

## ORIGINAL ARTICLE

# Copepod feeding in a coastal area of active tidal mixing: diel and monthly variations of grazing impacts on phytoplankton biomass

Doo B. Lee<sup>1</sup>, Hye Y. Song<sup>2</sup>, Chul Park<sup>2</sup> & Keun H. Choi<sup>3</sup><sup>1</sup> Division of Polar Climate Research, Korea Polar Research Institute, Incheon, Korea<sup>2</sup> Department of Oceanography and Ocean Environmental Sciences, Chungnam National University, Daejeon, Korea<sup>3</sup> Marine Living Resources Research Department, Korea Ocean Research and Development Institute, Ansan, Korea**Keywords**

Active tidal mixing bay; copepods; diel feeding rhythms; grazing impacts.

**Correspondence**Chul Park, Department of Oceanography and Ocean Environmental Sciences, Chungnam National University, 79 Daehangno, Yousoung-gu, Daejeon 305-764, Korea.  
E-mail: chulpark@cnu.ac.kr

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**Abstract**

This study examined monthly feeding rates and grazing impact on phytoplankton biomass, as well as diel feeding rhythms of four key copepod species in a tidally well mixed estuary (Asan Bay, Korean Peninsula). Monthly ingestion rates estimated based on gut pigment analysis were closely associated with their peak densities, but not with phytoplankton biomass, implying high ingestion may be related to reproductive output for population growth. The three smaller copepods, *Acartia hongii*, *Acartia pacifica* and *Paracalanus parvus*, showed feeding preference for smaller phytoplankton (<20 µm) with higher clearance rates, whereas the larger *Calanus sinicus* preferred larger phytoplankton. *Acartia pacifica* and *P. parvus* showed distinct increased nocturnal feeding rates as measured with gut fluorescence, whereas *A. hongii* showed no significant day–night differences. Copepod diel feeding patterns were not associated with food quantity, and endogenous physiological rhythm might be hypothesized as responsible for the observed diel feeding patterns. Grazing impact on phytoplankton biomass by the four copepods in the estuary was on average 8% (range 0.2–29.8%) of the phytoplankton standing stock, similar to values reported in other coastal waters. Very high copepod abundances but low daily carbon ration (<20% for all copepods) provided by feeding on phytoplankton indicate that copepods also grazed on other non-phytoplankton foods in Asan Bay.

**Introduction**

Feeding behavior plays an important role in the adaptive strategies of marine organisms (Kouassi *et al.* 2001). Feeding is also the main route for the transfer of energy and material from lower to higher trophic organisms within communities and, as such, its quantification is a key factor in understanding trophic interactions (Båmstedt *et al.* 2000).

Marine copepods are generally believed to feed in a characteristic day–night cycle. Some species show higher ingestion rates at night and others during the daytime; still others show no such cycles at all (Dagg & Grill 1980; Dagg

1985; Daro 1985; Kiørboe *et al.* 1985; Dagg & Walser 1987; Haney 1988; Roman *et al.* 1988; Saito & Taguchi 1996; Calbet *et al.* 1999). Food quantity, risk of predation, past feeding histories and genetically encoded endogenous rhythms have been ascribed as the primary reasons for diel feeding rhythms in copepods (Li *et al.* 2003).

In an estuary of active tidal mixing caused by a large tidal range, a high concentration of suspended particles is among the most important environmental characteristics for plankton ecology. Although copepods are generally well adapted to turbid environments (David *et al.* 2006), turbidity can have a variety of beneficial and adverse consequences for zooplankton feeding (Hart 1988;

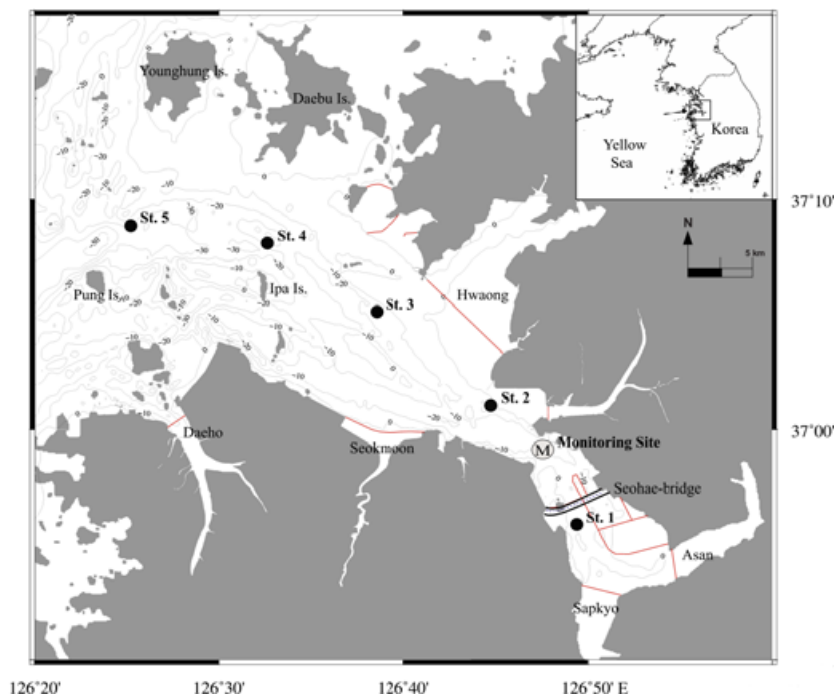


Fig. 1. Map of the sampling sites in Asan Bay, Korea.

Carrasco *et al.* 2007). Suspended particulate matter may impair the ability of a predator (*e.g.* zooplanktivorous fish) to locate prey (Gardner 1981). In addition, zooplankton capable of ingesting such particles may benefit nutritionally from this potential resource (Arruda *et al.* 1983). Strong turbulence and increased level of turbidity can decrease copepod feeding rates (Saiz *et al.* 2003). Egg production may also decrease due to lower food availability from lack of light and difficulty in selecting edible particles (Sautour & Castel 1995; Burdloff *et al.* 2000). Copepods in turbid estuarine environments can face chronic food limitation (Dagg & Grill 1980; Kimmerer *et al.* 2005), which may induce them to feed more constantly throughout the day, as compared to those in clearer waters that are exposed to a single patch of high food concentration during the day. Diel feeding rhythm may become weaker in coastal areas than in open seas, possibly due to relatively higher turbidity, which leads to reduced visual predation pressure (Vinyard & O'Brien 1976; Li *et al.* 2003). For instance, copepods living inside the Bohai Sea (north of the Yellow Sea, between China and Korea) showed relatively small amplitude of diel feeding rhythms, whereas copepods living in the bay-mouth area with relatively clear waters showed strong diel feeding rhythms (Li *et al.* 2003).

Two different approaches are generally used to estimate grazing rates; gut pigment analysis and food removal method. Gut content analysis provides information on mesozooplankton feeding with a tool sensitive enough to

measure chlorophyll *a* (Chl *a*) and derived pigments in zooplankton guts (Mackas & Bohrer 1976). This method is useful because of its analytical simplicity and the fact that it provides data directly from field zooplankton samples, thus not requiring incubation. It is especially useful in studying diel feeding patterns because it allows quantitative comparisons of feeding rates on phytoplankton in the field. The food removal method involves incubating zooplankton in bottles with food for fixed time, and then measuring the decrease in food concentration compared to that in control bottles with no grazers. This approach is the simplest direct method and the longest in use (Gauld 1951). However, potential limitations of laboratory incubations include the stress of capture, handling and confinement on zooplankton.

The aims of our study were (i) to estimate the feeding rates of abundant copepods to assess their food size selectivity in a coastal embayment of intense tidal mixing, (ii) to test the hypothesis that a diel feeding rhythm does not occur due to active tidal mixing and (iii) to evaluate the impact of copepod grazing on the phytoplankton community.

## Material and Methods

### Study site

Asan Bay is located in the western coast of the Korean peninsula and covers an area of about 90 km<sup>2</sup> (40 km long and 2.2 km wide with a mean depth of about 25 m).

A big tidal range of over 8 m at spring tide is a major characteristic, with tidal currents varying in speed and direction due to complex bottom topography and nearby islands. A maximum speed of just over  $1 \text{ m}\cdot\text{s}^{-1}$  in the channels has been reported (Park 2000). Studies on the mesozooplankton community in Asan Bay date back to the previous two decades (e.g. Park *et al.* 1998; Lee & Park 2002). *Acartia hongii* [formally known as *Acartia biflosa* and re-described by Soh & Suh (2000)], *Calanus sinicus*, *Acartia pacifica* and *Paracalanus parvus* account for about 50–80% of total copepod abundance, while their temporal distributions are closely related to seawater temperature (Park *et al.* 1991, 1998; Choi & Park 1993; Lee & Park 2002; Lee *et al.* 2006).

For the present study, five stations were sampled seasonally, from February to November in 2007 and monthly from January to December in 2008, to measure zooplankton abundance and copepod feeding rates (Fig. 1). Copepod feeding rates were determined by both gut pigment analysis and food removal method. To analyze copepod diel feeding rhythms, an additional monitoring station was visited in May, August and November of 2007 (Fig. 1). Water depths at the stations varied from 10 to 30 m, gradually increasing offshore: approximately 10 m at St. 1, 20 m at both St. 2 and St. 3, 25 m at St. 4, 30 m at St. 5, and 20 m at the additional monitoring site.

#### Environmental parameters

At all sampling events, vertical profiles of seawater temperature and salinity values were obtained using a YSI-6600 conductivity meter. Water samples were collected at three depths (surface, mid and bottom layer) using a 5-l Niskin sampler. Suspended particulate matter (SPM) was collected on pre-weighed Whatman GF/C filters by filtering 250–500 ml of seawater, after which the filters were dried at  $60^\circ\text{C}$  for 24 h and subsequently weighed. For Chl *a* concentration analysis, 250 ml seawater was taken at the three depths from each station at each sampling event and filtered onto GF/F filters. Pigments were extracted in 90% acetone overnight at  $4^\circ\text{C}$  in the dark. Chl *a* concentrations were measured with a UV-visible spectrophotometer following the method of Strickland & Parsons (1972).

#### Sampling for monthly copepod abundance, gut pigment analysis and ingestion rates

To estimate the abundance of copepods and other zooplankton groups, net samples were collected with a conical net (76 cm diameter,  $330 \mu\text{m}$  mesh size) that was towed obliquely from near bottom to the surface at about

$1\text{--}1.5 \text{ m}\cdot\text{s}^{-1}$  for about 3–5 min, thus filtering 17–149  $\text{m}^3$  of seawater for each sample as indicated by revolution counts of a flow-meter attached to the net. Three replicate samples were obtained during each sampling event. Samples were immediately fixed and preserved with buffered formaldehyde (pH 8, final concentration of *c.* 5%). In the laboratory, subsampling was done with a Folsom Plankton Splitter and the zooplankton subsamples were placed in a Bogorov chamber and examined under a dissecting microscope. Copepods were enumerated to species level if possible. The mean abundance of replicate samples was expressed as individual numbers per cubic meter ( $\text{ind}\cdot\text{m}^{-3}$ ).

For monthly feeding rate measurements, copepods were collected from additional tows with the same net used for the abundance study above. From the additional towed copepods, healthy individuals were immediately sorted out and transferred into 20-ml vials containing filtered seawater. The vials were frozen at  $-70^\circ\text{C}$  in liquid nitrogen container, brought back to the laboratory, and stored at  $-20^\circ\text{C}$  in the dark until gut pigment analyses was done within 2 months.

In the laboratory, female adult specimens of the four species, *A. hongii*, *C. sinicus*, *A. pacifica* and *P. parvus*, were sorted out from the frozen samples as rapidly as possible. About 100 individuals for smaller copepods (*A. hongii*, *A. pacifica* and *P. parvus*), and 50 individuals for the larger one (*C. sinicus*) were used for gut fluorescence analyses. Copepod body length was 1.0–1.2 mm (*A. hongii*), 2.1–3.3 mm (*C. sinicus*), 1.0–1.3 mm (*A. pacifica*), and 0.8–1.0 mm (*P. parvus*). Gut contents from the animals were extracted in centrifuge tubes containing 8 ml of 90% acetone for 24 h at  $4^\circ\text{C}$  in the dark. The fluorescence of the extract was measured using a Turner design trilogy fluorometer before and after acidification with 2–3 drops of 10% HCl. The chlorophyll and phaeopigment contents of each copepod species were calculated following Strickland & Parsons (1972). The gut pigment contents (G) were determined by directly summing these two values and were expressed as  $\text{ng Chl } a\cdot\text{eq. ind.}^{-1}$  (Dam & Peterson 1988; Head & Harris 1992). Ingestion rates (I,  $\text{ng Chl } a\cdot\text{eq. ind.}^{-1}\cdot\text{h}^{-1}$ ) were calculated from the measurements of gut fluorescence (Mackas & Bohrer 1976; Dagg & Wyman 1983) using the equation:

$$I = G \cdot k \cdot 60$$

where G is the gut pigment content ( $\text{ng Chl } a\cdot\text{eq. ind.}^{-1}$ ) and k is the gut evacuation rate constant ( $\text{min}^{-1}$ ). The gut evacuation rate constant (k) was derived from the following equation of Dam & Peterson (1988):

$$k = 0.0117 + 0.001794 \cdot T$$

where  $T$  is the seawater temperature ( $^{\circ}\text{C}$ ). This equation is based on the relationship between gut clearance time and temperatures covering large temperature ranges ( $-1$  to  $20$   $^{\circ}\text{C}$ ). We considered a phytoplankton carbon/chlorophyll ratio ( $C/\text{Chl } a$ ) of 50 and a copepod carbon content corresponding to 45% of the dry mass. The *in situ* grazing impacts of the adult females were calculated by multiplying individual ingestion rates with the corresponding species abundances and were expressed as the percentage of the depth-integrated  $\text{Chl } a$  concentrations.

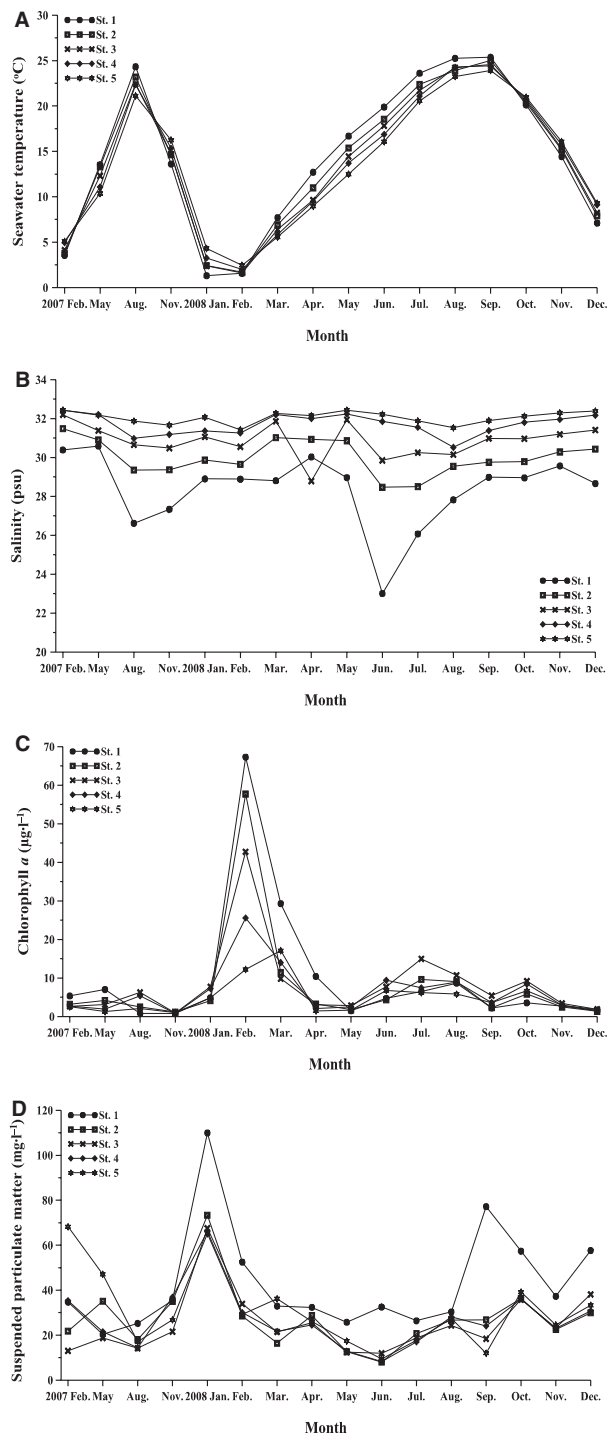
### Sampling for diel feeding rate measurements

Copepods for diel feeding rate measurements were collected with a 52-cm diameter net with  $200\ \mu\text{m}$  mesh at the 24 h monitoring site. The net was towed twice vertically from about 2 m above the bottom to the surface at 2-h intervals for a 24 h period. Zooplankton samples obtained from the first tow were preserved with buffered formalin for quantitative analyses as described above. From the second towed copepods, healthy individuals were immediately sorted for gut pigment analysis as described above.

### Feeding rates on size-fractionated phytoplankton

In the food removal method, feeding was measured as clearance rates (*i.e.* the volume swept clear by each individual copepod per unit time) on total and size-fractionated  $\text{Chl } a$ . Freshly caught healthy individuals were immediately sorted and transferred to 2.6-l polycarbonate bottles on site. Copepods for experiments were brought to the laboratory and acclimated for 24 h by placing the bottles in a container filled with natural seawater at *in situ* temperatures under a 12 h light:12 h dark cycle. In the laboratory, undamaged healthy adult females from the 2.6-l bottles were transferred into 2-l polycarbonate bottles filled with  $200\ \mu\text{m}$  prescreened seawater. Experimental bottles (two replicates per experiment) with copepods and a control bottle without copepods were placed in the dark for 24 h in the incubator at *in situ* seawater temperature. To prevent the food from sinking, the bottles were gently stirred every 3 h. Two subsamples of 250 ml [total  $\text{Chl } a$  and  $\text{Chl } a$  of nanophytoplankton ( $<20\ \mu\text{m}$ )] were taken from each bottle before and after 24 h incubation and filtered onto GF/F filters for  $\text{Chl } a$  measurements as described above. The copepods were strained through a sieve and their dry weight was measured after drying at  $60$   $^{\circ}\text{C}$ . Clearance rates of  $\text{Chl } a$  from total phytoplankton and nanophytoplankton were calculated from the equations in Frost (1972) and expressed in terms of  $\text{ml}$

### Copepod feeding in a coastal area of active tidal mixing



**Fig. 2.** Seasonal and monthly variations in depth-averaged environmental variables recorded at five stations in Asan Bay from February 2007 to December 2008 (A: seawater temperature, B: salinity, C:  $\text{Chl } a$  concentration, D: suspended particulate matter).

copepod $^{-1}\text{day}^{-1}$ .  $\text{Chl } a$  of the microphytoplankton ( $>20\ \mu\text{m}$ ) was obtained by subtracting nano  $\text{Chl } a$  from total  $\text{Chl } a$ .

## Statistical analysis

Cluster analysis was performed to examine the degree of co-occurrence among the 13 species of copepods with modified correlation coefficients ( $1-r_{ij}$ ) of abundance data. Relationships between the parameters copepod abundance, ingestion rate and environmental factors (seawater temperature, salinity and Chl *a* concentration) were tested using the Pearson correlation analysis. All statistical analyses were conducted using the SAS version 9.1.3 software package (SAS Institute Inc., 2005).

## Results

### Monthly variability

#### *Environmental variables*

In Asan Bay, depth-averaged seawater temperature showed a typical seasonal pattern observed in a temperate region, ranging from an average of 1.3 °C in February to 25.4 °C in September (Fig. 2A). Temperature differences among the stations within the same season were as large as 5 °C in spring and summer but nearly disappeared in winter (Fig. 2A). Temperature was higher in the inner part of the bay during spring and summer, gradually decreasing toward outer stations. The trend reversed during fall and winter, with higher temperatures found in the outer part of the bay. Such seasonal variation of spatial temperature distribution may reflect differential warming and cooling processes at stations of different depths (*i.e.* faster warming at shallow waters in spring and summer and slower cooling at deeper stations in fall and winter).

Temporal fluctuation of depth-averaged salinity was very small, except in the innermost bay, which is more affected by freshwater input (Fig. 2B), with low salinity being observed in the rainy summer season. Salinity differences among the stations were relatively small in winter and spring but larger in summer and autumn due to sporadic discharge of fresh water from nearby embankments.

Depth-averaged Chl *a* concentrations showed seasonal variations, being lowest in November 2007 and highest in February 2008, with a bloom appearing during the late winter-early spring period (Fig. 2C). In February 2008, Chl *a* concentration was highest in the inner part of the bay, whereas in July it was high in the outer part of the bay. The highest Chl *a* concentrations (up to 67  $\mu\text{g}\cdot\text{l}^{-1}$ ) were found in the inner part of the bay.

Depth-averaged suspended particulate matter (SPM) showed generally higher concentrations in the inner part of the bay (St. 1) except in February and May 2007 (Fig. 2D). In those months in 2007, SPM was higher in the outer part of the bay (St. 5).

#### *Mesozooplankton abundance and composition*

During the present study, 31 mesozooplankton taxa were identified, including 13 copepod species. Copepods contributed between 40 and 94% to total mesozooplankton abundance (Fig. 3). Decapoda, which ranked second in abundance after copepods and were represented mainly by larvae, only accounted for a significant portion of total numbers (23–37%) from June to August. Hydromedusa were relatively important only in spring, and Echinodermata and Mollusca larvae in summer and autumn. The chaetognath *Sagitta crassa* accounted for 1–9% of total mesozooplankton abundances throughout the year (Fig. 3).

Cluster analysis based on the degree of co-occurrence among the 13 copepods with modified correlation coefficients ( $1-r_{ij}$ ) of abundance data revealed two main groups at the 1.24 distance (Fig. 4). Group A comprised five copepod species (*Centropages abdominalis*, *Calanus sinicus*, *Eurytemora pacifica*, *Acartia hongii* and *Labidocera euchaeta*) that were mainly abundant in winter and spring. *Acartia hongii* was the most abundant copepod in the bay, representing on average ~40% of total mesozooplankton during the year, with peaks of 50–80% in spring and the lowest contribution (<30%) in summer and autumn (Table 1, Fig. 5). *Calanus sinicus* was most abundant in spring, contributing up to 13% of total mesozooplankton abundance in May (Table 1, Fig. 5). *Labidocera euchaeta* represented only 2% of total mesozooplankton abundance in winter, and *C. abdominalis* and *E. pacifica* ~1% in spring (Fig. 5).

Group B consisted of eight copepods (*Tortanus forcipatus*, *Centropages tenuiremis*, *Corycaeus affinis*, *Tortanus spinicaudatus*, *Paracalanus parvus*, *Labidocera bipinnata*, *Acartia pacifica* and *Pseudodiaptomus marinus*) that occurred mainly in summer and autumn. *Acartia pacifica* represented 11–21% of total zooplankton abundance only in July. *Paracalanus parvus* was abundant from August to September, constituting 33–59% of the abundance, with the remaining copepods accounting for <3% of total mesozooplankton abundance (Fig. 5).

In summary, *A. hongii*, *C. sinicus*, *A. pacifica* and *P. parvus* were the most dominant zooplankton in the bay, *Acartia*, *C. sinicus* in spring, *A. pacifica* in summer, and *P. parvus* in summer and autumn.

*Acartia pacifica* was generally distributed at relatively lower salinity with an abundance center located at salinity of about 27.5. *Calanus sinicus* occurred at areas of the highest salinity (32), and *A. hongii* and *P. parvus* were found at intermediate values (Fig. 6).

#### *Ingestion rates and grazing impact of copepods*

Gut pigment contents and ingestion rates of *Acartia hongii* ranged between 0.04 and 1.10, and between 0.09 and

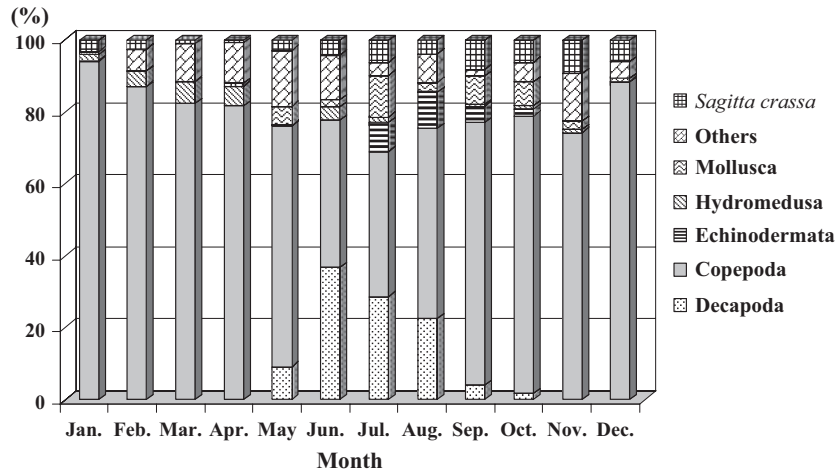


Fig. 3. Spatially averaged contribution (%) of major groups to total mesozooplankton abundance from January to December 2008.

1.21 ng Chl *a*-eq. ind.<sup>-1</sup>·h<sup>-1</sup>, respectively (Fig. 7A). The ingestion rate was highest in January, decreased gradually and increased again in November. The same rates in *Calanus sinicus* ranged from 0.04–7.25 and 0.12–16.44 ng Chl *a*-eq. ind.<sup>-1</sup>·h<sup>-1</sup>, respectively (Fig. 7B), with the highest ingestion rates recorded in May and November. *Acartia pacifica* and *Paracalanus parvus* showed similar feeding patterns, with increased feeding in August and September when they were more abundant (Table 1, Fig. 7C,D). The gut pigment contents were in the range of 0.11–0.39 ng Chl *a*-eq. ind.<sup>-1</sup> for *A. pacifica* and 0.01–0.32 ng Chl *a*-eq. ind.<sup>-1</sup> for *P. parvus*. The ingestion rates varied between 0.33 and 1.28 ng Chl *a*-eq. ind.<sup>-1</sup>·h<sup>-1</sup> for *A. pacifica* and between 0.02 and 1.09 ng Chl *a*-eq. ind.<sup>-1</sup>·h<sup>-1</sup> for *P. parvus*. The daily carbon ration ranged from 0.9 to 6.3% body C·day<sup>-1</sup> for *A. hongii*, from 0.2 to 18.4% body C day<sup>-1</sup> for *C. sinicus*, from 3.6 to 17.8% body C·day<sup>-1</sup> for *A. pacifica*, and from 0.3 to 12.7% body C·day<sup>-1</sup> for *P. parvus* (Table 2).

Copepod grazing impact on phytoplankton standing stock was highly variable between seasons and generally low for all of the four species examined (Table 2). *Acartia hongii* showed the largest impact, with a range of 0.23–14.65% (geometric mean of 1.93%) of the phytoplankton standing stock, with the highest value observed in April and the lowest in February. The impact of *A. pacifica* ranged from 0.65 to 8.05% (geometric mean of 1.73%), with the highest grazing impact recorded in August 2007. *Paracalanus parvus* had impact of between 0.01 and 26.58% (geometric mean of 0.70%) and *C. sinicus* had the lowest impact on phytoplankton, ranging from 0.001 to 6.42% (geometric mean of 0.11%).

Size selectivity in copepod feeding

Irrespective of the season and food concentrations, *Acartia hongii*, *Acartia pacifica* and *Paracalanus parvus*

had higher clearance rates of nanophytoplankton than of microphytoplankton (Table 3, *P* < 0.05 in *t*-tests for all comparisons). Selective feeding on smaller

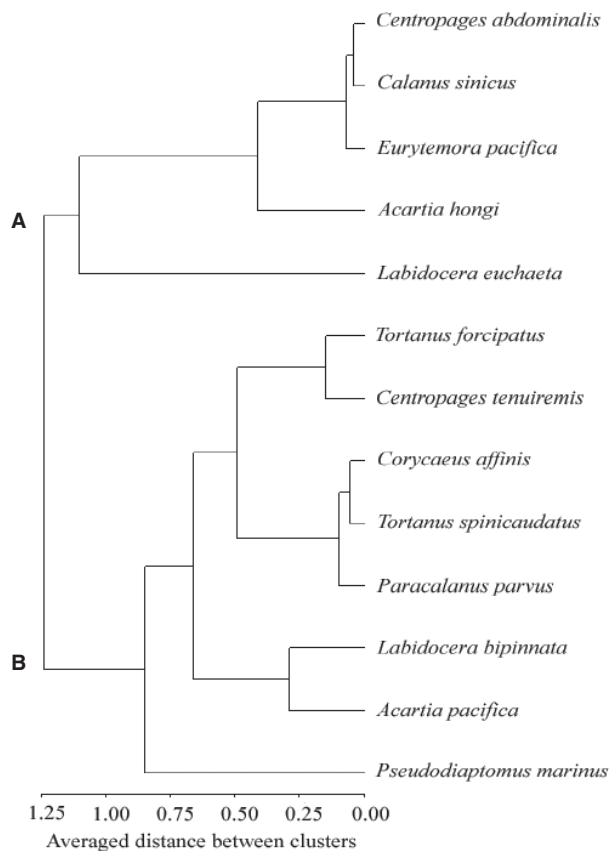


Fig. 4. Dendrogram showing the degree of co-occurrence among the 13 copepods obtained by the cluster analysis with modified correlation coefficients (1-r<sub>ij</sub>) of abundance data.

**Table 1.** Mean abundances (ind.·m<sup>-3</sup>, ± 95% confidence levels) of the four target copepod species and (in brackets) their percentage contribution to total mesozooplankton abundance. The averages are presented from data collected at five stations.

month/year	target species abundance, ind.·m <sup>-3</sup> (% of total numbers)											
	<i>Acartia hongii</i>		<i>Calanus sinicus</i>		<i>Acartia pacifica</i>		<i>Paracalanus parvus</i>					
	male	female	male	female	male	female	male	female				
02/07	37 ± 18.2 (19.6)	98 ± 49.6 (51.9)	<1 ± 0.2 (0.1)	6 ± 5.1 (3.0)	0 (0.0)	0 (0.0)	<1 ± 0.1 (0.1)	3 ± 1.1 (1.8)				
05/07	346 ± 239.1 (9.3)	2935 ± 2202.9 (79.2)	3 ± 2.3 (0.1)	5 ± 5.7 (0.1)	0 (0.0)	0 (0.0)	0 (0.0)	3 ± 1.3 (0.1)				
08/07	5 ± 6.3 (0.2)	20 ± 16.3 (1.0)	0 (0.0)	<1 ± 0.2 (0.0)	145 ± 194.5 (7.2)	279 ± 401.2 (13.8)	95 ± 76.0 (4.7)	987 ± 601.2 (48.9)				
11/07	1 ± 1.2 (0.5)	20 ± 12.7 (8.1)	<1 ± 0.2 (0.1)	<1 ± 0.7 (0.2)	<1 ± 0.1 (0.0)	<1 ± 0.5 (0.1)	4 ± 3.0 (1.4)	92 ± 69.6 (36.7)				
01/08	109 ± 76.4 (16.3)	345 ± 277.4 (51.8)	<1 ± 0.3 (0.0)	2 ± 2.1 (0.2)	0 (0.0)	0 (0.0)	1 ± 0.8 (0.1)	27 ± 14.7 (4.1)				
02/08	68 ± 25.9 (14.2)	249 ± 110.6 (51.8)	<1 ± 0.2 (0.0)	2 ± 0.9 (0.3)	0 (0.0)	0 (0.0)	0 (0.0)	6 ± 1.8 (1.3)				
03/08	254 ± 145.4 (20.8)	450 ± 272.9 (36.8)	<1 ± 0.2 (0.0)	2 ± 1.3 (0.1)	0 (0.0)	0 (0.0)	1 ± 0.9 (0.1)	5 ± 2.0 (0.4)				
04/08	172 ± 74.8 (8.9)	1251 ± 611.9 (64.9)	3 ± 3.7 (0.1)	6 ± 3.9 (0.3)	0 (0.0)	0 (0.0)	<1 ± 0.2 (0.0)	4 ± 4.1 (0.2)				
05/08	13 ± 8.0 (1.4)	463 ± 224.0 (48.1)	3 ± 2.8 (0.3)	11 ± 6.6 (1.1)	0 (0.0)	0 (0.0)	1 ± 0.9 (0.1)	13 ± 5.8 (1.4)				
06/08	6 ± 4.9 (1.5)	105 ± 45.5 (28.7)	<1 ± 0.2 (0.1)	1 ± 0.3 (0.2)	1 ± 0.9 (0.2)	<1 ± 0.6 (0.1)	2 ± 1.6 (0.5)	15 ± 11.5 (4.1)				
07/08	4 ± 3.4 (0.6)	27 ± 11.8 (3.4)	1 ± 0.9 (0.1)	2 ± 1.4 (0.2)	30 ± 35.0 (3.7)	57 ± 63.6 (7.2)	20 ± 26.3 (2.5)	100 ± 116.4 (12.6)				
08/08	2 ± 0.9 (0.2)	7 ± 4.9 (0.7)	<1 ± 0.1 (0.0)	<1 ± 0.3 (0.0)	41 ± 54.9 (4.2)	86 ± 96.6 (8.7)	14 ± 9.4 (1.4)	306 ± 102.0 (31.1)				
09/08	1 ± 1.1 (0.1)	4 ± 2.3 (0.3)	0 (0.0)	<1 ± 0.7 (0.0)	4 ± 5.1 (0.3)	17 ± 22.6 (1.5)	15 ± 10.6 (1.4)	637 ± 402.7 (57.7)				
10/08	1 ± 0.8 (0.3)	13 ± 8.2 (3.5)	<1 ± 0.1 (0.0)	0 (0.0)	12 ± 22.1 (3.1)	13 ± 24.4 (3.5)	6 ± 6.1 (1.7)	183 ± 60.4 (49.0)				
11/08	1 ± 0.9 (0.9)	31 ± 9.6 (20.6)	0 (0.0)	0 (0.0)	<1 ± 0.1 (0.0)	<1 ± 0.1 (0.0)	3 ± 2.0 (1.7)	31 ± 18.0 (20.3)				
12/08	49 ± 26.6 (13.7)	127 ± 52.9 (35.6)	<1 ± 0.1 (0.0)	1 ± 0.4 (0.2)	0 (0.0)	0 (0.0)	5 ± 2.5 (1.5)	83 ± 57.0 (23.2)				

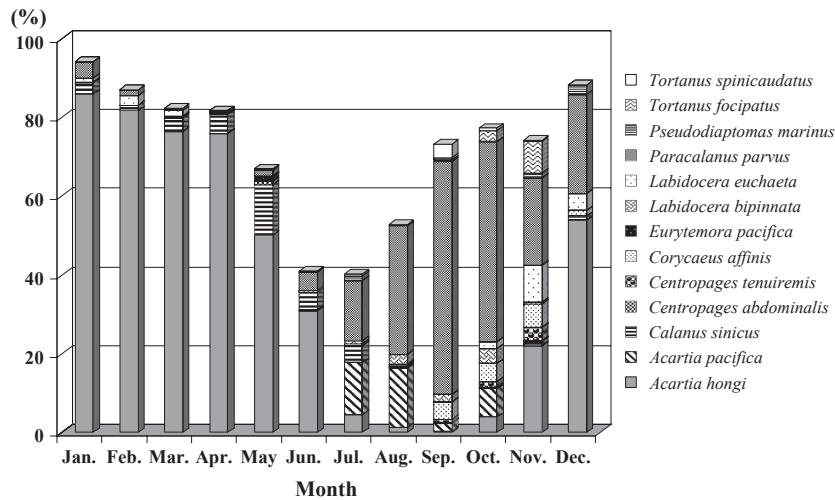


Fig. 5. Spatially averaged contribution (%) of the 13 copepods to total mesozooplankton abundance from January to December 2008.

phytoplankton was most prominent for *A. pacifica*. In contrast, *Calanus sinicus* showed double the clearance rate of micro- than of nano-phytoplankton in the single measurement that we could perform (Table 3).

#### Diel variability

##### Environmental parameters and copepod abundance

Environmental variables and the abundance of three copepods at the 24 h monitoring site are summarized in Table 4. Diel variations of seawater temperature and salinity were  $<1$  °C and 1 psu. The daily mean concentration of Chl *a* was lowest in November ( $0.7 \mu\text{g}\cdot\text{l}^{-1}$ ) and highest in May ( $5.2 \mu\text{g}\cdot\text{l}^{-1}$ ). Concentrations of suspended particulate matters were quite variable, ranging from 9.2 to  $34.3 \text{ mg}\cdot\text{l}^{-1}$  over a day, indicating an active tidal mixing occurring in the study area. Diel variation of copepod abundances was not periodic during the 24 h cycle, with no consistent relationship found between the abundance and the tidal phase (diel pattern for *Calanus sinicus* was not examined due to an insufficient number of specimens).

##### Copepod ingestion rates

Gut pigment contents and ingestion rates of *A. hongii* did not exhibit a diel rhythm in spring (*t*-test,  $P > 0.05$ ; Fig. 8A). The average gut pigment contents and ingestion rates were 0.09 and  $0.18 \text{ ng Chl } a\cdot\text{eq. ind.}^{-1}\cdot\text{h}^{-1}$ , respectively. On the other hand, both *Acartia pacifica* and *Paracalanus parvus* showed apparent diel feeding rhythms (Fig. 8B,C), with higher feeding rates at night. No consistent relationships were found

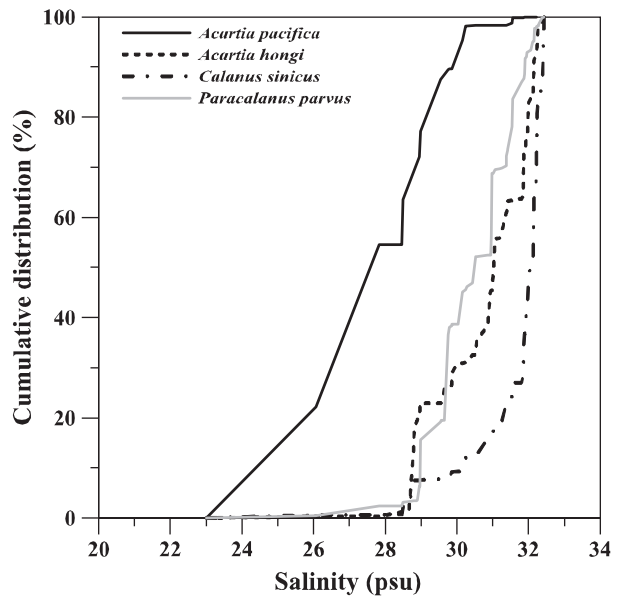
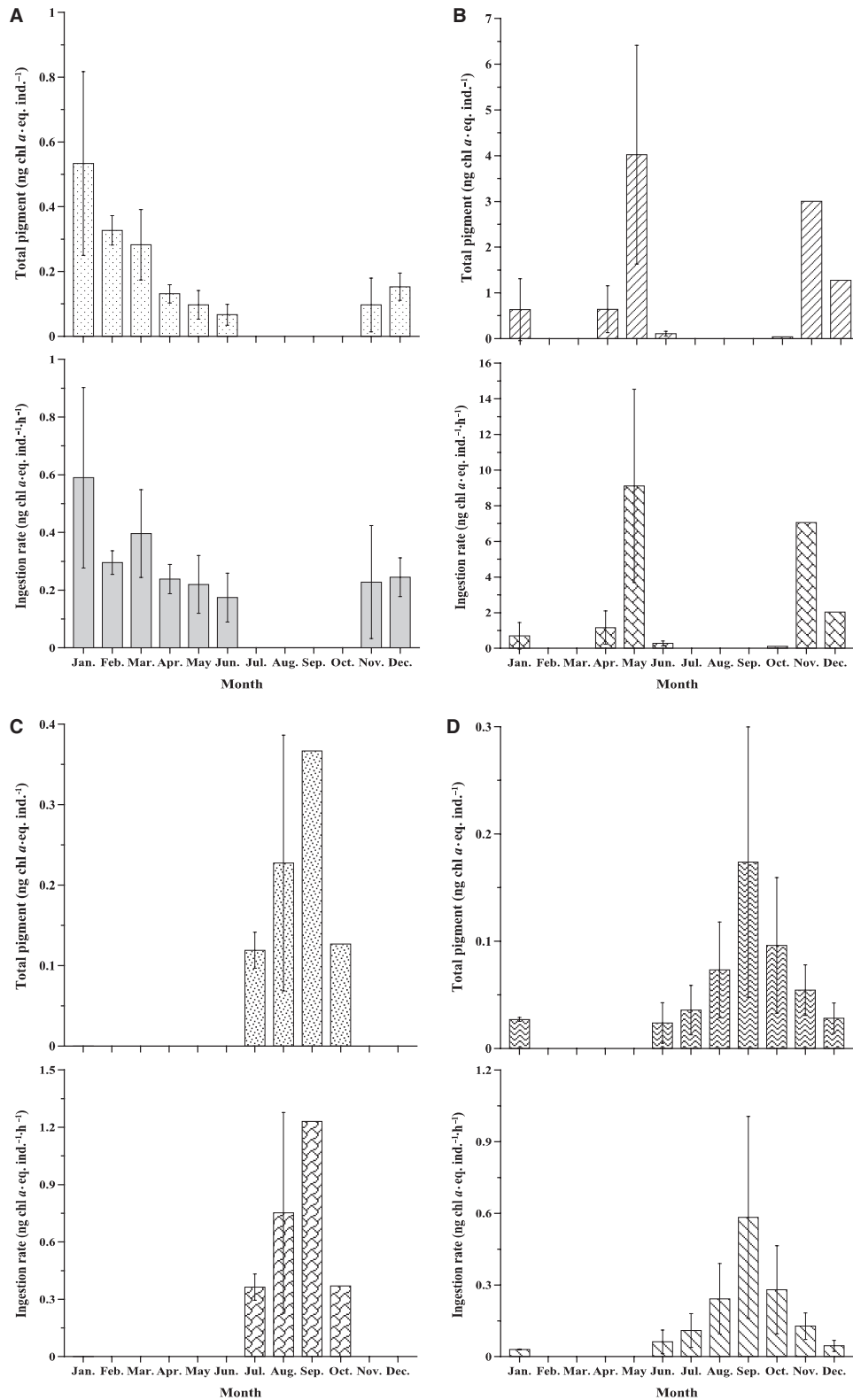


Fig. 6. Cumulative distribution of the four target copepod species along salinity gradient in the Asan Bay from January to December 2008.

between the gut pigment contents and tidal phase for all target species. The gut pigment contents of *A. pacifica* were between 0.03 and  $0.42 \text{ ng Chl } a\cdot\text{eq. ind.}^{-1}$ , with the ingestion rates ranging from 0.09 to  $1.36 \text{ ng Chl } a\cdot\text{eq. ind.}^{-1}\cdot\text{h}^{-1}$ . The corresponding rates of *P. parvus* varied from 0.01 to 0.15, and from 0.04 to  $0.47 \text{ ng Chl } a\cdot\text{eq. ind.}^{-1}\cdot\text{h}^{-1}$ , respectively. Day–night difference in ingestion rates for both species was significant (*t*-test,  $P < 0.05$ ), with *P. parvus* also showing a distinct diel feeding rhythm in autumn (Fig. 8D). The ingestion





**Fig. 7.** Monthly variations in the gut pigment content and ingestion rate of the four target copepod species (females) from January to December 2008 (A: *Acartia hongii*, B: *Calanus sinicus*, C: *Acartia pacifica*, D: *Paracalanus parvus*). Vertical bars indicate 95% confidence levels and lack of vertical bars indicate lack of replicate measurements.

**Table 2.** Values of copepod gut pigment content, carbon mass, gut passage time, daily carbon ration and *in situ* grazing impact obtained for *Acartia hongji* (A.h), *Calanus sinicus* (C.s), *Acartia pacifica* (A.p) and *Paracalanus parvus* (P.p) during the sampling periods. Empty cells indicate absence of datum.

month/year	mean gut pigment content (ng Chl a eq. ind <sup>-1</sup> )			copepod carbon mass (µg C·ind <sup>-1</sup> )			gut passage time (min)			mean gut carbon content (%)			daily carbon ration (% body C·day <sup>-1</sup> )			<i>in situ</i> grazing impact (%)			
	A.h	C.s	A.p	A.h	C.s	A.p	A.h	C.s	P.p	A.h	C.s	A.p	A.h	C.s	A.p	A.h	C.s	A.p	P.p
05/07	0.09			11.4			33	0.04			1.7			10.00					
08/07		0.20	0.06		9.2	12.1	20		0.11	0.03		7.9	2.2				8.05	13.27	
11/07			0.03			9.5	25			0.02			1.2					18.08	
01/08	0.53	0.63	0.03	11.9	82.8	14.7	50	0.22	0.04	0.01	6.3	1.2	0.3	3.81	0.10			0.01	
02/08	0.33			22.1			50	0.07			2.0			0.23					
03/08	0.28			9.8			50	0.14			4.0			1.78					
04/08	0.13	0.64		33.1	66.9		33	0.02	0.05		0.9	2.2		14.65	0.82				
05/08	0.10	4.02		11.4	106.0		25	0.04	0.19		2.3	10.9		9.13	6.42				
06/08	0.07	0.11		13.4	55.7		25	0.02	0.01		1.2	0.6		0.30	0.004				0.03
07/08		0.12	0.04		9.9	8.3	20		0.06	0.02		4.3	1.4				0.70	0.31	
08/08		0.23	0.07		9.2	12.1	17		0.12	0.03		10.2	2.5				1.31	1.17	
09/08		0.37	0.17		8.8	5.7	17		0.21	0.15		17.8	12.7				3.22	26.58	
10/08		0.04	0.13		67.7	13.2	20		0.003	0.05	0.04	0.2	3.6	2.9	0.001	0.001	0.65	0.67	
11/08	0.10	3.00	0.05	8.7	46.6	9.5	25	0.06	0.32	0.03	3.1	18.4	1.7	0.25	0.73				0.18
12/08	0.15	1.27	0.03	11.7	71.2	11.2	33	0.07	0.09	0.01	2.5	3.9	0.4	2.41	0.17				0.34

rates were about a third to a quarter lower in autumn compared with those in summer. The average gut pigment contents and ingestion rates were 0.03 and 0.07 ng Chl a eq. ind.<sup>-1</sup>·h<sup>-1</sup>, respectively, with the day-night difference being still significant (*t*-test, *P* < 0.05). The night-time to daytime ratio (N/D) of the gut pigment contents of *A. pacifica* and *P. parvus* were 3.1 and 3.4 in summer, respectively. The N/D ratio of *P. parvus* in autumn was slightly lower (2.3) than the other two species.

## Discussion

### Food quality, gut passage time and ingestion rates

Food quality can affect gut passage time in copepods and, consequently, the estimated ingestion rates. Different results were found for *Acartia tonsa*, which exhibited shorter gut passage time when it fed on diatoms than on dinoflagellates (Besiktepe & Dam 2002). However, in some cases no relations were established between food quality and gut passage time (Ellis & Small 1989; Tirelli & Mayzaud 2005). In the review of gut clearance rate constant, temperature and initial gut contents, Irigoien (1998) showed that copepods fed on laboratory grown phytoplankton cultures have shorter gut passage time than fresh caught copepods, which probably have a more variable diet (phytoplankton but also detritus and/or microzooplankton) than laboratory acclimated animals. In Asan Bay, phytoplankton exhibits seasonal variation in composition (Yi *et al.* 2005; Hyun *et al.* 2006). Microphytoplankton contributes 80% to the total Chl *a* in winter, when dominant species are *Thalassiosira* spp. and *Skeletonema costatum*. The phytoplankton size structure shifts from micro-size to nano-size class dominance in spring. Diatoms, Cryptophyceae and Cyanophyceae co-occur in summer and diatoms are again abundant in autumn. As the food composition is unlikely to change significantly overnight, potential diel food quality change may have very limited effects on our estimates of diel variations. Most copepods have a seasonal occurrence, appearing in large numbers within limited annual periods, during which the food composition is less likely to change dramatically. In addition, ingestion rates estimated with the two independent methods, gut pigment analysis (Table 2) and direct measurements of cell disappearance (Table 3), are within the same range of values (Shin & Choi 1992; Suzuki *et al.* 1999; Yang *et al.* 2009, 2010; this study). Therefore, our estimation based on the equation of Dam & Peterson (1988) does not differ significantly from those obtained with measured gut passage time.

**Table 3.** Clearance rates of the target copepods on size fractionated chl a. Data shown are mean  $\pm$  1 SD. [Correction added after online publication 31 October 2011 - 'Chl a concentration' and 'clearance rate' columns reformatted correctly].

month	experimental species	ind. l <sup>-1</sup>	seawater temperature (°C)		salinity (psu)	Chl a concentration ( $\mu\text{g l}^{-1}$ )		clearance rate (ml copepod <sup>-1</sup> day <sup>-1</sup> )
			<i>in situ</i>	incubation		micro Chl a (>20 $\mu\text{m}$ )		
						nano Chl a (<20 $\mu\text{m}$ )		
February	<i>Acartia hongji</i>	50	3.7	3–5	31.0	1.0	7 $\pm$ 1.4	
						1.3	62 $\pm$ 9.9	
March	<i>Acartia hongji</i>	50	6.5	5–7	31.2	2.1	25 $\pm$ 4.9	
						2.9	–	
April	<i>Acartia hongji</i>	40	10.4	9–11	30.8	0.2	4 $\pm$ 4.2	
						1.3	26 $\pm$ 0.7	
May	<i>Acartia hongji</i>	50	12.8	11–13	31.2	2.0	3	
						2.8	41	
May	<i>Calanus sinicus</i>	20	14.6	13–15	31.3	2.0	30 $\pm$ 0.0	
						2.9	17 $\pm$ 6.4	
July	<i>Acartia pacifica</i>	60	23.4	22–24	29.0	0.8	19 $\pm$ 1.4	
						0.6	131 $\pm$ 7.8	
August	<i>Paracalanus parvus</i>	20	24.5	23–25	30.3	4.0	–	
						2.5	51 $\pm$ 2.8	
October	<i>Paracalanus parvus</i>	30	20.6	19–21	30.7	7.8	0	
						1.4	11	
November	<i>Paracalanus parvus</i>	35	14.9	13–15	30.1	1.9	10 $\pm$ 5.7	
						1.2	17 $\pm$ 13.4	
December	<i>Acartia hongji</i>	33	8.3	7–9	31.0	0.5	7 $\pm$ 11.3	
						0.9	7 $\pm$ 7.8	

**Table 4.** Depth-averaged values of seawater temperature (T, °C), salinity (S, psu), Chl a concentration (Chl a,  $\mu\text{g l}^{-1}$ ), suspended particulate matters (SPM,  $\text{mg l}^{-1}$ ) and abundance (adult females and male, ind.·m<sup>-3</sup>) of the three copepods at the 24 h monitoring site.

time (h)	environmental variables											target species abundance, ind.·m <sup>-3</sup>				
	May				August				November			May	August		November	
	T	S	Chl a	SPM	T	S	Chl a	SPM	T	S	Chl a	SPM	<i>Acartia hongji</i>	<i>Acartia pacifica</i>	<i>P. parvus</i>	<i>P. parvus</i>
13:00	–	–	–	–	23.6	28.4	1.8	15.9	14.1	28.3	0.3	31.2	–	323	1677	651
15:00	12.6	31.2	4.3	20.1	23.3	29.0	3.2	13.6	14.3	28.7	0.5	26.0	5530	300	761	414
17:00	12.6	31.4	3.1	16.0	23.3	29.3	4.0	11.6	14.6	29.4	0.6	28.1	4124	510	1346	1137
19:00	12.5	31.3	3.9	13.8	23.1	29.5	4.1	9.2	14.7	29.6	0.4	23.2	4402	544	3441	2465
21:00	12.9	31.1	4.8	14.8	23.4	29.0	3.1	20.3	14.7	29.6	0.5	17.0	4395	755	2655	1177
23:00	13.3	30.9	7.1	21.8	23.8	28.1	1.9	15.1	14.5	29.2	0.9	27.2	1872	411	1228	1177
01:00	13.0	31.1	4.5	12.3	23.7	28.3	1.3	14.1	14.1	28.6	0.9	23.7	2831	531	817	849
03:00	12.6	31.3	5.2	18.4	23.3	29.1	3.3	17.4	14.3	29.0	0.8	29.2	4980	247	1511	661
05:00	12.2	31.5	5.0	15.9	22.9	29.7	4.3	25.1	14.6	29.4	0.8	21.4	4864	561	4258	888
07:00	12.5	31.3	4.8	15.3	22.9	29.7	2.6	13.6	14.6	29.5	0.7	22.9	4772	199	3076	1280
09:00	12.8	31.2	5.2	21.9	23.1	29.6	2.4	13.2	14.4	29.3	0.9	18.5	4071	422	1455	659
11:00	13.3	30.9	7.3	28.1	23.7	28.6	2.4	20.2	14.2	28.8	0.8	22.6	4191	449	1414	816
13:00	13.2	31.0	7.2	17.3	23.8	28.5	2.4	22.8	14.0	28.4	1.1	34.3	2520	924	3508	740

### Temporal variation of ingestion rates

Copepod ingestion rates generally increase with food concentration and water temperature (Bautista & Harris 1992; Dam & Lopes 2003; Jang *et al.* 2010). However, our investigations revealed that ingestion rates were not related to phytoplankton food concentration for any of

the copepods examined (Table 5). With respect to water temperature, *Acartia hongji* showed negative correlation with ingestion rate. Two summer copepods, *Acartia pacifica* and *Paracalanus parvus*, showed positive correlation with water temperature, but their ingestion rates were not related to phytoplankton biomass. Thus, the copepod ingestion rates of phytoplankton in Asan Bay may simply

reflect their seasonal abundance patterns (Table 1, Fig. 7A). *Acartia hongii* dominates the zooplankton communities from winter to spring and shows the highest ingestion rates in winter (Table 5). *Acartia pacifica* becomes more abundant with increasing water temperature (Tables 1 and 5) and shows its highest ingestion rates in September (Fig. 7C). Soh & Jeong (2003) reported that *A. hongii* occurs when seawater temperature is below 15 °C, whereas *A. pacifica* occurs above 20 °C in the southwestern waters of Korea, consistent with previous studies reporting that occurrences of these two species are mainly affected by seawater temperature (Lee & Park 2002; Lee *et al.* 2006, 2007; Park *et al.* 2008). *Paracalanus parvus* forms a large population in summer and dominates copepod community in the Yellow Sea (Sun *et al.* 2008). This species is abundant during summer and/or autumn in the outer parts of Asan Bay (Choi & Park 1993; Lee & Park 2002; Lee *et al.* 2007), and its ingestion rates also peak in September (Fig. 7D). *Calanus sinicus* is a cold-water copepod and shows low abundance throughout the year, with a slight increase in spring (Table 1, Fig. 5). Unlike other copepods, the ingestion rates of *C. sinicus* showed two peaks in May and November, which is consistent with egg production peaks observed during the same months (Park 1997). Ingestion rates were positively related to egg production rate of *Temora longicornis* (Peterson & Dam 1996). High ingestion rates may be closely related to reproductive efforts for the four target species in our present study.

#### Grazing impact on phytoplankton biomass

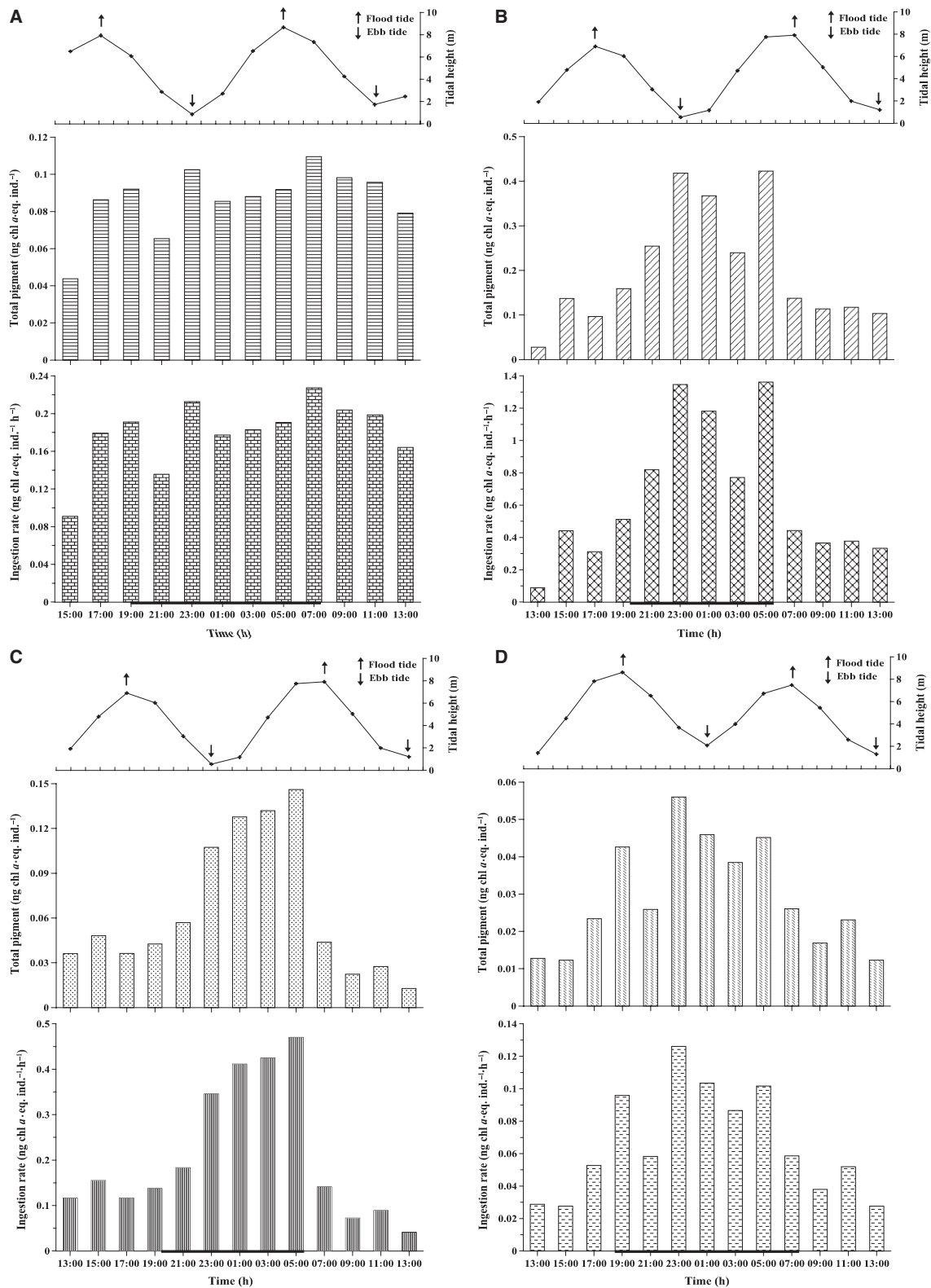
Grazing impact by copepods is a key factor in controlling composition and dynamics of phytoplankton communities in marine ecosystems (Sterner 1989; Kagami *et al.* 2002; Pagano *et al.* 2006). The grazing impacts of copepods on phytoplankton biomass are variable, ranging from <10% (Morales *et al.* 1991; Bautista & Harris 1992; Dagg 1995; Froneman 2000; Grunewald *et al.* 2002; Li *et al.* 2003) to nearly 70% of the standing stock (Kibirige & Perisinotto 2003). Grazing impact of *Acartia natalensis* on phytoplankton standing stock varied between 5 and 47% (Kibirige & Perisinotto 2003). Pagano *et al.* (2006) report relatively low impact (between 0.5 and 11%) of daily grazing pressure of metazooplankton on phytoplankton in the Senegal River Estuary (Western Africa). Sautour *et al.* (1996) show that grazing impact of herbivorous zooplankton, mainly *Paracalanus parvus* and *Temora longicornis*, on total phytoplankton stock, is low (9–14%). Li *et al.* (2003) report copepod grazing on phytoplankton to be about 12% (range 3–37%) of the Chl *a* concentration in the Bohai Sea. The grazing impact of copepods estimated in the present study was about 8%

(range 0.2–29.8%) of Chl *a* concentration (Table 2), similar to previous reports.

#### Copepod food selectivity

Although ingestion rates are similar to those reported in other studies (Table 6), daily carbon rations estimated in the present study (Table 2) are relatively lower than previously reported (Durbin *et al.* 1995; Atkinson 1996; Sautour *et al.* 1996; Froneman 2001; Fileman *et al.* 2007; Saiz *et al.* 2007). Very high copepod abundance but low values of daily carbon ration provided by feeding on phytoplankton biomass indicate other food resources were predated by copepods in Asan Bay. *Paracalanus parvus* (Kleppel 1993; Sautour *et al.* 1996) and *Acartia* species are generally known to be omnivorous (Bartram 1980; Irigoien *et al.* 1996; Rollwagen Bollens & Penry 2003; Yang *et al.* 2010). *Calanus sinicus* also ingests substantial amounts of non-phytoplankton prey (Yang *et al.* 2009; Jang *et al.* 2010). In a feeding study of *Acartia hongii* in Gyeonggi Bay, north of the present study area, microzooplankton accounted for >70% of the total carbon ration ingested by *A. hongii* throughout the year, even though microzooplankton represented only an average 13.7% of the total carbon available in the natural prey pool (Yang *et al.* 2010). The exception was during winter diatom blooming periods, in which *A. hongii* obtained approximately 60% of its carbon ration from phytoplankton (Yang *et al.* 2010). The egg production rate of *A. hongii* in Gyeonggi Bay was also higher in the presence of ciliates than when grazing on phytoplankton only (Youn & Choi 2007). *Paracalanus parvus* feed primarily on phytoplankton when phytoplankton dominates, but on a wide variety of particles (inorganic particles, detritus and heterotrophs) when phytoplankton biomass decreases (Kleppel 1993). In feeding experiments of *Calanus sinicus* in the East Sea/Japan Sea, heterotrophic protozoa constituted between 42.9 and 86.7% of the total carbon ration ingested by the copepod, although they represented on average 21.5% of the total available prey carbon (Yang *et al.* 2009). The copepods selected ciliate and heterotrophic dinoflagellate groups over other protozoa (Yang *et al.* 2009). Food selectivity is one of the most important processes in relation to adaptive strategies and competition for food resources between species. Coastal copepods have potential mechanisms for population stabilization, such as active food selection and prey switching (Saiz & Kiørboe 1995). Copepods in Asan Bay may integrate their phytoplankton diet with protozoans.

The consumption of phytoplankton by grazers strongly depends on their size structure (Bautista & Harris 1992). Size-selective grazing on phytoplankton by the four target copepods examined in our study showed that



**Fig. 8.** Tidal heights and diel variations in gut pigment content and ingestion rate of the three target copepod species (females) (A: *Acartia hongii*, B: *Acartia pacifica*, C: *Paracalanus parvus*, August, D: *Paracalanus parvus*, November) at the 24 h monitoring site. Dark horizontal bars on the x-axis indicate night hours.

**Table 5.** Correlation coefficients (*r*) between abundance (Abun, ind.·m<sup>-3</sup>), ingestion rate (I. R, ng Chl *a*-eq. ind.<sup>-1</sup>·h<sup>-1</sup>) of the four target copepods and environmental factors (seawater temperature, salinity and Chl *a* concentration) in Asan Bay, Korea from January to December 2008.

environmental factors	correlation coefficients ( <i>r</i> )							
	<i>Acartia hongji</i>		<i>Calanus sinicus</i>		<i>Acartia pacifica</i>		<i>Paracalanus parvus</i>	
	Abun	I. R	Abun	I. R	Abun	I. R	Abun	I. R
seawater temperature (°C)	-0.59*	-0.74*			0.62*	0.88**	0.67*	0.67**
salinity (psu)					-0.49**			
Chl <i>a</i> (µg·l <sup>-1</sup> )				-0.71**				

Asterisks indicate the level of significance at \**P* < 0.05 and \*\**P* < 0.1. Empty cells indicate no significant correlations.

**Table 6.** Comparison of gut pigment contents and ingestion rates of the copepod genera *Acartia*, *Calanus* and *Paracalanus* between the present study and previous reports.

species	gut pigment content (ng Chl <i>a</i> -eq. ind. <sup>-1</sup> )	ingestion rate (ng Chl <i>a</i> -eq. ind. <sup>-1</sup> ·h <sup>-1</sup> )	sources
<i>Acartia hudsonica</i>	0.42–2.17	0.79–6.07	Wlodarczyk <i>et al.</i> (1992)
<i>Acartia natalensis</i>	0.12–0.45	0.26–0.98	Kibirige & Perisinotto (2003)
<i>Acartia tonsa</i>		1.00–4.58	Kjørboe & Tiselius (1987)
<i>Acartia tonsa</i>	0.17–13.66		Durbin <i>et al.</i> (1990)
<i>Acartia spinicauda</i>	0.71–1.50		Tan <i>et al.</i> (2004)
<i>Acartia clausi</i>	0.06–1.77		Pagano & Saint Jean (1985)
<i>Acartia bifilosa</i>	0.06–0.66		Li <i>et al.</i> (2000)
<i>Acartia pacifica</i>	0.14–0.92		Li <i>et al.</i> (2000)
<i>Acartia</i> spp.		0.32–1.31	Saito & Hattori (1997)
<i>Paracalanus serrulus</i>	0.63–1.60		Tan <i>et al.</i> (2004)
<i>Paracalanus parvus</i>	0.04–0.48		Sautour <i>et al.</i> (1996)
<i>Paracalanus parvus</i>	0.07–0.48		Li <i>et al.</i> (2000)
<i>Calanus finmarchicus</i>	0.03–7.70		Durbin <i>et al.</i> (1995)
<i>Calanus euxinus</i>	3.42–21.28	12.67–59.60	Besiktepe <i>et al.</i> (1998)
<i>Calanus sinicus</i>		8.71–35.08	Uye & Yamamoto (1995)
<i>Calanus sinicus</i>	2.3		Tan <i>et al.</i> (2004)
<i>Acartia hongji</i>	0.04–1.10	0.09–1.21	This study
<i>Acartia pacifica</i>	0.03–0.42	0.09–1.36	This study
<i>Paracalanus parvus</i>	0.01–0.32	0.02–1.09	This study
<i>Calanus sinicus</i>	0.04–7.25	0.12–16.44	This study

clearance rates generally appear to be consistent with other reports (Table 3). Calanoid copepods are known to have efficient feeding on 10–20-µm particles (Sautour *et al.* 2000). *Acartia* species have been shown to select phytoplankton cells based on size (Paffenhöfer *et al.* 1982; Price *et al.* 1983; Tackx *et al.* 1989). Some *Acartia* species prefer a prey size of approximately 20 µm regardless of prey type (Rollwagen Bollens & Penry 2003) and they are more selective during periods of high food concentration. Small copepods (generally <1 mm in length), which include adults and copepodites of genus *Acartia* and *Paracalanus*, are capable of feeding at higher rates on nanoflagellates than on larger prey (Vargas & Gonzalez 2004). Meanwhile, the highest food capture efficiency of the larger *Calanus* species appears in the size range of 30–40 µm equivalent spherical diame-

ters (Levinsen *et al.* 2000). The larger copepod *C. sinicus* showed a preference for auto- and heterotrophic protozoa in the 20–50 µm size range, from a suite of available prey ranging from <3 to >100 µm in length (Yang *et al.* 2009).

#### Copepod diel feeding rhythms

Many calanoid copepods are known to feed in characteristic day–night cycles. The genus *Acartia* usually shows higher nocturnal feeding (Durbin *et al.* 1990; Wlodarczyk *et al.* 1992; Kouassi *et al.* 2001; Kibirige & Perisinotto 2003; Pagano *et al.* 2006). Peterson *et al.* (1990) and Wang & Fan (1997) reported diel feeding rhythms for *Paracalanus* spp., showing peak ingestion rates observed during the night with relatively small amplitude cycles. In

contrast, Saito & Taguchi (1996) reported that *Paracalanus* spp. do not show any significant diel feeding rhythms. In addition, Li & Wang (2000) showed that body size can affect diel feeding rhythm. For example, larger copepods (>500 µm) have diel feeding rhythms, whereas no rhythm is observed in smaller copepods (200–500 µm, mainly *Paracalanus parvus*, *Acartia bifilosa* and *Oithona similis*). In the present study, *Acartia pacifica* and *P. parvus* showed distinct nocturnal feeding, whereas *Acartia hongii* showed no significant day–night differences. Other factors that may influence diel feeding rhythm of copepods include quantity of food items, risk of predation, past feeding histories, and genetically encoded endogenous rhythm (Li *et al.* 2003), or a combination of these. Calbet *et al.* (1999) reported that copepods (*Acartia grani* and *Centropages typicus*) showed clear diel feeding rhythms at high food concentrations with significantly higher clearance rates during night-time. When food is limited, *A. grani* shows similar day and night clearance rates. In this study, Chl *a* concentration did not change during a day–night cycle (Table 4), and therefore this does not appear to be a factor, in comparison with the increased night feeding observed in *A. pacifica* and *P. parvus*. These species showed distinct day and night feeding rates in the period of low Chl *a* concentration, whereas *A. hongii* did not show diel feeding rhythm in the seasonal period of high Chl *a* concentration. Copepods can ingest food other than phytoplankton, such as protozoans as discussed above. Although protistan communities were not measured in this study, their concentration appears to be positively and closely related to the concentration of suspended particulate matter in coastal waters of the east coast of Yellow Sea (Choi *et al.* 2011). Considering the time scale of variation, the diel fluctuation of food concentrations may not be crucial in determining diel patterns of copepod feeding. The risk of predation is another possible cause of diel feeding rhythms. Diel feeding rhythm is relatively weak in coastal areas compared to open seas, possibly due to the relative high turbidity leading to reduced visual predation pressure (Vinyard & O'Brien 1976). The presence of diel feeding rhythm in the study area, which is subjected to shallow and active tidal mixing, implies that the risk of predation is not a key factor for diel feeding rhythm. The quality and quantity of food do not seem to work in such an active tidal mixing area either. As past feeding history is a composite of those factors already mentioned so far, the endogenous physiological rhythm might be hypothesized as a possible reason for the diel feeding patterns observed in *A. pacifica* and *P. parvus*, although this hypothesis must be more robustly tested.

In conclusion, the four copepods in this study exerted a significant impact on phytoplankton standing stock,

with ingestion rates as measured by both gut pigment analysis and food removal method being comparable to reported values in other estuaries and coastal waters. However, the daily carbon ration provided by phytoplankton consumption was only as large as 20% for all copepods, which suggests that the copepods also grazed on other non-phytoplankton food in Asan Bay. Increased night feeding of two copepods, with no apparent correlation with diel variation of food quantity/quality or predation, suggest that endogenous physiological rhythm might be a possible reason for the observed diel feeding patterns of the copepods in this estuary.

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### References

- Arruda J.A., Marzolf G.R., Faulk R.T. (1983) The role of suspended sediments in the nutrition of zooplankton in turbid reservoirs. *Ecology*, **64**, 1225–1235.
- Atkinson A. (1996) Subantarctic copepods in an oceanic, low chlorophyll environment: ciliate predation, food selectivity and impact on prey populations. *Marine Ecology Progress Series*, **130**, 85–96.
- Båmstedt U., Gifford D.J., Irigoien X., Atkinson A., Roman M. (2000) *ICES Zooplankton Methodology Manual*. Elsevier Academic Press, Amsterdam: 297–399.
- Bartram W.C. (1980) Experimental development of a model for the feeding of neritic copepods on phytoplankton. *Journal of Plankton Research*, **3**, 25–51.
- Bautista B., Harris R.P. (1992) Copepod gut contents, ingestion rates and grazing impact on phytoplankton in relation to size structure of zooplankton and phytoplankton during a spring bloom. *Marine Ecology Progress Series*, **82**, 41–50.
- Besiktepe S., Dam H.G. (2002) Coupling of ingestion and defecation as a function of diet in the calanoid copepod *Acartia tonsa*. *Marine Ecology Progress Series*, **229**, 151–164.
- Besiktepe S., Kideys A.E., Unsal M. (1998) *In situ* grazing pressure and diel vertical migration of female *Calanus euxinus* in the Black Sea. *Hydrobiologia*, **363**, 323–332.
- Burdloff D., Gasparini S., Sautour B., Etcheber H., Castel J. (2000) Is the copepod egg production in a highly turbid estuary (the Gironde, France) a function of the

- biochemical composition of seston? *Aquatic Ecology*, **34**, 165–175.
- Calbet A., Saiz E., Irigoien X., Alcaraz M., Trepas I. (1999) Food availability and diel feeding rhythms in the marine copepods *Acartia grani* and *Centropages typicus*. *Journal of Plankton Research*, **21**, 1009–1015.
- Carrasco N.K., Perissinotto R., Miranda N. (2007) Effects of silt loading on the feeding and mortality of the mysid *Mesopodopsis africana* in the St. Lucia Estuary, South Africa. *Journal of Experimental Marine Biology and Ecology*, **352**, 152–164.
- Choi K.H., Park C. (1993) Seasonal fluctuation of zooplankton community in Asan Bay, Korea. *Journal of the Korean Fisheries Society*, **26**, 424–437.
- Choi K.H., Kim Y.O., Lee J.B., Wang S.Y., Lee M.W., Lee P.G., Ahn D.S., Hong J.S., Soh H.Y. (2011) Thermal impacts of a coal power plant on the plankton in an open coastal water environment. *Journal of Marine Science and Technology* (in press).
- Dagg M.J. (1985) The effects of food limitation on diel migratory behavior in marine zooplankton. *Archiv für Hydrobiologie–Beiheft Ergebnisse der Limnologie*, **21**, 247–255.
- Dagg M.J. (1995) Ingestion of phytoplankton by the micro- and mesozooplankton communities in a productive subtropical estuary. *Journal of Plankton Research*, **17**, 845–857.
- Dagg M.J., Grill D.W. (1980) Natural feeding rates of *Centropages typicus* females in the New York Bight. *Limnology and Oceanography*, **25**, 597–609.
- Dagg M.J., Walser W.E. Jr (1987) Ingestion, gut passage, and egestion by the copepod *Neocalanus plumchrus* in the laboratory and in the Subarctic Pacific Ocean. *Limnology and Oceanography*, **32**, 178–188.
- Dagg M.J., Wyman K.D. (1983) Natural ingestion rates of the copepods *Neocalanus plumchrus* and *N. cristatus* calculated from gut contents. *Marine Ecology Progress Series*, **13**, 37–46.
- Dam H.G., Lopes R.M. (2003) Omnivory in the calanoid copepod *Temora longicornis*: feeding, egg production and egg hatching rates. *Journal of Experimental Marine Biology and Ecology*, **292**, 119–137.
- Dam H.G., Peterson W.T. (1988) The effect of temperature on the gut clearance rate constant of planktonic copepods. *Journal of Experimental Marine Biology and Ecology*, **123**, 1–14.
- Daro M.H. (1985) Feeding rhythms and vertical migration of marine copepods. *Bulletin of Marine Science*, **37**, 487–497.
- David V., Sautour B., Galois R., Chardy P. (2006) The paradox high zooplankton biomass-low vegetal particulate organic matter in high turbidity zones: what way for energy transfer? *Journal of Experimental Marine Biology and Ecology*, **333**, 202–218.
- Durbin A.G., Durbin E.G., Włodarczyk E. (1990) Diel feeding behavior in the marine copepod *Acartia tonsa* in relation to food availability. *Marine Ecology Progress Series*, **68**, 23–45.
- Durbin E.G., Campbell R.G., Gilman S.L., Durbin A.G. (1995) Diel feeding behavior and ingestion rate in the copepods *Calanus finmarchicus* in the southern Gulf of Maine during late spring. *Continental Shelf Research*, **15**, 539–570.
- Ellis S.G., Small L.F. (1989) Comparison of gut-evacuation rates of feeding and non-feeding *Calanus marshallae*. *Marine Biology*, **103**, 175–181.
- Fileman E., Smith T., Harris R. (2007) Grazing by *Calanus helgolandicus* and *Para-Pseudocalanus* spp. on phytoplankton and protozooplankton during the spring bloom in the Celtic Sea. *Journal of Experimental Marine Biology and Ecology*, **348**, 70–84.
- Froneman P.W. (2000) Feeding studies of selected zooplankton in the Kariega estuary, South Africa. *Estuarine, Coastal and Shelf Science*, **51**, 543–552.
- Froneman P.W. (2001) Seasonal changes in zooplankton biomass and grazing in a temperate estuary, South Africa. *Estuarine, Coastal and Shelf Science*, **52**, 543–553.
- Frost B.W. (1972) Effects of size and concentration of food particles on the feeding behaviour of the marine planktonic copepod *Calanus pacificus*. *Limnology and Oceanography*, **17**, 805–815.
- Gardner M.B. (1981) Effects of turbidity on feeding rates and selectivity of bluegills. *Transactions of the American Fisheries Society*, **110**, 446–450.
- Gauld D.T. (1951) The grazing rate of planktonic copepods. *Journal of the Marine Biological Association of the United Kingdom*, **29**, 695–706.
- Grunewald A.C., Morales C.E., Gonzalez H.E., Sylvester C., Castro L.R. (2002) Grazing impact of copepod assemblages and gravitational flux in coastal and oceanic waters off central Chile during two contrasting seasons. *Journal of Plankton Research*, **24**, 55–67.
- Haney J.F. (1988) Diel patterns of zooplankton behavior. *Bulletin of Marine Science*, **43**, 583–603.
- Hart R.C. (1988) Zooplankton feeding rates in relation to suspended sediment content: potential influences on community structure in a turbid reservoir. *Freshwater Biology*, **19**, 123–139.
- Head E.J.H., Harris L.R. (1992) Chlorophyll and carotenoid transformation and destruction by *Calanus* spp. grazing on diatoms. *Marine Ecology Progress Series*, **86**, 229–238.
- Hyun B.K., Sin Y.S., Park C., Yang S.R., Lee Y.J. (2006) Temporal and spatial variations of size-structured phytoplankton in Asan Bay. *Korean Journal of Environmental Biology*, **24**, 7–18 (in Korean with English abstract).
- Irigoien X. (1998) Gut clearance rate constant, temperature and initial gut contents: a review. *Journal of Plankton Research*, **20**, 997–1003.
- Irigoien X., Castel J., Gasparini S. (1996) Gut clearance rate as predictor of food limitation situations. Application to two estuarine copepods: *Acartia biflosa* and *Eurytemora affinis*. *Marine Ecology Progress Series*, **131**, 159–163.
- Jang M.C., Shin K., Lee T., Noh I. (2010) Feeding selectivity of calanoid copepods on phytoplankton in Jangmok



- Bay, south coast of Korea. *Ocean Science Journal*, **45**, 101–111.
- Kagami M., Yoshida T., Gurung T.B., Urabe J. (2002) Direct and indirect effects of zooplankton on algal composition in *in situ* grazing experiments. *Oecologia*, **133**, 356–363.
- Kibirige I., Perisintono R. (2003) *In situ* feeding rates and grazing impact of zooplankton in a South African temporarily open estuary. *Marine Biology*, **142**, 357–367.
- Kimmerer W.J., Ferm N., Nicolini M.H., Peñalva C. (2005) Chronic food limitation of egg production in populations of copepods of the genus *Acartia* in the San Francisco Estuary. *Estuaries*, **28**, 541–550.
- Kjørboe T., Tiselius P.T. (1987) Gut clearance and pigment destruction in a herbivorous copepod, *Acartia tonsa*, and determination of *in situ* grazing rates. *Journal of Plankton Research*, **9**, 525–534.
- Kjørboe T., Mohlenberg F., Riisgard H.U. (1985) *In situ* feeding rates of planktonic copepods: a comparison of four methods. *Journal of Experimental Marine Biology and Ecology*, **88**, 67–81.
- Kleppel G.S. (1993) On the diets of calanoid copepods. *Marine Ecology Progress Series*, **99**, 183–195.
- Kouassi E., Pagano M., Saint-Jean L., Arfi R., Bouvy M. (2001) Vertical migration and feeding rhythms of *Acartia clausi* and *Pseudodiaptomus hessei* (Copepoda: Calanoida) in a Tropical Lagoon (Ebrié, Côte d'Ivoire). *Estuarine, Coastal and Shelf Science*, **52**, 715–728.
- Lee C.R., Park C. (2002) Long-term variation of zooplankton composition and abundance in Asan Bay, Korea: is it influence of dyke construction? *The Yellow Sea*, **8**, 9–18.
- Lee C.R., Park C., Yang S.R., Sin Y.S. (2006) Spatio-temporal variation of mesozooplankton in Asan Bay. *Journal of the Korean Society of Oceanography*, **11**, 1–10 (in Korean with English abstract).
- Lee D.B., Park C., Yang S.R., Sin Y.S. (2007) Change in mesozooplankton community around the rainy season in Asan Bay, Korea. *Journal of the Korean Society of Oceanography*, **12**, 337–348 (in Korean with English abstract).
- 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 C., Wang R. (2000) Copepods feeding activities in the Laizhouwan Bay, Bohai Sea, in summer. *Oceanologia et Limnologia Sinica*, **31**, 23–28 (in Chinese with English abstract).
- Li C., Wang K., Wang R. (2000) The gut pigment contents of the dominant zooplankton species and their grazing pressure on the phytoplankton in the Weihe estuary. *Marine Fisheries Research*, **21**, 27–33 (in Chinese with English abstract).
- Li C., Wang R., Sun S. (2003) Grazing impact of copepods on phytoplankton in the Bohai Sea. *Estuarine, Coastal and Shelf Science*, **58**, 487–498.
- Mackas D.L., Bohrer R. (1976) Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. *Journal of Experimental Marine Biology and Ecology*, **25**, 77–85.
- Morales C.E., Bedo A., Harris R.P., Tranter P.R.G. (1991) Grazing copepod assemblages in the North-east Atlantic: importance of the small size fraction. *Journal of Plankton Research*, **13**, 455–472.
- Paffenhöfer G.-A., Strickler J.R., Alcaraz M. (1982) Suspension-feeding by herbivorous calanoid copepods: a cinematographic study. *Marine Biology*, **67**, 193–199.
- Pagano M., Saint Jean L. (1985) Premières données sur la nutrition d'*Acartia clausi* en Lagune Ebrié (Côte d'Ivoire) obtenues par des mesures de la fluorescence de broyats d'animaux. *Hydrobiologia*, **121**, 83–95.
- Pagano M., Champalbert G., Aka M., Kouassi E., Arfi R., Got P., Troussellier M., N'Dour E.H., Corbin D., Bouvy M. (2006) Herbivorous and microbial grazing pathways of metazooplankton in the Senegal River Estuary (West Africa). *Estuarine, Coastal and Shelf Science*, **67**, 369–381.
- Park C. (1997) Seasonal distribution, eggs production and feeding by marine copepod *Calanus sinicus* in Asan Bay, Korea. *Journal of the Korean Society of Oceanography*, **32**, 85–92.
- Park M.J. (2000) Modeling of sediment transport and bank formation in a macro tidal sea. *Journal of the Korean Society of Oceanography*, **35**, 1–10.
- Park C., Choi K.H., Moon C.H. (1991) Distribution of zooplankton in Asan Bay, Korea with Comments on vertical migration. *Bulletin of the Korean Fisheries Society*, **24**, 472–482.
- Park C., Lee P.G., Lee C.R. (1998) Seasonal variation on abundance, species occurrence and species diversity of zooplankton in Asan Bay, the Yellow Sea over the last eight years. *The Yellow Sea*, **4**, 40–48.
- Park C., Lee D.B., Lee C.R., Yang S.R., Jung B.G. (2008) Variation in planktonic assemblages in Asan Bay during the winter-spring bloom. *Journal of the Korean Society of Oceanography*, **13**, 308–319 (in Korean with English abstract).
- Peterson W.T., Dam H.G. (1996) Pigment ingestion and egg production rates of the calanoid copepod *Temora longicornis*: implications for gut pigment loss and omnivorous feeding. *Journal of Plankton Research*, **18**, 855–861.
- Peterson W.T., Painting S.J., Hutchings L. (1990) Diel variations in gut pigment contents, diel vertical migration and estimates of grazing impact for copepods in the southern Benguela upwelling region in October, 1987. *Journal of Plankton Research*, **12**, 259–281.
- Price H.J., Paffenhöfer G.-A., Strickler J.R. (1983) Modes of cell capture in calanoid copepods. *Limnology and Oceanography*, **28**, 116–123.
- Rollwagen Bollens G.C., Penry D.L. (2003) Feeding dynamics of *Acartia* spp. copepods in a large, temperate estuary (San

- Francisco Bay, CA). *Marine Ecology Progress Series*, **257**, 139–158.
- Roman M.R., Ashton K.A., Gauzens A.L. (1988) Day/night differences in the grazing impact of marine copepods. *Hydrobiologia*, **167/168**, 21–30.
- Saito H., Hattori H. (1997) Diel vertical migration and feeding rhythm of copepods under sea ice at Saroma-ko Lagoon. *Journal of Marine Systems*, **11**, 191–203.
- Saito H., Taguchi S. (1996) Diel feeding behavior of neritic copepods during spring and fall blooms in Akkeshi Bay, eastern coast of Hokkaido, Japan. *Marine Biology*, **125**, 97–107.
- Saiz E., Kiørboe T. (1995) Predatory and suspension feeding of the copepod *Acartia tonsa* in turbulent environments. *Marine Ecology Progress Series*, **122**, 147–158.
- Saiz E., Calbet A., Broglio E. (2003) Effects of small-scale turbulence on copepods: the case of *Oithona davisae*. *Limnology and Oceanography*, **48**, 1304–1311.
- Saiz E., Calbet A., Atienza D., Alcaraz M. (2007) Feeding and production of zooplankton in the Catalan Sea (NW Mediterranean). *Progress in Oceanography*, **74**, 313–328.
- SAS Institute Inc. (2005) *SAS/STAT Software, Version 9.1.3*. SAS Institute Inc., Cary, NC.
- Sautour B., Castel J. (1995) Comparative spring distribution of zooplankton in three macrotidal European estuaries. *Hydrobiologia*, **311**, 139–151.
- Sautour B., Artigas L.F., Herbland A., Laborde P. (1996) Zooplankton grazing impact in the plume of dilution of the Gironde estuary (France) prior to the spring bloom. *Journal of Plankton Research*, **18**, 835–853.
- Sautour B., Artigas L.F., Delmas D., Herbland A., Laborde P. (2000) Grazing impact of micro- and mesozooplankton during a spring situation in coastal waters off the Gironde estuary. *Journal of Plankton Research*, **22**, 531–552.
- Shin K.S., Choi J.K. (1992) The feeding behavior of the marine planktonic copepod, *Calanus sinicus* and *Acartia clausi* (*A. omorii*). *Journal of the Korean Society of Oceanography*, **27**, 11–18 (in Korean with English abstract).
- Soh H.Y., Jeong H.G. (2003) Spatio-temporal distribution of Genus *Acartia* (Copepoda: Calanoida) in the southwestern waters of Korea. *Korean Journal Environmental Biology*, **21**, 422–427.
- Soh H.Y., Suh H.L. (2000) A new species of *Acartia* (Copepoda, Calanoida) from the Yellow Sea. *Journal of Plankton Research*, **22**, 321–337.
- Sterner R.W. (1989) The role of grazing in phytoplankton succession. In: Simmer U. (Ed.), *Plankton Ecology: Succession in Plankton Communities*. Springer Verlag, Berlin: 107–170.
- Strickland J.D.H., Parsons T.R. (1972) *A Practical Handbook of Seawater Analysis*, 2nd edn, Vol. 167. Bulletin/Fisheries Research Board of Canada, Ottawa: 1–310.
- Sun X.H., Sun S., Li C.L., Zhang G.T. (2008) Seasonal and spatial variation in abundance and egg production of *Paracalanus parvus* (Copepoda: Calanoida) in/out Jiaozhou Bay, China. *Estuarine, Coastal and Shelf Science*, **79**, 637–643.
- Suzuki K., Nakamura Y., Hiromi J. (1999) Feeding by the small calanoid copepod *Paracalanus* sp. on heterotrophic dinoflagellates and ciliates. *Aquatic Microbial Ecology*, **17**, 99–103.
- Tackx M.L.M., Bakker C., Francke J.W., Vink M. (1989) Size and phytoplankton selection by Oosterschelde zooplankton. *Netherlands Journal of Sea Research*, **23**, 35–43.
- Tan Y., Huang L., Chen Q., Huang X. (2004) Seasonal variation in zooplankton composition and grazing impact on phytoplankton standing stock in the Pearl River Estuary, China. *Continental Shelf Research*, **24**, 1949–1968.
- Tirelli V., Mayzaud P. (2005) Relationship between functional response and gut transit time in the calanoid copepod *Acartia clausi*: role of food quantity and quality. *Journal of Plankton Research*, **27**, 557–568.
- Uye S., Yamamoto F. (1995) *In situ* feeding of the planktonic copepod *Calanus sinicus* in the Inland Sea of Japan. *Bulletin of the Plankton Society of Japan*, **42**, 123–139.
- Vargas C.A., Gonzalez H.E. (2004) Plankton community structure and carbon cycling in a coastal upwelling system. II. Microheterotrophic pathway. *Aquatic Microbial Ecology*, **34**, 165–180.
- Vinyard G.L., O'Brien W.J. (1976) Effects of light and turbidity on the reactive distance of Bluegill (*Lepomis macrochirus*). *Journal of Fishery Research Board Canada*, **33**, 2845–2849.
- Wang R., Fan C. (1997) Copepods feeding activities and its contribution to downwards vertical flux of carbon in the East China Sea. *Oceanologia et Limnologia Sinica*, **28**, 579–587 (in Chinese with English abstract).
- Wlodarczyk E., Durbin A.G., Durbin E.G. (1992) Effect of temperature on low feeding thresholds, gut evacuation rate, and diel feeding behavior in the copepod *Acartia hudsonica*. *Marine Ecology Progress Series*, **85**, 93–106.
- Yang E.J., Kang H.K., Yoo S.J., 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.
- Yang E.J., Ju S.J., Choi J.K. (2010) Feeding activity of the copepod *Acartia hongii* on phytoplankton and micro-zooplankton in Gyeonggi Bay, Yellow Sea. *Estuarine, Coastal and Shelf Science*, **88**, 292–301.
- Yi S.H., Sin Y.S., Yang S.R., Park C. (2005) Seasonal characteristics of phytoplankton distribution in Asan Bay. *Ocean and Polar Research*, **27**, 149–159 (in Korean with English abstract).
- 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.