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In situ feeding of the planktonic copepod *Calanus sinicus* in the Inland Sea of Japan, examined by the gut fluorescence method[1, 2]

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Abstract

We investigated in situ feeding of adult females of the planktonic copepod *Calanus sinicus* in the Inland Sea of Japan by the gut fluorescence method. Unlike many empirical observations of food-dependent feeding in copepods, no correlation was found between in situ gut pigment of *C. sinicus* and ambient chlorophyll *a* concentration. This might partly be due to the large (up to 13-fold) variability in individual gut content, which persisted throughout the day. The *C. sinicus* population showed a diel feeding periodicity; mean gut pigment was significantly higher at night than during the day. Gut evacuation rate increased linearly with increasing temperature. Daily pigment ingestion rates were estimated at 3 stations where gut pigment data over 24 h were available. They varied from 209 to 842 ng pigment indiv.$^{-1}$ d^{-1}. Assuming that the population biomass of *C. sinicus* at these stations was 32 mg C m^{-3} (the average biomass in Osaka Bay), the population would have consumed 13 to 85% of the phytoplankton standing crop per day.

Key words: *Calanus sinicus*, copepod, feeding, gut pigment, Inland Sea of Japan

The calanoid copepods of the genus *Calanus* are perhaps the most dominant and productive planktonic crustaceans in the temperate and boreal waters of the world oceans. *Calanus sinicus*, which is distributed in the East China Sea, the Yellow Sea and the coastal waters of Japan (Hulsemann 1994), is the most southerly-distributed species of this genus in the northern hemisphere. In the Inland Sea of Japan, this species is common and one of the most important copepods in terms of biomass (Uye et al. 1987). In spite of its importance as a secondary producer in this area (Uye et al. 1987, Huang et al. 1993a), knowledge of its feeding ecology is limited (Ito & Imai 1986, Uye 1986).

The gut fluorescence method (Mackas & Bohrer 1976) has often been used to study the feeding of herbivorous zooplankton. This method has the following advantages compared to the conventional laboratory incubation method: 1) effects of confinement of zooplankton in bottles are eliminated by instant capture of the animals in their natural habitats, 2) gut pigment content of an animal and gut evacuation rate give the grazing rate of the animal just prior to capture, 3) the technique

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[2] 消化管蛍光法による浮遊性カイアシ類 *Calauns sinicus* の瀬戸内海における摂餌生態
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is so sensitive that a single copepod can be used for measurement, and 4) the procedure is simple and quick.

We investigated the feeding of *C. sinicus* in the Inland Sea of Japan as well as in controlled laboratory conditions using the gut fluorescence method. In this paper we describe the gut pigment content in relation to ambient chlorophyll, along with individual variability in gut pigment, diel variation in gut pigment and gut evacuation rate at different temperatures. We also estimate the daily pigment ingestion rate and discuss the grazing impact by *C. sinicus* on the phytoplankton community.

Materials and Methods

Calanus sinicus were collected at various locations in the Inland Sea of Japan during 10 cruises of the *Toyoshio Maru* (Hiroshima University), *Tansei Maru* (Tokyo University) and *Daini Hayashio Maru* (chartered by the Technological Institute of Chugoku) from June 1991 to June 1994. Zooplankton were sampled by vertical hauls of a Norpac net (mouth diameter: 0.45 m, length: 2 m, mesh opening: 300 μm, with a 2-liter volume cod-end) from near-bottom depths (ca. 10 to 50 m) to the surface. The contents of the cod-end were released into 3-liter plastic dishes, and adult females of *C. sinicus* were sorted out immediately using a wide-mouthed pipette.

Gut pigment content of *C. sinicus* was quantified by fluorometry (Mackas & Bohrer 1976). Our protocol was as follows, unless otherwise specified. The copepods, sorted on a small glass dish, were individually picked out by the first antenna by a pair of tweezers, dipped for ca. 1 s in filtered (Whatman GF/C) seawater or distilled water to remove adhering phytoplankton, and transferred into plastic tubes containing 6 ml of N,N-dimethylformamide (DMF) (Suzuki & Ishimaru 1992). The operation from collection of the animals to immersion in DMF required at most 5 min. These tubes were kept at $-20°C$ in darkness until analysis (>24 h). The copepods were not ground, since our preliminary test showed no significant differences in the recovery of pigment with or without grinding. Chlorophyll *a* and pheopigments (as chlorophyll equivalents) were determined by a Turner Designs (Model 10) fluorometer before and after acidification (Parsons et al. 1984a). The gut pigment content of each copepod was expressed as the sum of chlorophyll *a* and pheopigments. Since the gut pigment was near zero for copepods that had been starved in filtered seawater for 2 days, no correction for background was made.

Gut pigment content in relation to ambient chlorophyll

Gut pigment content was examined during daytime at stations in Hiroshima Bay, Iyo Nada, Beppu Bay and Bungo Channel (Figure 1) during 7 cruises. At each station, vertical profiles of temperature, salinity and in vivo fluorescence were obtained by a cast of a Sea Bird CTD with a Sea Tech fluorometer attached. Two-hundred ml of water from a 3-m depth was filtered with a glassfiber (Whatman GF/C) filter. The filter was introduced into a plastic tube containing 6-ml DMF and then kept at $-20°C$ in darkness for later determination of extracted chlorophyll *a* by a fluorometer. Data from extracted chlorophyll were used in the calibration for

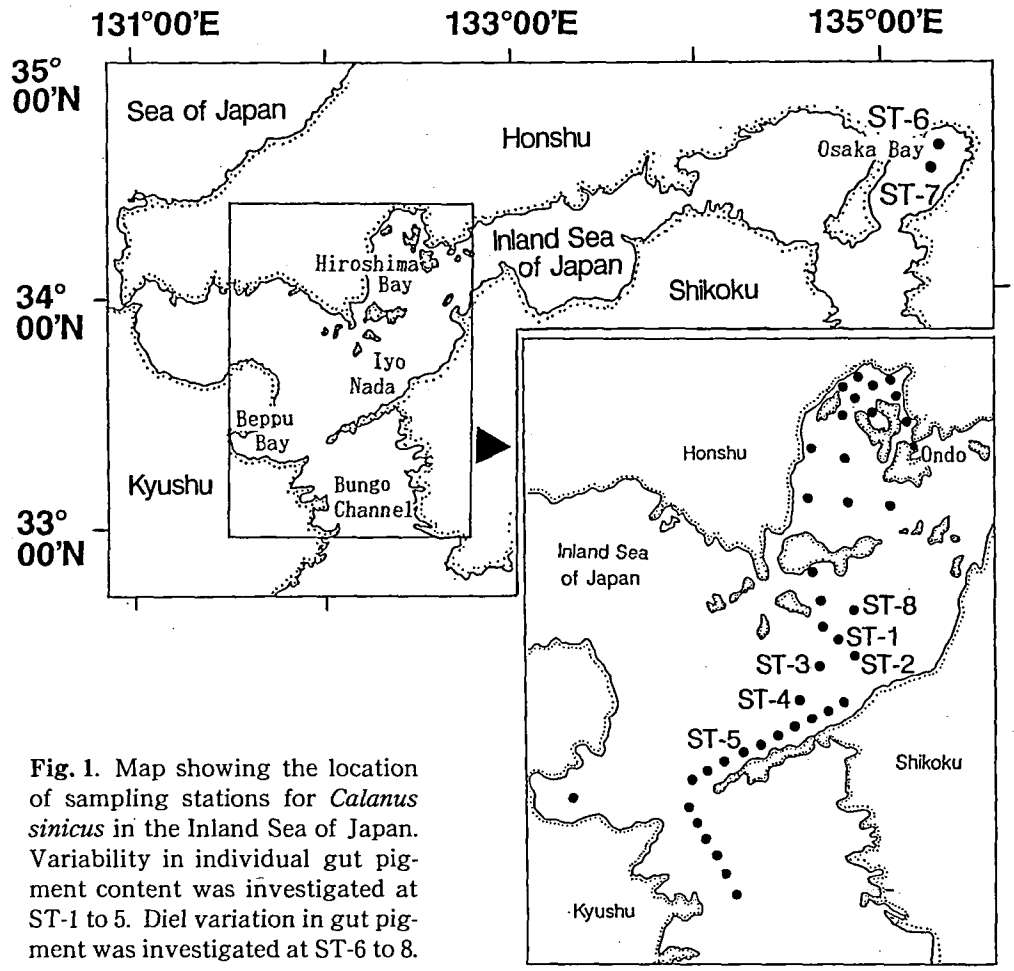

Fig. 1. Map showing the location of sampling stations for *Calanus sinicus* in the Inland Sea of Japan. Variability in individual gut pigment content was investigated at ST-1 to 5. Diel variation in gut pigment was investigated at ST-6 to 8.

converting in vivo fluorescence to chlorophyll concentration. The water column average for chlorophyll was determined by dividing the integrated chlorophyll values through the water column by the depth. At each station, 2 to 8 copepods were picked from the zooplankton sample and processed as described above.

Individual variability

The variability in individual gut pigment content was investigated at 5 stations (ST-1 to ST-5) in Iyo Nada (Figure 1) on 28 and 29 July 1993. Fifty-two to 107 specimens were picked from consecutively collected samples and processed as described above.

Variation under constant food supply

Approximately 200 *C. sinicus* were isolated from the zooplankton samples taken in Hiroshima Bay in the afternoon of 18 May 1992, and introduced into a Plexiglass cylinder with a 300-μm sieve on the bottom, which was immersed in a 5-liter glass

beaker containing 4-liter filtered seawater. They were starved until the following morning when the cultured diatom *Thalassiosira weissflogii* was added to the beaker (chlorophyll: 9.3 $\mu g\ l^{-1}$). At 3 to 30 min intervals samples, each of which consisted of 3 to 5 copepods, were taken and processed as above. Temperature was maintained at 20±1°C.

Diel variation

Diel variations in gut pigment content were investigated at 3 stations (ST-6, 7 and 8, Figure 1) during different seasons. At ST-6, 1 to 4 copepods were isolated as described above at 20-min to 2-h intervals from 10:00 on 30 June to 09:00 h on 1 July 1991. Vertical profiles of in vivo fluorescence were obtained at 3-h intervals. Fifteen specimens were collected at 2 to 4-h intervals from 07:00 h on 3 December to 07:00 h on 4 December 1993 at ST-7, where only one series of vertical chlorophyll profile data was available. At ST-8, 20–30 copepods were pipetted onto a 500-μm sieve, rinsed with filtered seawater and placed on a glassfiber (Whatman GF/C) filter. The filter was placed in a cryovial and frozen in liquid nitrogen. One to 3 similar lots were taken at 0.7 to 3-h intervals from 11: 30 h on 26 June to 11: 00 h on 27 June 1994. Vertical in vivo fluorescence data were obtained at 3-h intervals. Upon return to the land laboratory, the copepods were thawed at room temperature (ca. 20°C) and were individually soaked in DMF as described above for the later determination of their gut pigment contents.

Gut evacuation rate

The gut evacuation rate of *C. sinicus* was investigated mainly on board ship during cruises in Hiroshima Bay and Iyo Nada. On-shore laboratory examinations were also conducted using copepods sampled at Ondo, Kure, to supplement the above experiments. The gut evacuation rate was determined at 8 to 20°C, close to the ambient temperatures at the sampling sites. In each experiment, 30 to 50 copepods were transferred to a Plexiglass cylinder with a 300-μm sieve on the bottom, which was immersed in a bucket containing ca. 4-liter filtered seawater with the cultured diatom *T. weissflogii* in suspension (chlorophyll: 8.5 to 75 $\mu g\ l^{-1}$). After feeding for 3 to 4 h, they were rinsed 3 times in a bucket containing filtered seawater. A plastic dish was applied to the bottom of the cylinder so that the water inside the cylinder remained at a 1.5-cm depth during transfer. After the third rinse (ca. 1 min after the first), the cylinder was left immersed in the bucket, and 2 to 5 copepods were removed for analysis at 2 to 5-min intervals over the first 50 min and then at 10-min intervals thereafter.

Results

Gut pigment content in relation to ambient chlorophyll level

The gut pigment contents of *Calanus sinicus* varied depending on the cruise. The pigment level was relatively high but the data plots were scattered widely in April and September 1992, while it was uniformly low, in spite of large chlorophyll

variation, in May and June 1992 and May 1993 (Figure 2). The minimum and maximum gut pigment contents of *C. sinicus* in the field were 0.66 and 28.2 ng, respectively. There was no significant correlation between gut pigment content and ambient chlorophyll level during any individual cruise, or when data from all cruises were compiled (Figure 3).

Chlorophyll was always less abundant than pheopigments in the guts of *C. sinicus*, averaging 12.4% (range: 6.9 to 20.5%) of total pigment content. There was no indication that the percentage composition of chlorophyll increased with increasing ambient chlorophyll level.

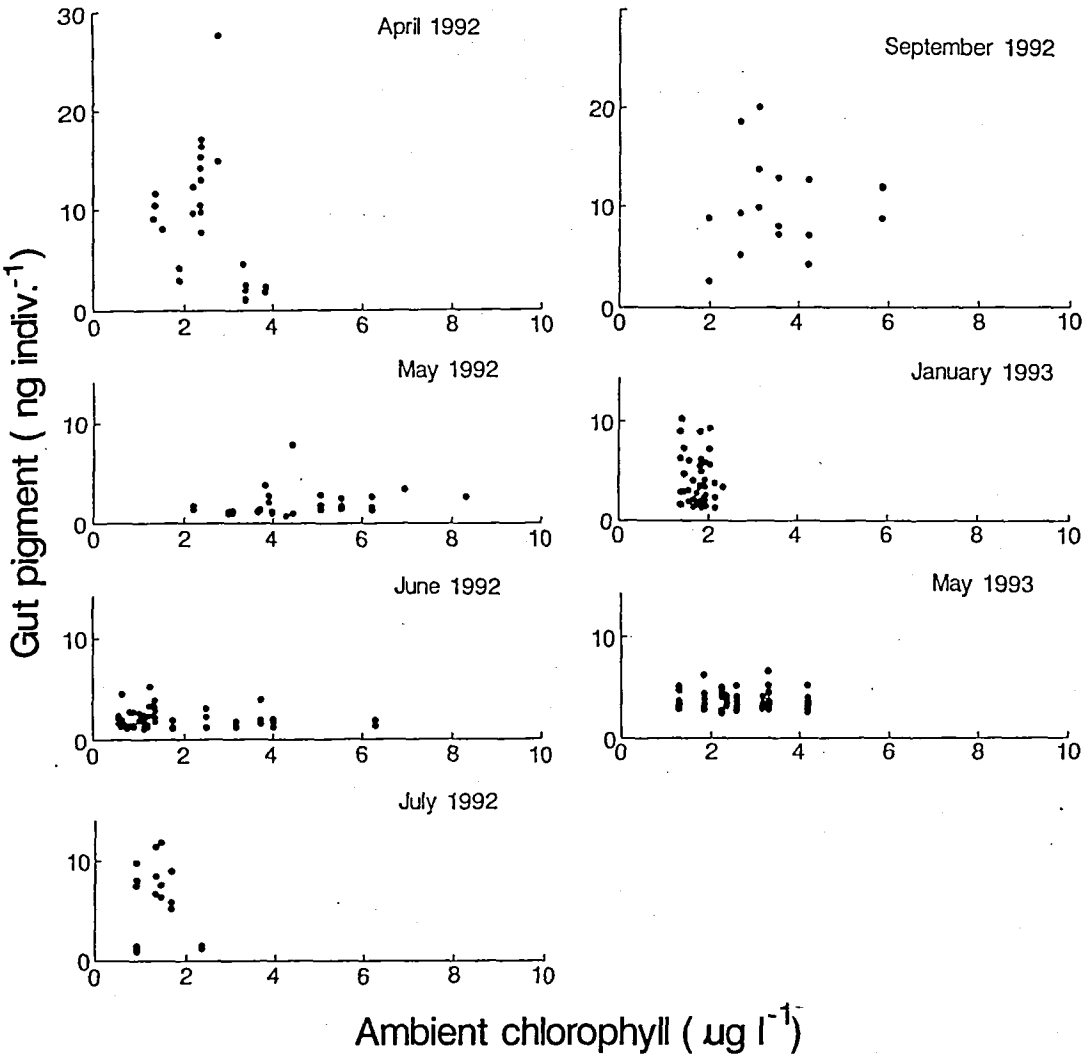

Fig. 2. Relationship between gut pigment content of *Calanus sinicus* and average ambient chlorophyll concentration during 7 cruises from April 1992 to May 1993.

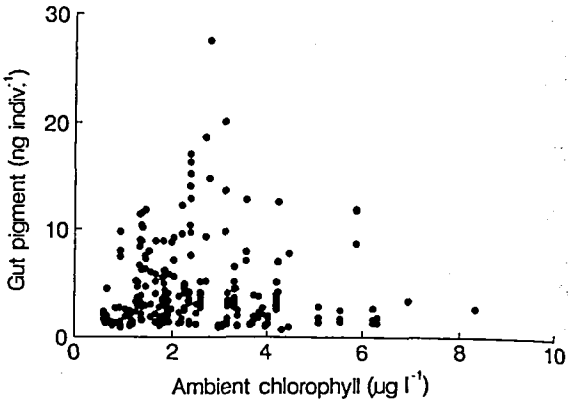

Fig. 3. Composite relationship between the gut pigment content of *Calanus sinicus* and the average ambient chlorophyll concentration from the 7 cruises shown in Fig. 2.

Individual variability

Due to similar vertical hydrographic conditions at ST-1 to ST-4 (ST-5 was vertically more homogeneous), the vertical profiles of chlorophyll showed a more or less similar pattern (the difference between the maximum and minimum chlorophyll concentrations in the water column was less than 3-fold) and the water column average of these stations fell within the narrow range between 1.11 and 1.93 $\mu g\ l^{-1}$. *Calanus sinicus* were thought to have been abundant in the water column at depths deeper than 30 m, since they were rare in the zooplankton samples taken with the net towed from the 30-m depth.

Large variations in individual gut pigment were apparent even among individuals collected at the same station (Figure 4). The variability was smallest (5-fold) at ST-1 and largest (13-fold) at ST-3. The distribution of individual gut pigment was skewed toward lower values, especially at ST-1, 2 and 4. The coefficient of variation was larger at ST-2, 3 and 5 (50 to 54%) than at ST-1 and 4 (33 to 39%).

Variation under constant food supply

Starved *C. sinicus* started feeding immediately after exposure to diatom food, showing a rapid increase in gut pigment from 0.50 to 21.5 ng indiv.$^{-1}$ for the initial 30 min (Figure 5). After the first peak, the gut contents decreased and were relatively constant around 10 ng indiv.$^{-1}$ until the second peak (21.6 ng indiv.$^{-1}$), 90 min after exposure. Thereafter, the gut pigment level was relatively low, and varied irregularly within the range of 2.2 and 9.5 ng indiv.$^{-1}$.

Diel variation

A strong diel variation in gut pigment content was observed in all investigations (Figure 6); the nighttime mean was significantly ($p < 0.05$, t-test) higher than the daytime mean. However, the pattern of variation differed from one station to another. At ST-6 (average chlorophyll: 0.46 $\mu g\ l^{-1}$), the gut pigment contents were low during the day (mean: 0.83 ng indiv.$^{-1}$). Just after sunset, they increased rapidly and maintained a high level throughout the night (mean: 2.9 ng indiv.$^{-1}$), decreasing

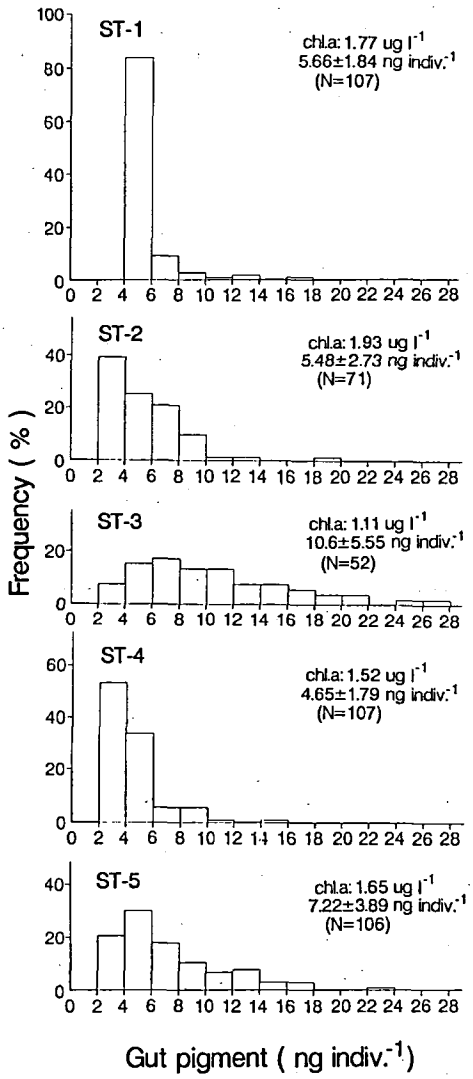

Fig. 4. Frequency distribution of individual gut pigment content of *Calanus sinicus* at ST-1 to 5. Average ambient chlorophyll concentration, mean individual gut pigment (±SD) and the number of specimens examined are also shown.

rapidly around dawn. AT ST-7 (average chlorophyll: 0.79 $\mu g\ l^{-1}$), where the gut pigment levels were several-fold higher than the other stations, the gut contents did not show a sharp increase around sunset, but rather showed a gradual increase over the nighttime hours toward dawn. Daytime and nighttime means were 6.7 and 9.9 ng indiv.$^{-1}$, respectively. At ST-8 (average chlorophyll: 1.1 $\mu g\ l^{-1}$), gut pigment contents showed two peaks over the night.

Since the numbers of copepods examined at each time point were relatively high at ST-7 (15) and St-8 (15 to 75), the interindividual differences in gut pigment distribution at each sampling time point was examined (Figures 7 & 8). At ST-7 in December, the coefficient of variation was smallest (40%) at 07: 00 h on 3 December and largest (74%) at 05:00 h on 4 December. It was greater for daytime data (68%, n: 105) than for nighttime data (50%, n: 75). At ST-8 in June, the coefficient of

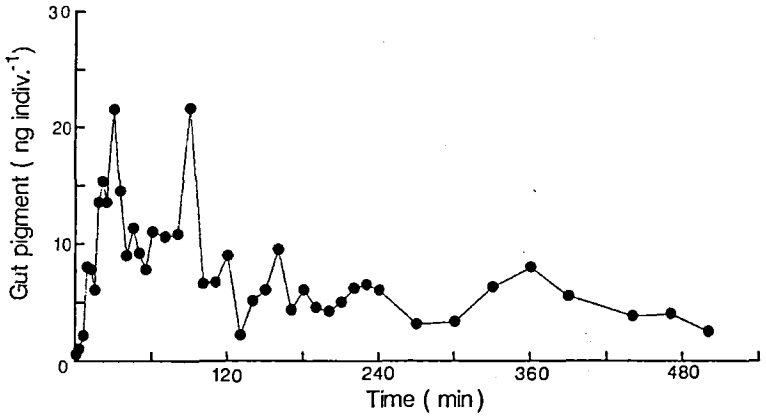

Fig. 5. Time series of the gut pigment of *Calanus sinicus* exposed continuously to a diatom suspension, after starvation for ca. 18 h in filtered seawater.

variation was smallest (26%) at 02: 00 h on 27 June and greatest (65%) at 17: 00 h on 26 June. Unlike December, the variation was greater for nighttime data (62%, n: 233) than for daytime data (46%, n: 475).

Gut evacuation rate

In filtered seawater, gut pigment content decreased quickly for the initial 20 to 30 min, and slowed thereafter. The copepods that were starved for 60–90 min still retained a portion of their last meal in the gut (Figure 9). Instantaneous gut evacuation rate was calculated using the non-linear least square method for data obtained for the first 30 min, where it was assumed that gut evacuation is an exponential process.

The calculated gut evacuation rate was 0.0436 min^{-1} at 8°C, giving a mean gut residence time of 22.9 min, and it increased with increasing temperature to 0.0823 min^{-1} (mean gut residence time: 12.2 min) at 20°C (Figure 10). The linear least square method was applied to describe the relationship between gut evacuation rate (E, min^{-1}) and temperature (T, °C):

$$E=0.0222+0.00278T. \qquad (r=0.804, p<0.01) \qquad (1)$$

Daily ingestion rate

Daily pigment ingestion rates were calculated at ST-6, 7 and 8, where diel gut pigment data were available. Gut evacuation rate was able to be calculated from the average temperatures at these stations (i.e. 20.3, 17.3 and 17.9°C at ST-6, 7 and 8, respectively) using equation (1). Assuming feeding was constant around each sampling time point, the ingestion rate at each sampling can be calculated from:

$$I=G\times E, \qquad (2)$$

where I is the ingestion rate (ng indiv.$^{-1}$ min^{-1}), G is the gut pigment content (ng indiv.$^{-1}$) and E is the gut evacuation rate (min^{-1}). The ingestion rates were

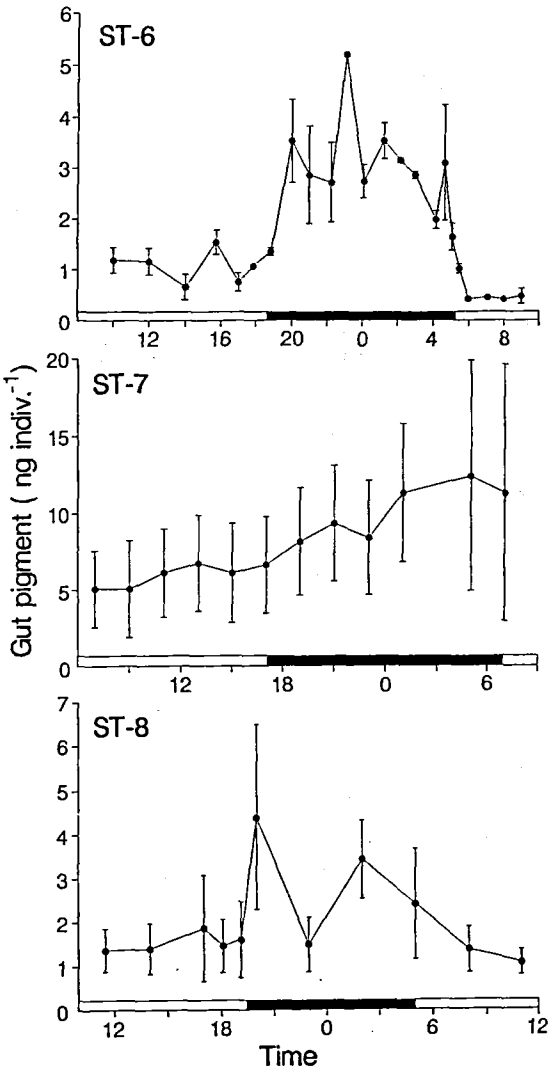

Fig. 6. Diel variation in mean gut pigment content of *Calanus sinicus* at ST-6 (June 1991), ST-7 (December 1993) and ST-8 (June 1994). Vertical lines denote SD.

integrated over 24 h to give a daily pigment ingestion rate. The values obtained were 209, 842 and 212 ng indiv.$^{-1}$ d^{-1} at ST-6, 7 and 8, respectively (Table 1). These were converted to 8.4, 33.7 and 8.5 μg C indiv.$^{-1}$ d^{-1}, respectively, using a carbon-chlorophyll conversion factor of 40 (Parsons et al. 1984b). Assuming that the body carbon weight of *C. sinicus* was 50 μg, the average carbon content of an adult female (Uye 1988), the specific ingestion rate was 0.17, 0.67 and 0.17 d^{-1}, respectively.

Discussion

Ito & Imai (1986) and Uye (1986) demonstrated a saturation type of functional response of *Calanus sinicus* when they were incubated in bottles containing different concentrations of phytoplankton in suspension. From these results, one would

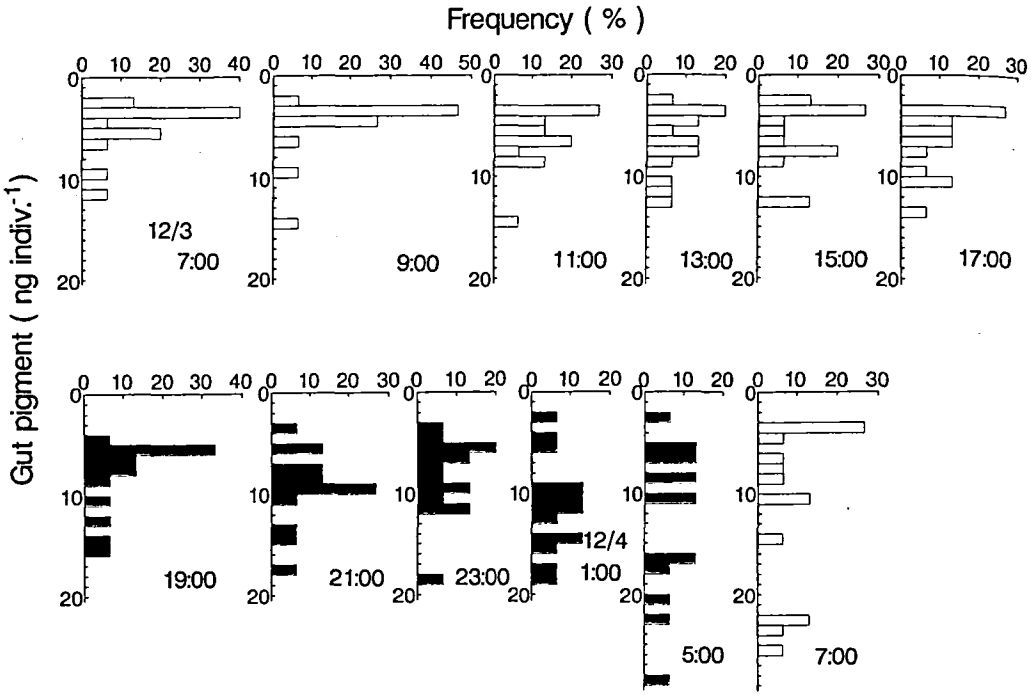

Fig. 7. Frequency distribution of individual gut pigment content of *Calanus sinicus* at each sampling time at ST-7. Open and solid columns denote daytime and nighttime, respectively.

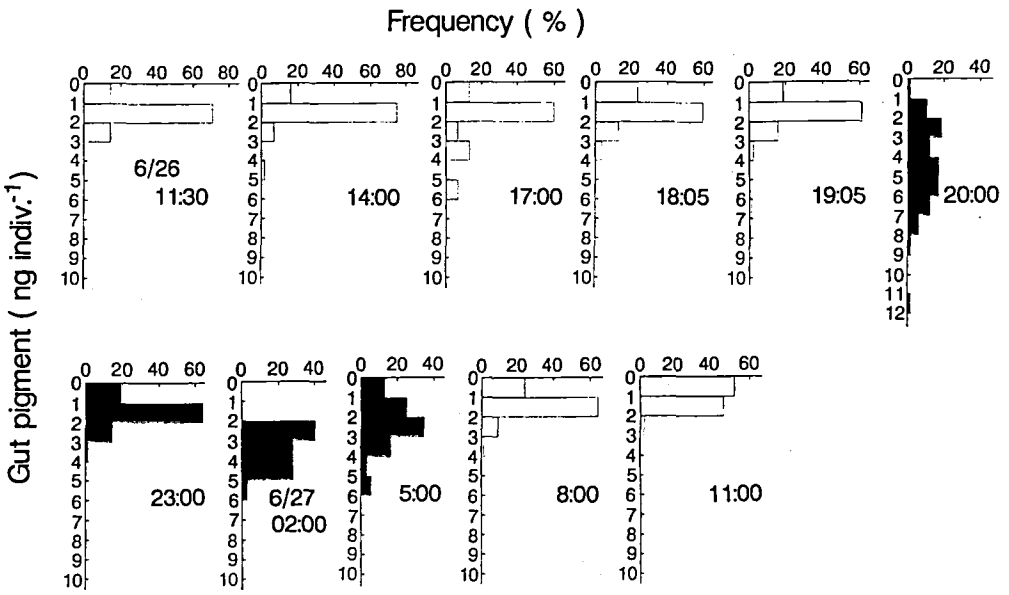

Fig. 8. Frequency distribution of individual gut pigment content of *Calanus sinicus* at each sampling time at ST-8. Open and solid columns denote daytime and nighttime, respectively.

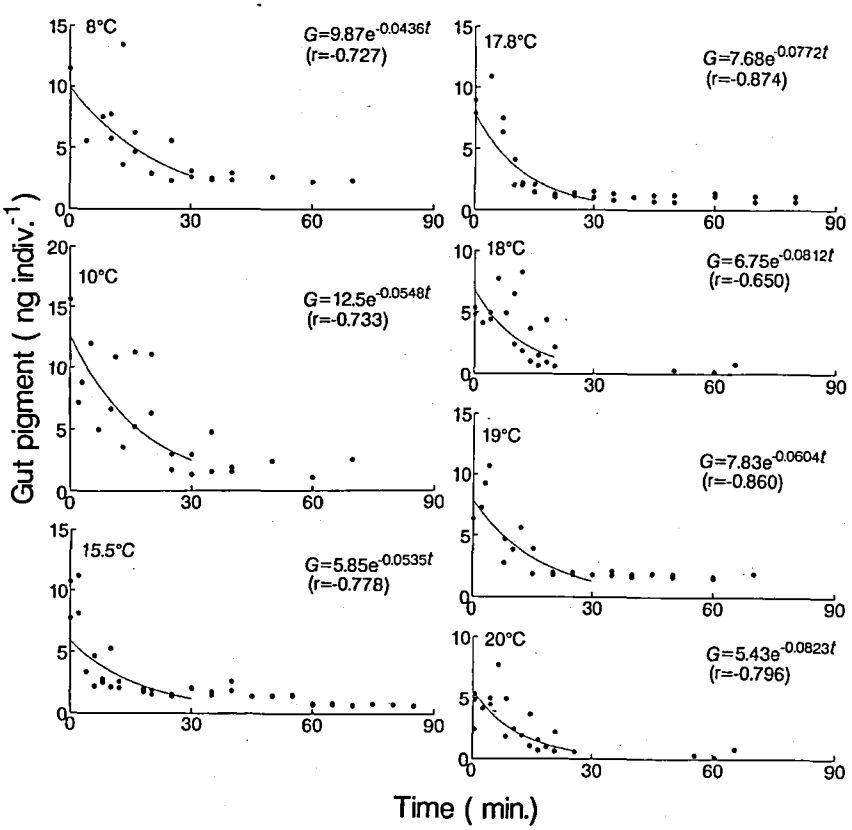

Fig. 9. Decrease of the gut pigment content (G, ng indiv.$^{-1}$) of *Calanus sinicus* with time (T, min) after transfer to filtered seawater at 7 different temperatures. Exponential gut evacuation rate (E, min^{-1}) can be described by the non-linear regression equation: $G=G_0e^{ET}$.

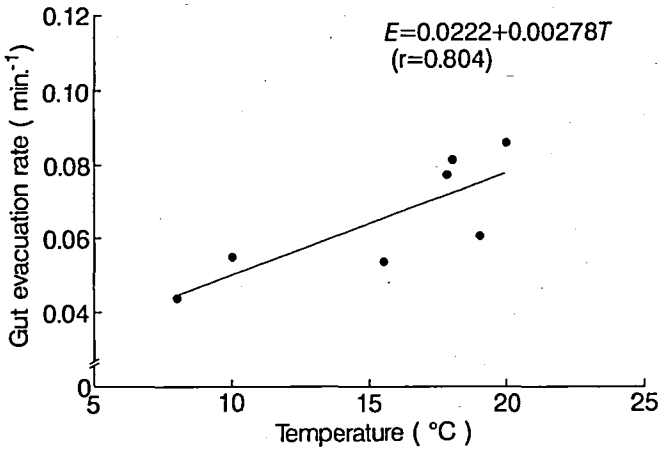

Fig. 10. Relationship between the gut evacuation rate of *Calanus sinicus* and temperature.

Table 1. In situ pigment ingestion rate of *Calanus sinicus* at 3 stations in the Inland Sea of Japan.

Station	Average chlorophyll ($\mu g\ l^{-1}$)	Ingestion rate (ng indiv.$^{-1}$ d^{-1})	Population ingestion rate ($\mu g\ m^{-3}\ d^{-1}$)*
ST-6	0.46	209	135
ST-7	0.79	842	544
ST-8	1.05	212	137

* assuming that the population carbon biomass was 32 mg m^{-3} and the specific ingestion rate was uniform within the population. See text.

expect to see a correlation between the concentration of available food and the degree of fullness of the gut. We conducted egg production experiments concurrently with the present gut pigment investigations, and our unpublished data show that the egg production rate of *C. sinicus* increased with increasing ambient chlorophyll concentration and was never saturated within the range of chlorophyll concentrations encountered. This suggests that the growth rate of this species is food-limited in the Inland Sea of Japan, and implies that gut pigment levels should be positively correlated to ambient chlorophyll levels. On the contrary, *C. sinicus* showed no such correlation (Figures 2 & 3). Absence of the correlation was reported for *Neocalanus plumchrus* and *N. cristatus* (Dagg & Wyman 1983) and also *Calanus glacialis* and *C. finmarchicus* (Tande & Båmstedt 1985). These contrasting results may be due to gut pigment measurements only giving a snapshot of the recent (i.e. minutes to hours) feeding history of copepods, while egg production measurements reflect the feeding condition integrated over several days.

The lack of a positive correlation between gut pigment and ambient chlorophyll may have been due to various causes, among which the large individual variability in gut pigment (Figure 4), that was persistently observed throughout the day (Figures 7 & 8) may be the most important. Such large individual variation is not only characteristic of field-caught copepods (Kleppel et at. 1988, Ohman 1988, Rodriguez & Durbin 1992) but is also commonly observed in copepods in the laboratory even though exposed continuously to their phytoplankton food (Mackas & Burns 1986, Durbin et al. 1990). For example, Durbin et al. (1990) reported that the gut pigment of *Acartia tonsa*, which were kept in a suspension of *Thalassiosira weissflogii* at 8°C, varied ca. 50-fold during the day and 100-fold at night, being of a much larger variability than that observed in *C. sinicus* in the field (max: 13-fold). These studies indicate that the feeding of copepods is intermittent and not synchronous within the whole population even under a continuous food supply.

A rapid increase in gut pigment concentration has been commonly observed when starved copepods are transferred to a phytoplankton suspension (Figure 5, Mackas & Bohrer 1976, Mackas & Burns 1986), and their feeding is probably synchronous until their guts are filled. After peaking, their gut pigment content decreases and, at the same time, feeding synchronization is probably lost, since feeding episodes are probably randomly phased between individuals once they have filled their guts. Intermittent feeding activity was indicated by the occasional peaks in the gut pigment of *C. sinicus* maintained in a food suspension (Figure 5). Hence, gut fullness of copepods might be regulated by episodic on-off feeding

activity even if food is continuously available.

Since *C. sinicus* is omnivorous, the variability in gut pigment content may result from different degrees of omnivory by individual copepods. Microzooplankton such as copepod nauplii and nonpigmented heterotrophic ciliates have been shown to be important prey for copepods of the genus *Calanus* (Landry 1981, Ohman & Runge 1994), and are likely to have contributed significantly to the diet of *C. sinicus* particularly at stations where the preferred size class of phytoplankton prey was scarce. Heterogeneity in phytoplankton spatial distribution and differences in copepod body size may also be additional factors influencing the variability. To reduce such individual variation, it is recommended to pool the data from as many grouped copepods as possible.

The gut evacuation rate of *C. sinicus* was temperature-dependent, as found for other copepod species (Kiørboe et al. 1982, Dagg & Wyman 1983, Dam & Peterson, 1988). Dam & Peterson (1988) combined their data together with those reported previously and proposed the following linear regression equation to describe the composite relation between the gut evacuation rate of copepods (E, min^{-1}) and temperature (T, °C):

$$E=0.0117+0.001794T. \quad (3)$$

Compared to the rates calculated from the above equation (0.0296 and 0.0476 min^{-1} at 10 and 20°C, respectively), the gut evacuation rates of *C. sinicus* calculated from equation (1) were higher (0.050 and 0.0778 min^{-1}, respectively), indicating that this species has higher gastric activity. This, in turn, demands rapid handling from sample collection to pigment extraction, since gut contents may continue to be evacuated during that period. In our study, copepods were soaked in DMF within 5 min of collection. If copepods were starved for the 5 min at 20°C, ca. 30% of their initial gut pigment would have been lost. Accordingly, our pigment data were underestimated and this might also contribute to the high variability between individuals. To reduce this problem, copepods upon collection should immediately be frozen, e.g. in liquid nitrogen, or anesthetized, e.g. in 3-aminobenzoic acid ethyl ester (MS-222) solution (Ohman 1988, Durbin et al. 1990) or carbonated water (Kleppel et al. 1988), prior to sorting.

Although we investigated the diel feeding periodicity at only 3 stations during different seasons, we always observed a strong diel feeding rhythm (Figure 6), as widely reported among other marine copepods (Dagg et al. 1989, Durbin et al. 1990, Ishii 1990, Checkley et al. 1992, and others). *Calanus sinicus* performs a pronounced diel vertical migration (Uye et al. 1990, Huang et al. 1992), but this behavior is likely to be induced by exogenous factors, e.g. abundance of predators (Ohman et al. 1983, Bollens & Frost 1989, Huang et al. 1993b). Diel feeding periodicity is commonly seen in copepods both in the presence of diel migration (Simard et al. 1985, Båmstedt & Tande 1988, Dagg et al. 1989) and in its absence (Head et al. 1985, Daro 1988). This implies that diel rhythm in feeding is endogenous and is probably triggered by a diel change in light intensity (Stearns 1986).

The coefficient of variation can be used as an index of the synchrony of

individual feeding events. Results obtained at ST-7 and 8 (Figures 7 and 8) showed no consistent day/night difference in synchrony. The sharp increase in gut pigment content immediately after the evening twilight, as seen at ST-8 (Figure 6), was not the result of synchronized feeding but rather simply the result of an elevation in the mean gut content (see Figure 8, at 20 h). The above results suggest that highly synchronized feeding, as shown implicitly in the case of exposure to phytoplankton prey after starvation (Figure 5), seldom occurs in natural *C. sinicus* populations (see also Figure 4) and that synchrony is not required for active feeding (Kleppel et al. 1988, Rodriguez & Durbin 1992).

The gut pigment levels observed in *C. sinicus* were similar to those found in *C. pacificus* whose body size is comparable (prosome length: 2.0 to 2.5 mm). The maximum gut pigment content of *C. sinicus* observed under laboratory and field conditions was 21.6 and 28.2 ng indiv.$^{-1}$, respectively. Gut pigment levels of 30 to 50 ng indiv.$^{-1}$ were observed for *C. pacificus* fed dense concentrations of cultured algae in the laboratory (Mackas & Burns 1986). Typical pigment levels for *C. pacificus* in the field are 4 to 14 ng indiv.$^{-1}$ (Dagg et al. 1989, Landry et al. 1994), although values as high as 50 to 80 ng indiv.$^{-1}$ have been observed (Kleppel & Pieper 1984, Ohman 1988).

Aspects of the degradation of pigments in the copepod gut have been hotly debated over the last decade (cf. Conover et al. 1986, Wang & Conover 1986, Kiørboe & Tiselius 1987, Mayzaud & Razouls 1992). Estimated rates of degradation have varied from 0 (Ishii 1990) to 99% (Conover et al. 1986), averaging ca. 30% (Dam & Peterson 1988). The evidence regarding pigment degradation is still conflicting, as the methods used to examine it are subject to a variety of errors (Durbin et al. 1990, Peterson et al. 1990). No correction was made for pigment degradation in the calculation of ingestion rates for *C. sinicus* (Table 1) in this study.

We have attempted to estimate the grazing impact of the *C. sinicus* population upon the phytoplankton standing stock. As we did not sample for copepod biomass during this study, we assume a biomass (copepodites and adults) of 32 mg C m^{-3} for ST-6, 7 and 8, the average biomass in Osaka Bay in June 1985 (Uye unpublished data). We also assume that the specific ingestion rate is uniform within the population. The pigment ingestion rate by the whole population is calculated to be 135, 544 and 137 μg m^{-3} d^{-1} at ST-6, 7 and 8, respectively (Table 1), which corresponds to 29, 85 and 13% of the chlorophyll standing stock at each respective station. These results indicate that *C. sinicus* can play a significant role as a phytoplankton grazer in the Inland Sea of Japan.

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