

Diel vertical migration and feeding rhythm of copepods in a shallow, food-abundant embayment

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Abstract: We examined diel vertical migration (DVM) and diel feeding rhythm (DFR) of copepods in Akkeshi Bay during the fall bloom and tested the predation preventive hypothesis on both behaviors. The dominant copepods aggregated in the near-bottom layer during the day, and after sunset, dispersed through the water column. However, the magnitudes of the DVMs were not extensive, as the rises in the median depth of the populations (MD) from daytime to nighttime were less than 3.3 m. The differences between the nighttime and daytime average MDs were insignificant ($p > 0.05$) in 7 of 13 categories of copepods. The usual pattern of DFR was observed in every layer in the water column. Most of the copepods did not exploit the chlorophyll maximum layer and decreased their ingestion rate during the day. However, these copepods were not food limited, as their daily ingestion rates were 3–4 times higher than their daily food requirements. Both the daytime near-bottom aggregation and the daytime decrease in feeding activity are thought to help decrease the predation risk from visual predators. The observed diel behaviors of copepods could be thought of as a preventive behavior for avoiding visual predators in a food-abundant shallow environment.

Key words: copepod, vertical migration, feeding rhythm, visual predator, phytoplankton bloom

Introduction

Diel vertical migration (DVM) and diel feeding rhythm (DFR) are commonly observed in zooplankton behaviors (e.g. Haney 1988). Although these diel behaviors often occur concurrently, they are thought to be independent of each other (Stearns 1986; Saito & Hattori 1997). Most recent studies have supported the theory that DVM and DFR are behaviors for preventing predation by visual predators (Bollens & Frost 1989; Bollens & Stearns 1992; Durbin et al. 1990; Giguère & Northcote 1987; Gliwicz 1985, 1986; Huang et al. 1993; Iwasa 1982; Lampert 1989, 1993; Levy 1990; Ohman et al. 1983; Stearns 1986; Stich & Lampert 1981, 1984). However, many theories have been proposed for the adaptive significance of both behaviors, especially DVM, and it has been shown that factors other than predation prevention also influence both behaviors (e.g., McLaren 1963; Lampert 1989). Food concentration and food distribution in the water column are other factors that influence DVM. In food-limited

waters, zooplankton cease DVM, and become distributed in the surface layer throughout the day to avoid starvation (Huntley & Brooks 1982). In eutrophic or vertically homogeneous waters, zooplankton remain at depth throughout the day because there is no disadvantage to foraging in this layer and there is the advantage of reducing predation risk by visual predators (Gliwicz & Pijanowska 1988; Pijanowska & Dawidowicz 1987). In stratified water with a food-abundant surface layer and a food-limited deep layer, zooplankton show extensive DVM (Lampert 1989).

On the other hand, the influence of food concentration on DFR is still under debate. Continuous feeding without obvious DFR in oligotrophic waters or in the food-scarce deep layer has been observed (Dagg & Walser 1987; Dagg et al. 1989; Tsuda & Sugisaki 1994). Contrary to these results, Durbin et al. (1990) and Durbin et al. (1995) showed that copepods continued DFR even when in a state of starvation due to food-limitation, and Landry et al. (1994) pointed out that the day-night difference in grazing intensity was usually inversely correlated to food concentration. Factors other than food concentration possibly led to these contradictory results.

Akkeshi Bay (Fig. 1), on the eastern coast of Hokkaido, Japan, is a shallow eutrophic embayment. During the spring and fall phytoplankton blooms, the water column in the bay is weakly stratified (Motoda et al. 1977; Saito & Taguchi 1996). Although predator abundance is not well known in Akkeshi Bay, the coastal area is, in general, a nursery ground for fish and the predation pressure on zooplankton by visual predators is estimated to be higher in this area than in the open ocean (Kimmerer 1991). In such coastal environments, avoidance of visual predators may be more important than efforts to avoid starvation. Therefore, the following diel behaviors of zooplankton are expected during the fall bloom in Akkeshi Bay: (1) zooplankton will be distributed in the dimly lit, deeper layer during the day because the low irradiance will decrease the predation risk from visual predators, (2) DVM will be extensive when the food concentration in the deep layer is low but will be absent or confined to a small range when food is abundant, even in the deeper layer, (3) DFR will be apparent because small amounts or an absence of gut contents during the day serves to protect them from visual predators through enhanced transparency, and a high food concentration allows them to feed enough during the night to exceed their daily energy requirements.

In order to test these predictions, we determined DVM and DFR of copepods during the fall bloom in Akkeshi Bay. Variabilities in the patterns of DVM and DFR by species or stages have been reported elsewhere (Saito & Taguchi 1996; Saito & Hattori 1997). The present paper discusses the reasons for these variabilities.

Materials and Methods

Sampling was carried out at Stn 3, in the central part of Akkeshi Bay (Fig. 1), on 14–15 October 1992. Sunset on 14 October was 1641 h and sunrise on 15 October was 0532 h. Bottom depth was 15–16 m. Zooplankton were collected every 4 h at 0, 2.5, 5, 7.5, 10 and 14 m using an NIPR-sampler fitted with 330- μ m mesh netting (Fukuchi et al. 1979). The NIPR-sampler collects plankton at a fixed position using screw-induced water flow. Zooplankton were collected twice at each sampling layer. One sample was used for enumeration (4.65 m³ filtered volume) and the other (1.55 m³) was used for gut pigment analysis. Samples used for the enumeration were preserved with buffered 5% formalin-seawater. Copepods, which dominated the zooplankton assemblages, were sorted by species, stage and sex.

Gut pigment contents of copepods were analyzed for adult females and males of *Acartia*

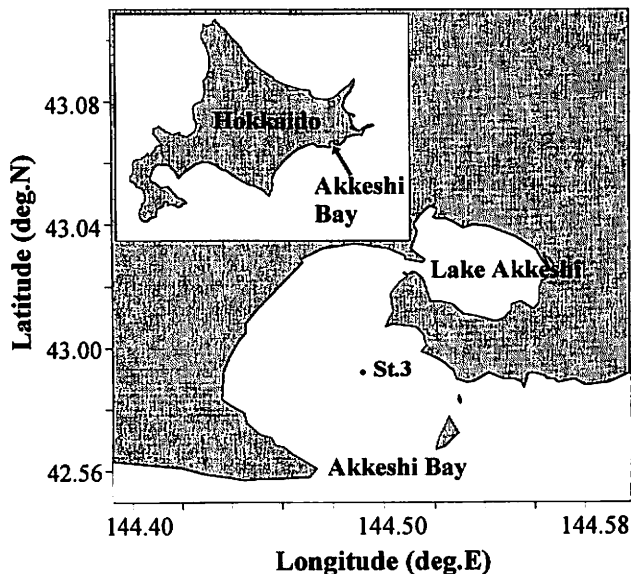


Fig. 1. Location of the station in Akkeshi Bay.

omorii, adult females of *Paracalanus* sp., adult females of *Pseudocalanus newmani*, and adult females and males and copepodid stage V (CV) of *Centropages abdominalis*. Samples for the gut pigment analysis were immediately filtered onto a 100- μm nylon mesh screen and rinsed with sea water filtered through a GF/F glass fiber filter (FSW). The filters were then kept in the dark at -20°C . Upon returning to the laboratory, copepods on the filters were sorted by species, stage and sex under a dissecting microscope and put into 5 ml of 90% acetone to extract chlorophyll *a* and pheopigments. In general 30 animals were used in each analysis for *Acartia*, *Paracalanus*, and *Pseudocalanus*, 10 animals for adult *Centropages*, and 15 for *Centropages* CV. Sorting was done under subdued light through a red filter and samples were kept chilled. Gut pigment contents (chlorophyll+pheopigments) were determined using a Turner Designs Model 10 fluorometer (Holm-Hansen et al. 1965). The average ratio of chlorophyll to chlorophyll+pheopigments in the guts was 0.12 ± 0.050 (mean \pm 1 S.E.) in the present study.

In order to determine the gut evacuation rate constant (k : min^{-1}), copepods were collected at 0130 h on 15 October, with a ring net (45 cm diameter and 1.8 m long) fitted with 330- μm mesh that was vertically towed from 14 m to the surface. The copepods collected were immediately rinsed with FSW and transferred into a 10-liter bottle filled with FSW. To monitor the decrease in the gut pigment contents of the copepods, subsamples were filtered onto 100- μm nylon mesh at 5-min intervals for 20 min, and copepods were treated as they were for the analysis of gut pigment contents. Only adult females of *Acartia omorii* and adult females of *Paracalanus* sp. were collected in sufficient numbers for gut pigment analysis in each subsample. Gut evacuation rate constants (k : min^{-1}) were calculated by fitting the data to the exponential decay model (Dagg & Grill 1980),

$$G_t = G_0 e^{-kt} \quad (1)$$

where G_0 and G_t are gut pigment contents (ng individ $^{-1}$) at time 0 and time t after the transport of copepods to an experimental bottle.

The degradation rate of pigments to non-fluorescent matter during passage through the copepod gut was determined using the silica: pigment ratio method (Conover et al. 1986). Copepods were collected with an NIPR-sampler from 5, 10, and 14 m, and transferred into a

plastic bottle filled with FSW. *Acartia omorii* and *Paracalanus* sp. were selected, rinsed with FSW twice and transferred into 1-liter bottles filled with FSW. The experimental bottles were incubated for 3 h in a water bath with surface-derived running seawater. During the incubation, the experimental bottles were covered with black plastic to prevent photo-degradation of pigments (SooHoo & Kiefer 1982). After the incubation, copepods were removed with 330- μm mesh and fecal pellets were recovered on 20- μm nylon mesh. The fecal pellets thereby collected were rinsed with FSW and refiltered onto a Nuclepore filter with a pore size of 10 μm . The filters were kept in the dark at -20°C until analysis of pigment and biogenic silica content (Paasche 1980). Water samples were collected at the same depths at which the copepods were sampled, were filtered onto Nuclepore filters with a pore size of 2 μm and pigment and biogenic silica content of the phytoplankton were analyzed. Assuming that biogenic silica is not destroyed during passage through the gut, the pigment destruction rates (D) were then calculated as

$$D = \left[1 - \frac{S_A / P_A}{S_F / P_F} \right], \quad (2)$$

where S_A and S_F are the concentrations of biogenic silica in the water and feces, and P_A and P_F are the concentrations of pigments in the water and feces, respectively.

The grazing rate of copepods (I) was calculated by the following equation (Mackas & Bohrer 1976),

$$I = \frac{1}{1-D} kG, \quad (3)$$

where G is the gut pigment content.

Water samples were taken after each sampling of copepods from 0, 5, 10, and 14 m using a bucket or Niskin bottle. The samples collected were successively filtered onto Nuclepore filters with pore sizes of 10, 2, and 0.2 μm , and chlorophyll- a concentrations were determined by fluorometry. Temperature and salinity were measured with an Allec Electronics CTD model AST-1000 at each sampling. A vertical profile of photosynthetically available radiation (PAR) was measured at 1400 h on 15 October using a Biospherical Instruments underwater radiometer Model PUV-500. An Aanderaa current meter model RCMS4S was moored at a depth of 5 m and used to monitor current speed and direction at 1-min intervals.

Results

Hydrography

The vertical difference in temperature was small, ranging between 12.5 and 13.4°C. On the other hand, a halocline was observed above the 5-m layer (Fig. 2). Temperature and salinity profiles did not change greatly throughout the sampling period. The current speed was low and steady during the investigation, averaging 1.5 cm s^{-1} . Total chlorophyll- a concentration ($>0.2 \mu\text{m}$) was highest at 5 m, where it reached 10 $\mu\text{g l}^{-1}$, and was lowest in the near-bottom layer (Fig. 2). Total chlorophyll- a standing stock (0–14 m) during the investigation was $84.0 \pm 14.8 \text{ mg m}^{-2}$ (mean ± 1 S.E.) with chlorophyll $a > 10 \mu\text{m}$ accounting for $83.3 \pm 1.8\%$ of the total, chlorophyll a 10–2 μm for $12.0 \pm 1.8\%$, and chlorophyll a 2–0.2 μm accounting for $4.6 \pm 1.5\%$ (Table 1). PAR values at 5, 10, and 14 m were 10%, 1.1% and 0.27% of that at the surface, respectively.

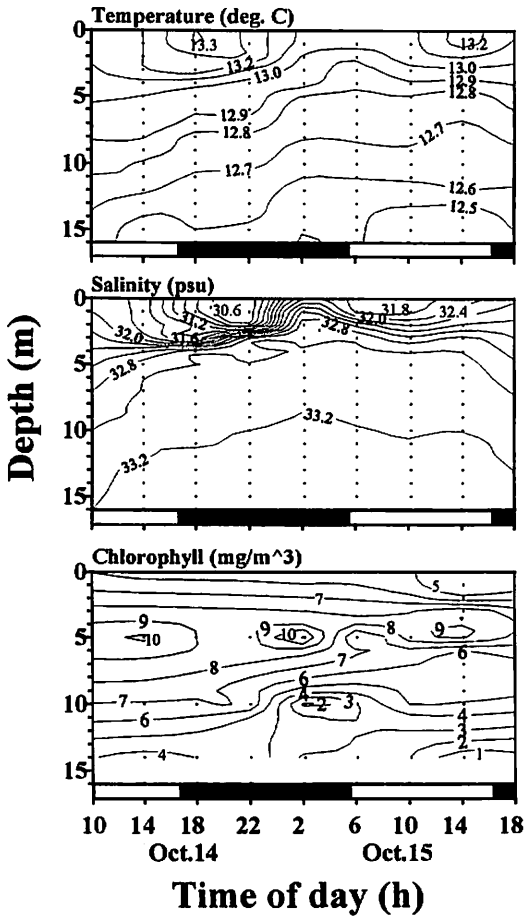


Fig. 2. Diel change in vertical distribution of temperature (°C; top), salinity (psu; middle) and chlorophyll *a* concentration (mg m⁻³; bottom). Dots show depth and time of samplings. Open and closed bars indicate day and night, respectively.

Diel Vertical Distribution of Copepods

Acartia omorii was the dominant species in the copepod assemblages, accounting for 24.4% of the copepods by number. Adult females aggregated in the near-bottom layer during the day and migrated to the shallower layer after sunset (Fig. 3). The median depth of the population (MD) of adult females was significantly shallower at night than during the day (Table 2). Adult males of *A. omorii* showed a DVM pattern that was similar to that of adult females. However, they ascended to a shallower layer than adult females at night. At midnight, 42% of the adult males but less than 18% of the females reached the layer shallower than 5 m.

Table 1. Mean and 1 S.E. of chlorophyll *a* concentration (>0.2 μm) and size distribution in each sampling (n=7).

	Total chl. <i>a</i> (mg m ⁻²)	>10 μm	Frequency (%) 10–2 μm	2–0.2 μm
Mean	84.0	83.3	12.0	4.6
1 S.E.	14.8	1.8	1.8	1.5
C. V. (%)*	17.6	2.1	14.9	32.5

*: Coefficient of variation expressed as a percent of the mean.

A DVM pattern similar to that of *A. omorii* was observed for adult females of *Paracalanus* sp., adult females of *Clausocalanus arcuicornis*, and copepodid stages I to III (CI–III) and IV–VI (CIV–VI) of *Calanus pacificus*. Differences between the mean MDs of these categories during the day and night ranged between 1.9 and 2.8 m and were statistically significant (Student's *t*-test, $p < 0.05$) (Table 2). Adult females and males of *Pseudocalanus newmani* showed a similar DVM pattern. However, the day-night differences in the mean MDs (1.5 m for females and 1.3 m for males) were smaller than they were in the above groups and insignificant. In the sampling period between 0223 and 0308 h, the densest layer of copepods in the water column was found in the near-bottom layer again. Adult females of *Paracalanus* sp. were an exception (Fig. 3).

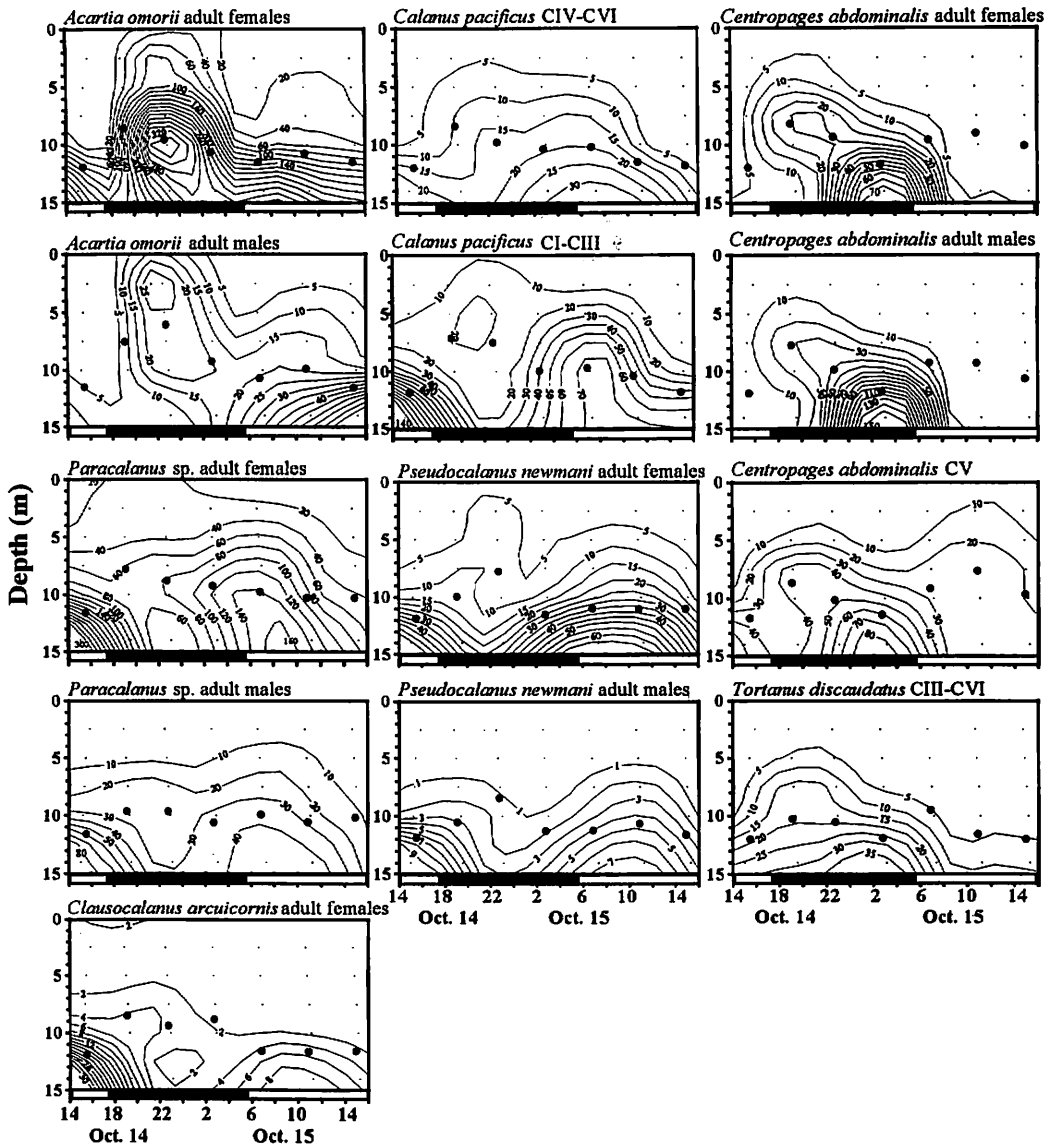


Fig. 3. Diel change in the vertical distribution of copepods (ind. m^{-3}). Closed circles show the median depth of the population (MD). Dots show depth and time of samplings. Open and closed bars indicate day and night, respectively.

Table 2. Mean \pm 1 S.E. of the median depths of the population (MD: m) during day and night and the difference between those during the day and night. Significance levels (p) of mean MD between day and night were tested by the Student's t -test, ns signifies non-significance ($p > 0.05$).

Species, stage & sex	Day	MD (m) Night	Day-Night	P
<i>Acartia omorii</i> CVI females	11.4 \pm 0.49	9.6 \pm 1.03	1.8	<0.05
CVI males	10.9 \pm 0.78	7.6 \pm 1.59	3.3	<0.01
<i>Paracalanus</i> sp. CVI females	10.5 \pm 0.77	8.6 \pm 0.72	1.9	<0.05
CVI males	10.5 \pm 0.75	10.0 \pm 0.55	0.5	ns
<i>Pseudocalanus newmani</i> CVI females	11.2 \pm 0.43	9.7 \pm 1.85	1.5	ns
CVI males	11.4 \pm 0.53	10.1 \pm 1.49	0.3	ns
<i>Clausocalanus arcuicornis</i> CVI females	11.7 \pm 0.18	8.9 \pm 0.45	2.8	<0.01
<i>Centropages abdominalis</i> CVI females	10.2 \pm 1.27	9.7 \pm 1.77	0.5	ns
CVI males	10.3 \pm 1.27	9.8 \pm 2.00	0.5	ns
CV	9.7 \pm 1.55	10.0 \pm 1.37	-0.3	ns
<i>Calanus pacificus</i> CIV-CVI	11.4 \pm 0.79	9.5 \pm 1.02	1.9	<0.05
CI-CIII	10.9 \pm 1.07	8.2 \pm 1.55	2.7	<0.05
<i>Tortanus discaudatus</i> CVI females	11.3 \pm 1.20	10.9 \pm 0.87	0.4	ns

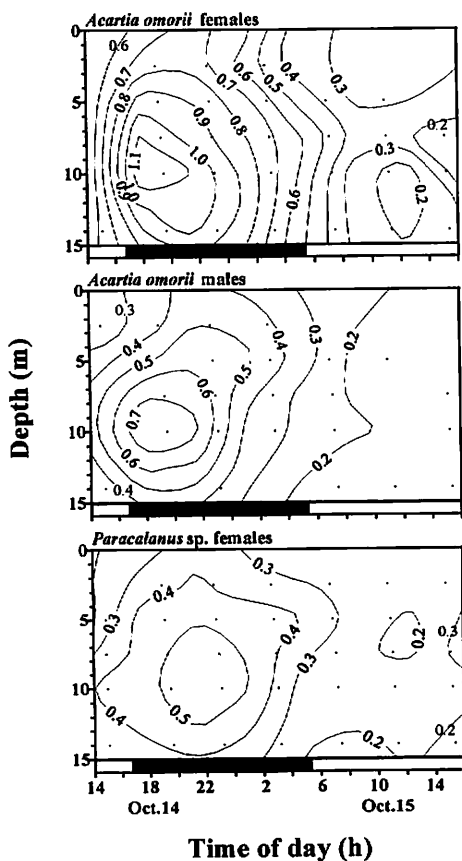


Fig. 4. Diel change in gut pigment contents of copepods (ng Pig. ind.⁻¹). Adult females of *Acartia omorii* (top), adult males of *A. omorii* (middle) and adult females *Paracalanus* sp. (bottom). Open and closed bars indicate day and night, respectively.

Daytime aggregation in the near-bottom layer and dispersion into the shallower layer after sunset were also observed for adult males of *Paracalanus* sp., adult females, males and CV of *Centropages abdominalis*, and CIII to CVI of *Tortanus discaudatus*. However, these categories re-aggregated in the near-bottom layer at midnight (Fig. 3). The rises in the MD at night from the MD during the day for these categories were less than 0.5 m and were insignificant (Table 2).

Diel Change in Gut Pigment Contents

Vertical and diel changes in the gut pigment contents of adult females and males of *Acartia omorii* and adult females of *Paracalanus* sp., accounting for 31–67% of copepod assemblages in number, are shown in Fig. 4. These 3 categories of copepods showed similar DFR patterns. Gut pigment contents increased after sunset and decreased again between midnight and sunrise in every sampling layer. Mean gut pigment contents at night at each depth (\overline{G}_{ZN}) were always higher than those during the day (\overline{G}_{ZD}) (Table 3). The ratios of $\overline{G}_{ZN}:\overline{G}_{ZD}$ were in the range between 2.0 and 3.3 for adult females of *A. omorii*, between 1.9 and 3.0 for adult males of *A. omorii*, and between 1.2 and 1.8 for adult females of *Paracalanus* sp. (Table 3). Gut pigment contents were usually higher between 5 and 10 m than at other depths during the night,

Table 3. Mean \pm 1 standard error of gut pigment contents of *Acartia omorii* and *Paracalanus* sp. at each sampling depth during nighttime (\overline{G}_{ZN}) and daytime (\overline{G}_{ZD}). Number of replicates is given in parentheses. ND signifies no data.

Species & sexes	Depth (m)	\overline{G}_{ZN} (ng Pig ind. ⁻¹)	\overline{G}_{ZD} (ng Pig ind. ⁻¹)	$\overline{G}_{ZN}:\overline{G}_{ZD}$
<i>Acartia omorii</i> females	0	0.67 \pm 0.11 (3)	0.34 \pm 0.12 (4)	2.0
	2.5	0.64 \pm 0.20 (3)	ND	—
	5	0.82 \pm 0.15 (3)	0.30 (2)	2.8
	7.5	0.91 \pm 0.19 (3)	0.44 \pm 0.039 (3)	2.1
	10	1.0 \pm 0.24 (3)	0.31 \pm 0.20 (3)	3.3
	14	0.94 \pm 0.22 (3)	0.31 \pm 0.16 (4)	3.0
	Mean	0.83	0.37	2.3
	S.E.	0.15	0.058	0.58
<i>Acartia omorii</i> males	0	0.40 \pm 0.062 (3)	0.21 (1)	1.9
	2.5	0.43 \pm 0.10 (3)	ND	—
	5	0.54 (2)	0.17 (2)	3.2
	7.5	0.54 \pm 0.23 (3)	0.18 (2)	3.0
	10	0.61 \pm 0.39 (3)	0.24 (2)	2.5
	14	0.38 (1)	0.15 \pm 0.089 (4)	2.5
	Mean	0.50	0.20	2.6
	S.E.	0.093	0.037	0.53
<i>Paracalanus</i> sp. females	0	0.30 \pm 0.079 (3)	0.24 \pm 0.057 (4)	1.2
	2.5	0.35 \pm 0.069 (3)	0.30 \pm 0.008 (3)	1.2
	5	0.52 \pm 0.10 (3)	0.42 \pm 0.34 (4)	1.2
	7.5	0.47 \pm 0.13 (3)	0.26 \pm 0.12 (4)	1.8
	10	0.51 \pm 0.23 (3)	0.33 \pm 0.098 (4)	1.5
	14	0.36 \pm 0.079 (3)	0.21 \pm 0.099 (4)	1.7
	Mean	0.42	0.29	1.4
	S.E.	0.092	0.085	0.27

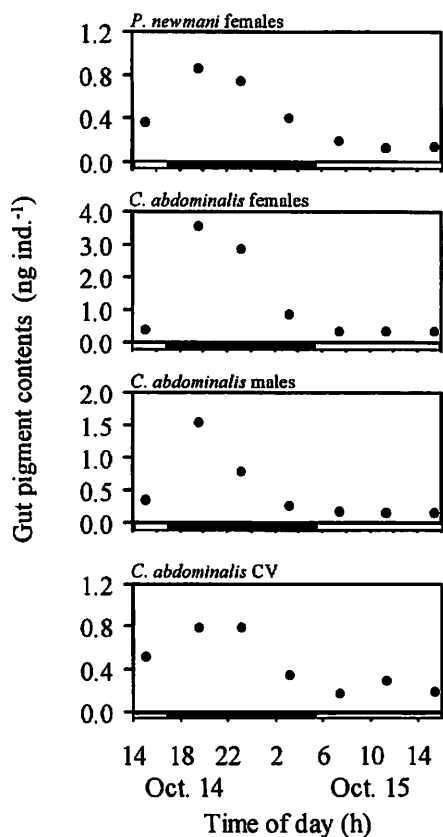


Fig. 5. Diel change in gut pigment contents (ng Pig. ind.⁻¹) of adult females of *Pseudocalanus newmani* and adult females, adult males and CV of *Centropages abdominalis* at 14 m. Open and closed bars indicate day and night, respectively.

while, on the other hand, vertical differences in gut pigment contents were small during the day (Fig. 4, Table 3).

Gut pigment contents of adult females of *Pseudocalanus newmani* and adult females, adult males and CV of *Centropages abdominalis* during the day were not examined due to an insufficient number of specimen except for the 14-m sample. Therefore, diel changes in gut pigment contents for these categories are shown only at 14 m (Fig. 5). The DFR patterns of *P. newmani* and *C. abdominalis* closely resembled those of *A. omorii* and *Paracalanus* sp. Gut pigment contents at night were always higher than those during the day. The ratios of $\bar{G}_{14N} : \bar{G}_{14D}$ in *P. newmani* and adult females and males of *C. abdominalis* were higher than those of *A. omorii* and *Paracalanus* sp. (Table 4). The ratios of $\bar{G}_{14N} : \bar{G}_{14D}$ were positively related to the prosome lengths of copepods ($p < 0.01$, Student's *t*-test, Fig. 6).

Table 4. Mean ± 1 standard error in gut pigment contents of *Pseudocalanus newmani* and *Centropages abdominalis* at 14 m during nighttime (\bar{G}_{14N}) and daytime (\bar{G}_{14D}). Number of replicates is given in parentheses.

Categories	\bar{G}_{14N} (ng Pig ind. ⁻¹)	\bar{G}_{14D} (ng Pig ind. ⁻¹)	$\bar{G}_{14N} : \bar{G}_{14D}$
<i>Pseudocalanus newmani</i> adult females	0.67 \pm 0.24 (3)	0.21 \pm 0.11 (4)	3.2
<i>Centropages abdominalis</i> adult females	2.4 \pm 1.4 (3)	0.37 \pm 0.021 (4)	6.6
adult males	0.87 \pm 0.65 (3)	0.21 \pm 0.0921 (4)	4.2
CV	0.64 \pm 0.26 (3)	0.29 \pm 0.16 (4)	2.2

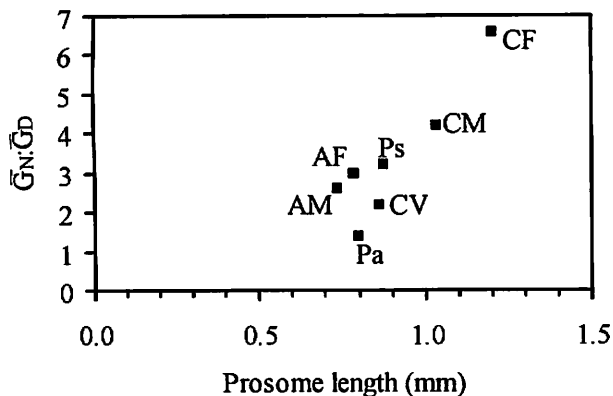


Fig. 6. The relationship between the ratio of mean gut pigment contents at night to that during the day (\bar{G}_N/\bar{G}_D) at 14 m and the prosome length of copepods. AF and AM indicate adult females and males of *Acartia omorii*, respectively. Pa and Ps refer to adult females of *Paracalanus* sp. and adult females of *Pseudocalanus newmani*, respectively. CF, CM and CV indicate adult females, adult males and copepodid stage V of *Centropages abdominalis*, respectively.

Gut Evacuation Rate Constant, Pigment Degradation Rate and Grazing Pressure

Gut evacuation rate constants of adult females of *Acartia omorii* and *Paracalanus* sp. are shown in Table 5. The biogenic silica: pigment ratios were lower in the fecal pellets than in the phytoplankton in each sampling layer (Table 6). Therefore, we assumed chlorophyll degradation was negligible during the present study. Ingestion rates of adult females and males of *A. omorii* and adult females of *Paracalanus* sp. were calculated using equation (3) and a pigment degradation rate of 0. For adult males of *A. omorii*, a gut evacuation rate constant of 0.069, which was obtained at Stn 3 in Akkeshi Bay, was used for the calculation (Saito & Taguchi 1996). Grazing rates for each category (GR: ng pig. $m^{-3} h^{-1}$) are shown in Fig. 7. The depth in which the maximum grazing rate (GR_{max} depth) occurred in adult females of *A. omorii* rose from the near-bottom layer during the day to 10 m after sunset. A similar pattern of diel change was observed for adult males of *A. omorii*, but the GR_{max} depths at night were shallower than those of adult females, reaching 2.5 m at midnight. The GR_{max} depths of *Paracalanus* sp. were observed at 10–14 m throughout the day with one exception (7.5 m at 1843–1939 h). Daily grazing rates were lowest in the surface layer for each category (Table 7), and were highest at the near-bottom layer for adult females of *A. omorii* and at 10 m for adult males of *A. omorii* and adult females of *Paracalanus* sp. The grazing pressure, i.e., the amount grazed daily by these 3 categories of copepods expressed as a percentage of chlorophyll standing stock, was less than 0.5% at each depth, and 0.14% over the whole water column (Table 7). The average daily grazing rates per individual were calculated from the daily grazing rate of each category in the water column divided by the average density of each category in the water column. These values were 2.9 to 4.2 times higher than the daily food requirement for metabolic demand (Table 7).

Table 5. Gut evacuation rate constant (k), and gut pigment contents (G_0) of females of two species of copepod. G_0 refers to the gut pigment contents at the start of the evacuation experiment.

Species and sex	$k \pm S.E.$ (min^{-1})	G_0	r^2 *1	p *2
<i>Acartia omorii</i> females	0.053 ± 0.016	1.2	0.73	<0.05
<i>Paracalanus</i> sp. females	0.082 ± 0.016	0.36	0.90	<0.01

*1 Coefficient of determination for fits to the exponential model.

*2 Significance level (Student's t -test).

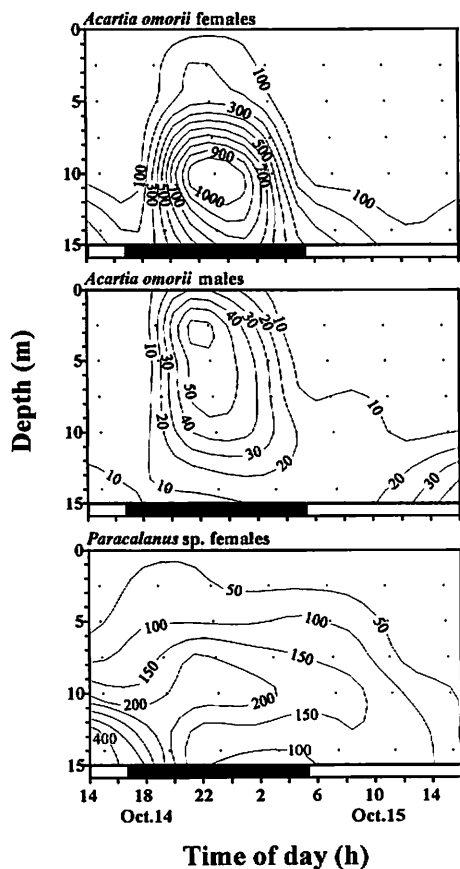


Fig. 7. Diel change in grazing pressure of copepods (ng Pig. m⁻³ h⁻¹). Adult females of *Acartia omorii* (top), adult males of *A. omorii* (middle) and adult females of *Paracalanus* sp. (bottom). Open and closed bars indicate day and night, respectively.

Discussion

Copepods aggregated at the near-bottom layer during the day (Fig. 3). The near-bottom layer appeared to be less favorable than the shallower layers for the feeding of herbivorous copepods because it had the lowest food concentration in the water column and also possibly because the quality of food might be low due to the irradiance being insufficient for phyto-

Table 6. Biogenic silica (BioSi) and pigments in phytoplankton and fecal pellets collected at different depths. *D* refers to chlorophyll degradation rate estimated by equation (2).

Depth (m)	BioSi	Pigments	BioSi : Pigments	<i>D</i>
Phytoplankton (μg l ⁻¹)				
0	411	8.0	51	
5	456	12	37	
10	300	7.4	41	
14	538	5.7	94	
Mean	440	9.4	47	
Fecal pellets (μg)				
5	177	6.4	28	<0
10	97	2.9	34	<0
14	56	1.3	44	<0

plankton growth (Fig. 2). In spite of the unfavorableness of the near-bottom layer for feeding, the dimness of the layer is advantageous for copepods as it would decrease the predation risk from visual predators. Akkeshi Bay and Lake Akkeshi (Fig. 1) are important nursery grounds for flatfish, and several commercially important species spawn in these areas during summer and autumn (Minami 1995). Shisyamo smelt (*Spirinchus lanceolatus*), whose main food source is copepods, migrate to the coastal area for spawning in autumn (Watanabe et al. 1996). Although their biomass and feeding rate are unknown, it is likely that predation pressure on copepods by these fish strongly influence the copepods' behavior. Therefore, copepods might select a daytime habitat to minimize predation risk, even though it would mean a decrease in the quantity and/or quality of food.

The copepods that aggregated in the near-bottom layer during the day dispersed into the shallower layer after sunset (Fig. 3), although the DVM was not extensive. The differences between mean MDs at night and those during the day were at most 3.3 m, and were insignificant in 7 of 13 categories of copepods examined (Table 2). One of the reasons for the less extensive or insignificant DVM was the relatively high food concentration in the near-bottom layer. The daily ingestion rates of *Acartia omorii* and *Paracalanus* sp. were 3 to 4 times higher than their daily food requirements for metabolic demand during this study (Table 7) even though the DVM was not extensive. Gut pigment contents of *Pseudocalanus newmani* and *Centropages abdominalis* from the near-bottom layer (Fig. 4) were comparable to or higher than

Table 7. Daily grazing rate of copepod categories ($\mu\text{g Pig. m}^{-3} \text{d}^{-1}$). Grazing pressure refers to the means percentage of the sum of ingestion rates by adult females and males of *Acartia omorii* and adult females of *Paracalanus* sp. to chlorophyll-*a* standing stock (Chl. *a*). Carbon ingestion rates were calculated using a C : Chl ratio of 40 (Taguchi et al. 1994). Food Req. refers to the daily requirement of food to meet metabolic demand.

Depth (m)	<i>Acartia omorii</i> females	<i>Acartia omorii</i> males	<i>Paracalanus</i> sp. Females	Chl. <i>a</i> (mg m^{-3})	Grazing pressure (%)
0	0.64	0.17	0.49	5.30	0.025
2.5	1.53	0.42	0.93	7.17* ¹	0.040
5	1.70	0.41	1.80	9.04	0.043
7.5	5.48	0.48	3.12	6.71* ¹	0.135
10	9.17	0.51	4.28	4.39	0.318
14	9.24	0.38	3.63	2.91	0.455
0-14 m	70.8	5.90	36.4	84.0	0.135
	($\mu\text{g Pig. m}^{-2} \text{d}^{-1}$)	($\mu\text{g Pig. m}^{-2} \text{d}^{-1}$)	($\mu\text{g Pig. m}^{-2} \text{d}^{-1}$)	(mg m^{-2})	
Density (ind. m^{-2})	1167	192	892		
Pig. Ingestion ($\mu\text{g ind.}^{-1} \text{d}^{-1}$)	0.061	0.031	0.041		
C Ingestion ($\mu\text{g ind.}^{-1} \text{d}^{-1}$)	2.4	1.2	1.6		
Food Req.* ² ($\mu\text{g C ind.}^{-1} \text{d}^{-1}$)	0.57	0.41	0.52		

*¹ Interpolated from values at sampling layers above and below.

*² Calculated from the respiration rate using the equation by Ikeda (1985). The values used for respiratory quotient and assimilation efficiency were 1.0 and 0.69, respectively (Parsons et al. 1984; Conover 1966). Copepods weight values were taken from Saito & Taguchi (1996).

those reported in similar sized copepods in food-abundant environments (Dagg & Grill 1980; Head & Harris 1987; Kiørboe et al. 1982; Nicolajsen et al. 1983; Saito & Taguchi 1996; Tiselius 1988). These results suggest that the copepods in the present study were able to find enough food for growth or reproduction with a less extensive or insignificant DVM.

In the present study, the smallest DVMs were observed for the carnivorous copepod *Tortanus discaudatus* and the omnivore *Centropages abdominalis* (Fig. 3, Table 2). The near-bottom layer might be the most favorable layer for foraging and survival for *T. discaudatus* because the concentration of prey copepods was high throughout the day and the dim light minimized predation by visual predators during the day. Thus, the advantages of DVM for *T. discaudatus* were insignificant. The favorable food environment and lower predation risk in the near-bottom layer may also explain the small DVM of *C. abdominalis*. There, they can select the feeding mode (either filter feeding for small particles such as phytoplankton or raptorial feeding for zooplankton); copepods eggs and nauplii are also possible prey foods for them (Paffenhöfer & Knowles 1980; Ohtsuka et al. 1996). In the present study, it is likely that the concentrations of copepod eggs and early stages of nauplii were high in the near-bottom layer because adult female copepods were concentrated in this layer for most of the day and therefore were likely to lay their eggs there.

Most of the copepod species descended prior to the increase in irradiance accompanying dawn (Fig. 3). Although pre-dawn descents have been observed elsewhere (Simard et al. 1985; Runge & Ingram 1991; Saito & Hattori 1997), the hypothesis that this migration is to prevent predation by visual predators cannot explain this behavior. We can only speculate on possible reasons, e.g., an endogenous rhythm (Enright & Hamner 1967), satiation of feeding (Pearre 1973; Simard et al. 1985), and non-visual predator avoidance (Kimmerer 1991). However, factors other than visual predators also influence the pattern and timing of DVM.

Results in the present study were dependent on the samples collected with an NIPR-sampler at certain depths. Although the sampling effectiveness of the NIPR-sampler for copepods of the genus *Pseudocalanus* and chaetognaths of the genus *Sagitta* is comparable to a ring net (45 cm of diameter) (Nishiyama et al. 1987), the underestimation through avoidance of sampling gear, especially for larger species, and/or patchy distribution on a scale finer than the sampling interval was impossible to avoid as in all studies that entail field sampling of zooplankton. In the present study, lower biomass of *Centropages abdominalis* during the day than that at night was obvious (Fig. 3). Although we have no data on their distribution in layers deeper than 14 m, dense distribution just above the bottom (15–16 m) during the day, which has been observed for some neritic copepods (Anraku 1975), is a possible reason for the day-night difference in observed biomass of *C. abdominalis*.

Gut pigment contents were higher at night than during the day at all depths (Table 3, Fig. 4). Since zooplankters with full guts are more conspicuous to visual predators than are zooplankters with empty guts, which are nearly transparent (Zaret 1972), the usual DFR pattern, which is similar to that observed in the present study, is considered to be advantageous in reducing the predation risk from visual predators. According to this hypothesis, the daytime ingestion rate in the dim deep layer is expected to be higher than that in the surface layer. However, no obvious trend with depth was observed in the ingestion rate (Table 3). The threshold light level for feeding of visual predators is quite low (Batty et al. 1990). Even in the near-bottom layer, where the light level was 0.27% of that at the surface, the dimness was assumed to be insufficient to completely prevent predation by visual predators.

The selectivity of zooplankton by visual predators increases with the body size and visibility of the zooplankton (Brooks & Dodson 1965; O'Brien et al. 1976; Zaret 1972). Zaret &

Kerfoot (1975) showed that the visibility of prey is a more important selective factor for visual predators than prey size. In the present study, the $\bar{G}_N:\bar{G}_D$ ratios at 14 m were positively related to the prosome length of copepods (Fig. 6). The $\bar{G}_N:\bar{G}_D$ ratios of *Acartia* and *Paracalanus* observed in the present study were comparable to those previously reported in Akkeshi Bay during phytoplankton blooms, but the $\bar{G}_N:\bar{G}_D$ ratio of *Pseudocalanus* was lower than that previously reported (Saito & Taguchi 1996). Bollens & Stearns (1992) showed that daytime gut fullness was lower in the presence of visual predators than in their absence. Therefore, the ratio is not a constant value for each species or size, but is influenced by variable factors. It is not known how variable the ratio is. However, the ratio may reflect the vulnerability of different copepods to visual predators.

The metabolic or demographic advantage hypothesis on the adaptive significance of DVM (McLaren 1963, 1974; Enright 1977; Enright & Honegger 1977) is correlated with the hypothesis that the DFR is the result of DVM (e.g. Gauld 1953). The studies mentioned above did not assert that DVM was the controlling factor for DFR. However, they implied that a diel vertical migrator would show a DFR and concluded that zooplankton decreased their grazing pressure on phytoplankton to achieve effective use of their resources. In the present study, the upward migration and the increase in gut pigment contents were observed after sunset (Figs 3, 4). On the other hand, gut pigment contents of adult females and males of *Acartia omorii* and adult females of *Paracalanus* sp. in the period between midnight and sunrise were still twice that of those during the day, even though downward migration had started. Surface-dwelling copepods also showed a DFR (Fig. 4). These results confer with the conclusions of previous reports that DFR is a behavior that is independent of DVM (Dagg et al. 1989; Saito & Hattori 1997; Stearns 1986; Tang et al. 1994).

The grazing pressures of adult *Acartia omorii* and adult females of *Paracalanus* sp., which dominated the copepod assemblages, were less than 0.5% of the standing crop of phytoplankton in each layer and 0.14% when averaged over the water column (Table 7). The impact of copepod grazing on the phytoplankton community has been found to be insignificant during the phytoplankton bloom in Akkeshi Bay (Saito & Taguchi 1996; Taguchi & Fukuchi 1975). This was due, not to a low feeding activity, but to a low standing stock of copepods in the bay. Other unknown factors, e.g., diatom toxicity (Ivanora & Poulet 1993), or predation (Uye et al. 1992), might inhibit reproduction or recruitment success of copepods in the shallow, food-abundant waters of Akkeshi Bay.

In the present study, the DVM and DFR of copepods expected by the predation preventive hypothesis were indeed observed in the shallow, food-abundant waters of Akkeshi Bay. The present results suggest that the daytime aggregation of the copepods at the near-bottom layer and the daytime decrease in ingestion rate are selected to reduce the predation risk from visual predators. Although these behaviors were disadvantageous for feeding efficiency, abundant food during the phytoplankton bloom in Akkeshi Bay made it possible for copepods to find enough food for growth and reproduction regardless. The observed differences in diel behaviors between species, sexes, and different stages might be due to the differences in their vulnerability to visual predators and to differences in the vertical distribution of food for each category.

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