ingestion rates than *A. omorii*, and its ingestion rate was strongly correlated with food density in phytoplankton sized > 20 µm ($r^2 = 0.904$, $P = 0.013$; Fig. 9). The results indicated that the high abundance of *A. steueri* in winter and spring can affect the biomass and composition of phytoplankton sized > 20 µm. Copepods feed more as their body size increases (Hansen et al. 1997). Paffenhöfer (1970) found that the total body length of an adult female copepod is directly related to the amount of food available during rearing. Larger copepods have greater gut volume because they require greater amount of energy for the metabolism associated with increased body sizes (Tseng et al. 2008, 2009). The variation in ingestion rates between *A. steueri* and *A. omorii* is because of the difference in their body lengths. In this study, the mean prosome length of adult females *A. omorii* was 873.2 ± 45.6 µm ($n = 10$), while that of adult females *A. steueri* was 1031.4 ± 72.7 µm ($n = 10$). By integrating observations on sex ratios, particularly on April 14 when the ratio approached 1:1, we further enriched our understanding of these dynamics. This balanced sex ratio among adults offered a pivotal moment to dissect the impact of physiological differences between the sexes on feeding behavior, especially as *A. steueri* demonstrated peak

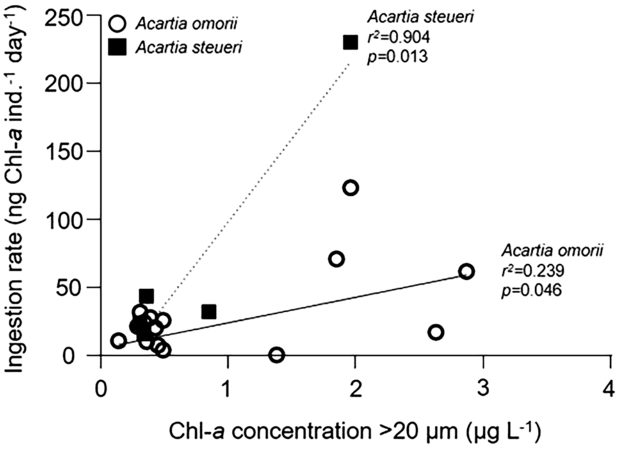


Fig. 9 Correlation between ingestion rate and micro-phytoplankton (> 20 µm) biomass (Chl-*a* concentration) for adults of *Acartia* species (*Acartia omorii* and *A. steueri*)

clearance rates and grazing pressures on micro-phytoplankton during this period. The additional energy requirements for oogenesis in adult females, necessitating a higher intake than their male counterparts (Roncalli et al. 2020), likely influenced these observed feeding behaviors and grazing pressures. This finding highlights the importance of considering both the species and size of copepods when studying their role in the food chain and energy transfer in coastal ecosystems. Further research is needed to fully understand the mechanisms associated with the differences in feeding behavior and ingestion rates in the two species, taking in consideration the different life cycle stages, different energetic needs of the two sexes, and in the same female sex in different ovogenesis periods (when producing diapause and subitaneous eggs).

Conclusions

In Jangmok Bay, the occurrence and abundance of *A. omorii* and *A. steueri* are closely linked to water temperature. T-S analysis indicated that *A. omorii* has a broader environmental tolerance, with a temperature range of 6.2 to 17.1 °C and a salinity spectrum of 31.8 to 33.5. However, *A. steueri* prefers a narrower temperature window of 6.5 to 12.8 °C and a salinity range of 32.2 to 33.5. This variation in temperature preference is critical to understanding their patterns of coexistence and competition, especially for micro-phytoplankton (> 20 µm), which is a key food resource. Our observations demonstrate the challenges that both *A. omorii* and *A. steueri* might face regarding food availability, and adaptability to temperature variations when their habitats overlap. Furthermore, this study sheds light on the adaptive feeding strategies of these species, suggesting a complex interplay between dietary preferences and environmental conditions. The findings particularly highlight *A. omorii*'s potential for broader dietary flexibility of adults, which may be vital for its survival in environments with limited food sources. Additional research is required to explore alternate food sources for these copepods and understand the impact of changing phytoplankton communities on their feeding behaviors and interspecies competition. Such investigations are crucial for a deeper comprehension of their ecological roles and the broader implications for the health of coastal marine ecosystems.

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Author contributions SYC and HYS conceived the study and conducted the literature search. SYC, EHL, MHS, and M-C Jang collated data from the literature. SYC analyzed and visualized the data. SYC and HYS wrote the original draft of the manuscript, which was revised by all the authors.

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Data availability Data will be made available from the corresponding authors upon reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethical approval The authors declare that all applicable guidelines for sampling, care and experimental use of animals in the study have been followed.

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