# Grazing of Various Developmental Stages of Pseudodiaptomus marinus (Copepoda : Calanoida) on Naturally Occurring Particles[1,2]

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## Abstract

Comparative grazing experiments of various developmental stages and sexes of the inshore marine copepod *Pseudodiaptomus marinus* on naturally occurring particles were carried out. The feeding behavior was similar between both sexes of the adult, but different between developmental stages. The adult females were capable of consuming almost all particles from 2.8 to 63.3 $\mu$m diameter, showing selectivity for larger particles (ca. 50 $\mu$m) where the peak of particle concentration occurred. The nauplii consumed mainly smaller particles ($<30 \mu$m). The consumption by copepodites was intermediate between that of the nauplii and adult females, since they fed upon both smaller and larger particles. Such intraspecific differences of grazing behavior may lead to the effective utilization of heterogeneous natural food resources.

The ingestion rates of the adult females increased linearly with the increase of particle concentrations, without indications of the threshold nor saturation response. The amount of ingested carbon rarely met the requirement for potential egg production which was observed for the wild population. Thus, it was surmised that the adult females could ingest sufficient food deposited on the sea-bottom during a daytime epibenthic phase to attain predicted egg production.

Since the copepods are the major constituents of the herbivorous zooplankton, their feeding behavior has been studied by numerous workers (MARSHALL 1973, CONOVER 1978a, for review). Despite this, many questions still remain unanswered. One of the questions which has not been fully answered is how feeding behavior differs between developmental stages and sexes. Most studies have been conducted with adults, usually adult females. However, younger stages are usually much more abundant than older stages in natural copepod populations. Therefore, to estimate their grazing impact, it is necessary to know how grazing behavior changes through development. The grazing of various developmental stages has been compared for laboratory-reared copepods (MULLIN & BROOKS 1967, 1970, HARRIS & PAFFEN-HÖFER 1976, PAFFENHÖFER 1971, PAFFENHÖFER & HARRIS 1976) fed with cultured phytoplankton. However, no work, to our knowledge, has been performed on the grazing of immature stages of copepods on naturally occurring particles, except for works by ALLAN et al. (1977) and POULET (1977). The second question is how the feeding rate of copepods is affected by the change in concentration of available food. Saturation-type feeding (i.e. ingestion rate is proportional to concentration of food up to a certain level, above which it becomes

constant or "saturated") has been frequently observed in laboratory studies (CORNER et al. 1972, FROST 1972). Saturation of ingestion rate has also been observed for copepods feeding on natural phytoplankton assemblages (PARSONS et al. 1967). On the contrary, CONOVER (1978b) and MAYZAUD & POULET (1978) have criticized the saturation-type model, and proposed a linear model to describe the relationship between feeding rate and food supply under natural conditions.

The present investigation has been conducted primarily to answer above-mentioned questions by examining the grazing of the inshore marine copepod *Pseudodiaptomus marinus* on naturally occurring particles.

## Materials and Methods

Since our preliminary data showed that *P. marinus* is most abundant in early summer and fall (UYE et al. 1982, 1983), the present feeding experiments were carried out by using specimens from the fall population peak of 1978-1982, when the surface water temperature at the sampling sites ranged from 16.8 to 22.3°C. The water samples were taken at Tomo, Fukuyama, with a 6-1 Van Dorn water bottle at a depth of ca. 5 m. Zooplankton were collected by vertical or oblique tows with a 0.45 m net (330 μm mesh opening) either at Tomo or Fukuyama Harbor, the distance between these sites being ca. 10 km. Since adults of *P. marinus* are nocturnal migrators, i.e. they are distributed rather homogeneously in the water column at night (VALBONESI & HARADA 1980), only the nighttime collections yielded a sufficient catch of this species. Hence, sampling was usually made from 19 to 22 hrs local time. Zooplankton concentrated in the cod-end were diluted into 2-1 plastic bottles containing surface seawater, which were then filled to the top with additional seawater before being screw-capped. The water and animals were then transported to the laboratory, which required ca. 30 min.

Adult females and males of *P. marinus* were sorted from the mixed zooplankton samples with pipettes and used immediately for grazing experiments. However, nauplii and copepodites were so rare in these samples that they were obtained from a stock culture. To begin the stock culture, several hundred gravid females were sorted into 2-1 glass dishes containing glassfiber (Whatman GF/C) filtered seawater. After the nauplii were permitted to hatch from eggs for a period of 2 days, they were transferred to 1-1 glass beakers containing filtered seawater with *Pavlova lutheri*, *Dunaliella tertiolecta* and *Thalassiosira* sp. added as food. They were kept in a constant temperature room (20-22°C, 12L-12D light cycle). Nauplii (NV and VI) were sorted from the beakers after 7-9 days of culture by taking advantage of their positive phototaxis, and copepodites (CIII-V) were individually pipetted after 14-17 days of culture.

First, we examined differences in the feeding behavior of various developmental stages and sexes of *P. marinus* in response to the same size composition of the food particles. For each grazing experiment, 20 adult females and males, 40 copepodites and several hundred nauplii were picked out, rinsed with filtered seawater and each group was placed into a 500 ml glass bottle containing natural seawater filtered through a 102 μm sieve to remove larger

particles. Each bottle was wrapped with a dark vinyl bag and attached to a grazing wheel rotating at 1–2 rpm. The experiments were run for 15–24 h in a temperature controlled room (20–22°C). At the end of the experiments, the copepods were checked for survival and removed by sieving with a 102 μm mesh net. The animals were preserved with formalin for later analysis of developmental stages and body length measurement. The particle size distribution of the seawater before and after the experiment was determined with a Coulter Counter (Model B or ZB) using an orifice of 140 μm diameter. The quantity of particles consumed for each size group was calculated from the difference of the particle concentration before and after the grazing.

Second, we conducted a series of grazing experiments with adult females of *P. marinus* in order to observe the relationship between their ingestion rate and particle concentration of the seawater. During the course of this experiment, we occasionally observed the formation of several small lumps of aggregates of 2–3 mm diameter in the grazing chambers. Since these lumps were removed by sieving with a 102 μm mesh net, the lump formation caused overestimation of the copepod ingestion rate. The decrease of particle concentration due to aggregate formation in control bottles (containing no animals) ranged from 18.9 to 26.0 % (mean: 22.0 %) of the initial concentration for the seawater with concentrations from 3.10 to 4.47 ppm. Visual observations indicated that the aggregate formation was more pronounced in control bottles than in grazing bottles, because of more water agitation in grazing bottles by copepod feeding activity. We assumed rather arbitrarily that the decrease of particle concentration in grazing bottles was one half in control bottles (i.e. 11 % of the initial concentration), since the degree of the lump formation in grazing bottles was impossible to measure.

For discussion of the allocation of ingested energy in the adult female, particulate organic carbon (POC) concentrations were measured using a CHN analyzer (Yanagimoto Co., Model MT-3), after filtering the natural seawater, which had been prefiltered through a 102 μm sieve, with a precombusted glassfiber filter (Whatman GF/C). The respiration rate of adult females was measured by incubating 40–45 individuals into several dark BOD bottles (ca. 100 ml) filled with oxygen-saturated seawater for 18–20 h at 20°C. The growth rate was estimated from data on egg production (UYE et al. 1982).

## Results

### *Grazing of Various Developmental Stages and Sexes*

Six grazing experiments were carried out to examine differences in the grazing behavior between nauplii, copepodites and adult females (Experiments I & II), between nauplii and adult females (Experiments III & IV) and between adult females and males (Experiments V & VI) (Figs. 1 and 2). The particle size distribution of the natural seawater differed in each experiment, but larger particles (ca. 50 μm diameter) were most abundant in most of the experiments. The smaller particles (ca. 5 μm) were also abundant in Experiments II–IV, showing bimodal distribution. Microscopic observation revealed that *Ditylum brightwellii* constituted the larger particles and unidentified flagellates were the major constituents of the smaller
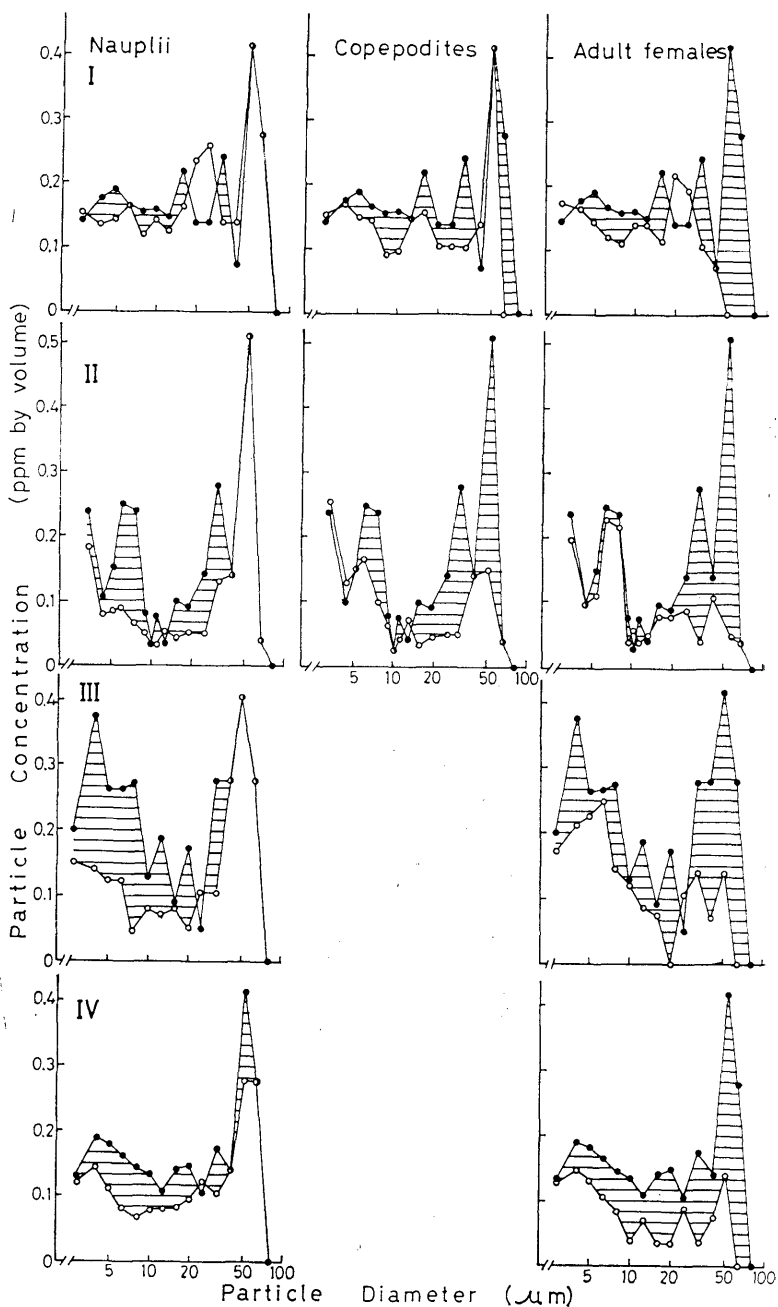
Fig. 1. Comparative feeding between nauplii, copepodites and adult females of *Pseudodiaptomus marinus* on natural particles. Particle size-biomass distribution before and after the grazing is expressed as filled and open circles, respectively. Hatched area denotes consumption by grazing.
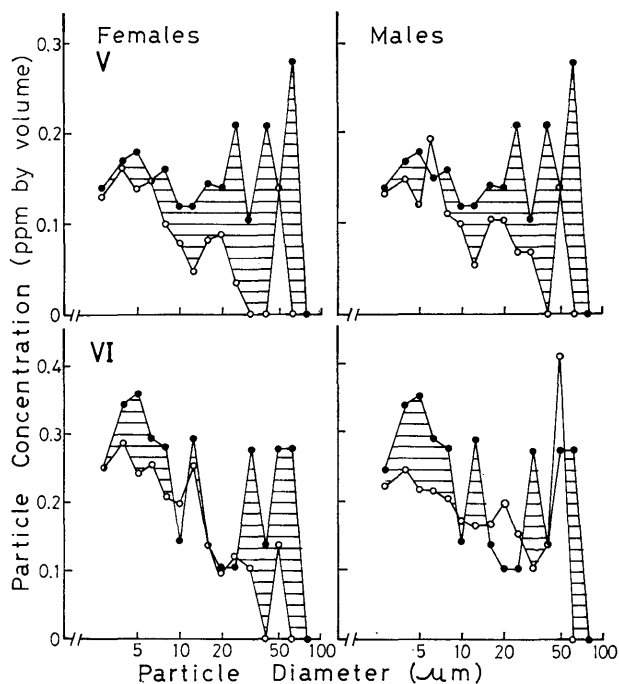
Fig. 2.  Comparative feeding between adult females and males of *Pseudo-diaptomus marinus* on natural particles. Symbols as in Fig. 1.

particles.  Nonliving organic particulate matter was abundant throughout the experiments. The total particle concentration varied from 2.263 ppm in Experiment V to 3.297 ppm in Experiment VI.  Adult females were able to consume almost all particles from 2.8 to 63.3 $\mu$m diameter.  Their consumption, however, differed greatly depending on particle size and concentration.  The particles of ca. 50 $\mu$m diameter were always grazed most abundantly by the adult females, indicating higher feeding selectivity for larger particles.  The peaks of smaller and intermediate particles were also grazed at slightly higher rates than particles between peaks, with the exception of Experiment II, where they grazed few on the peak of small particles.  On the other hand, the particles consumed by nauplii were predominantly those smaller than ca. 30 $\mu$m diameter, the peak of larger particles was not consumed, excepting in Experiment IV.  Copepodites were able to consume larger particles, as were adult females. However, in Experiment II, they grazed the peak of smaller particles as did nauplii, while adult females did not graze it well.  It was also observed that the particles with biomass peaks were abundantly consumed; this was especially apparent in Experiment II.  Fig. 2 shows that the feeding behavior of adult males was essentially the same as that of adult females, while a slight difference was observed in the consumption of particles with 12 and 50 $\mu$m diameter in Experiment VI.

We calculated the feeding efficiency, i.e. the rate of consumption of each particle size category in terms of percentage of the initial particle concentration (Fig. 3).  In this case, the

feeding efficiency of the negative consumption was assumed to be zero.　For all developmental stages, the efficiency was not homogenous over the spectra, indicating selective feeding on certain size categories.　The rate was always higher on larger particles for adult females and copepodites, but on smaller and intermediate particles for nauplii.　Fig. 3 also indicates that higher efficiencies often coincided with the biomass peaks, but this was not evident for nauplii.
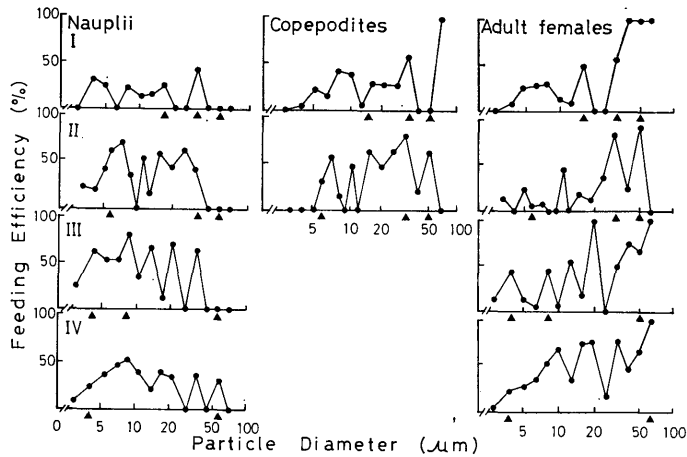


Fig. 3. Comparison of the feeding efficiency of nauplii, copepodites and adult females of *Pseudodiaptomus marinus*.　Triangles denote the position of peaks of particle concentration.
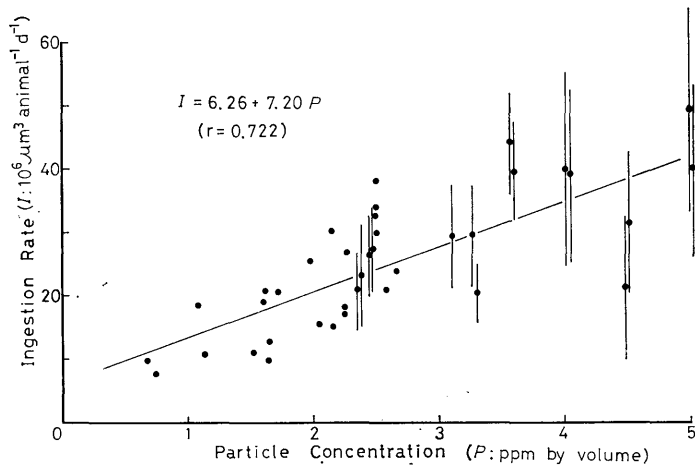


Fig. 4.　Ingestion rates of an adult female of *Pseudodiaptomus marinus* at various particle concentrations expressed as volume. (See text)

### Ingestion Rates of Adult Females at Various Particle Concentrations

A total of 38 grazing experiments were performed in seawater with particle concentrations ranging from 0.66 to 5.02 ppm.　The aggregated lump formation was observed on 15 occasions, where the total particle concentrations were higher than 2.38 ppm.　In these cases, the ingestion

rates were expressed as vertical bars (Fig. 4).  When aggregate formation is as abundant as in controls, the rate become the lower end of the bar, but when aggregate formation is few, it is close to the upper end of the bar.  The relationship between ingestion rate ($I$, in $10^6 \mu m^3 \cdot$ animal$^{-1}$ d$^{-1}$) and particle concentration ($P$, in ppm) is shown in Fig. 4.  Minimization of the sum of square variance was used as the criterion for fitness of the models.  The best fit to the data was a linear model rather than a rectilinear or curvilinear model, although the difference of the variance was minor between these models, given by the following equation:

$$I = 6.26 + 7.20\,P \quad (r = 0.722).$$

These results indicated that neither feeding saturation nor cessation took place for *P. marinus* within the range of particle concentration of the present study.

*Ingestion Rates of Adult Females in Relation to Respiration and Growth Rates*

The relationship between particle volume concentration ($P$, in ppm) and particulate organic carbon concentration (POC, in $\mu$gC $\cdot$ l$^{-1}$) was determined for 34 seawater samples with volume concentration ranging from 1.07 to 7.70 ppm, giving the following equation (Fig. 5):

$$POC = 101.8 + 97.8\,P \quad (r = 0.923).$$

By using this regression equation, the data from the grazing experiments were converted from the particle volume basis to carbon basis (Fig. 6).  The ingestion rate ($Ic$, in $\mu$gC) can be expressed as:

$$Ic = -0.12 + 0.0072\,POC.$$

The respiration rate of an adult female of *P. marinus* was calculated as 2.83 $\mu$lO$_2 \cdot$animal$^{-1}$ d$^{-1}$.  Assuming the respiration quotient (RQ) is 0.8, an animal respired 1.21 $\mu$gC $\cdot$ d$^{-1}$.  The growth rate was estimated from the egg production since somatic growth would be negligible in mature females.  The specific daily egg production rate at 20°C was 0.183 (UYE et al.
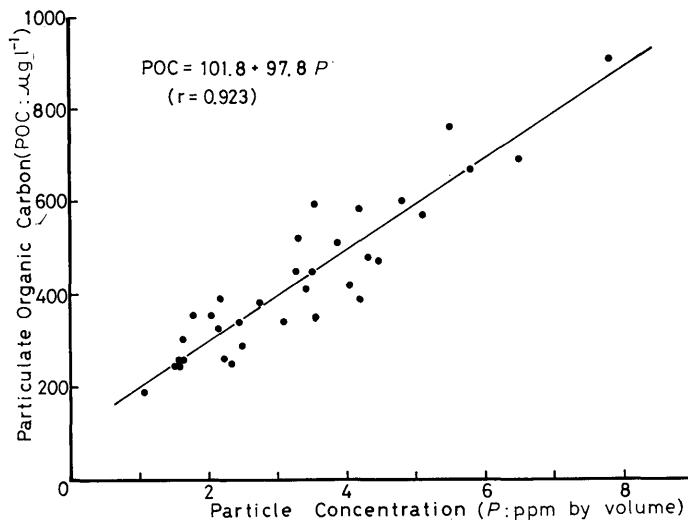


Fig. 5.  Relationship between particulate organic carbon concentration and particle volume concentration.
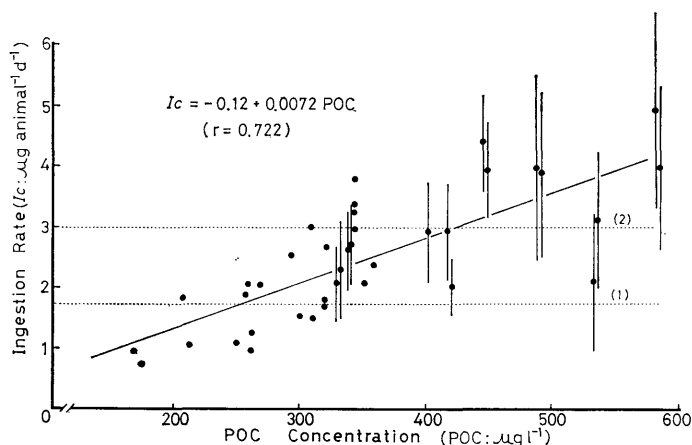
Fig. 6. Ingestion rates of an adult female of *Pseudodiaptomus marinus* at various particle concentrations expressed as carbon. Lines denote the estimated food requirements for metabolism (1), and for metabolism plus predicted egg production (2).

1982), which, multiplied by the average body carbon weight of an animal (4.89 $\mu$gC), gives the daily egg production rate: 0.89 $\mu$gC $\cdot$ animal$^{-1}$ d$^{-1}$. The ingestion rates which would be needed for metabolism and metabolism plus predicted egg production were calculated using an assimilation efficiency of 0.7 as 1.73 and 3.00 $\mu$gC $\cdot$ animal$^{-1}$, respectively. These tow values are indicated by horizontal lines in Fig. 6. The ingestion rates were usually higher than the requirement for metabolism, but in 9 experiments at lower concentrations, the ingestion rates did not meet that requirement. The ingestion rates more than estimated to be necessary for egg production were observed in 11 experiments at higher concentrations. In most cases, the animal ingested more than for metabolism, but less than for potential egg production.

## Discussion

### *Grazing of Various Developmental Stages and Sexes*

There was no discernible difference in grazing behavior between adult females and males of *P. marinus*, while the difference was apparent between developmental stages (Figs. 1 & 2). In studies using laboratory cultures of algae, many investigators have reported that adult females of copepods filter larger cells at higher rates than the smaller cells (MULLIN 1963, RICHMAN & ROGERS 1969, PAFFENHÖFER 1971, FROST 1972, 1977). This fact is commonly attributed to a better retention efficiency for larger particles by filtering setae (NIVAL & NIVAL 1976, FROST 1977). However, in studies using natural particle assemblages of seawater (POULET 1973, 1974), adult females of *Pseudocalanus minutus* were able to consume particles between 4 and 100 $\mu$m diameter, but on the average intermediate particles were more readily eaten than the larger particles. They opportunistically shifted their grazing pressure from one size range to another depending on where the particle peak occurred. RICHMAN et al.

(1977) also investigated the grazing of adult females of *Eurytemora affinis*, *Acartia tonsa* and *A. clausi* on natural distributions of particles. These three species demonstrated similar capabilities for grazing over a broad range of particle size, with selection on larger particles as well as biomass peaks. The results of the grazing experiment on multiple-peak distributions suggested that the copepods first fed on larger particles and then successively switched to biomass peaks of smaller size categories. This phenomenon can not be explained solely by the simple mechanical filtering by a fixed sieve of the feeding appendages. In the present experiment, the particle size was most important for adult females of *P. marinus* since they always showed higher selectivity for large-sized particles, where the biomass peak also occurred. The shift of grazing pressure from larger particles to smaller ones was not obvious.

Since copepodites of *P. marinus* could consume larger particles, their grazing behavior is more like that of adult females. However, smaller and intermediate particles were more important for them than for the adults. Copepodites may possess the feeding appendages as functional as those of the adults, but they have smaller mesh size than the adults as demonstrated for *Acartia clausi* by NIVAL & NIVAL (1976). POULET (1977) examined the grazing of copepodites of *Pseudocalanus minutus* on naturally occurring particles, consisting mainly of smaller particles ($<22\,\mu$m diameter). The importance of fine particles was also suggested for copepodites of this species since they obtained more food than the adults on particles smaller than 10 $\mu$m. The selective feeding observed in the present study (Fig. 3) is also common for copepodites of other species (ALLAN et al. 1977, POULET 1977).

In comparison with the feeding of copepodites and adults of *P. marinus*, the most striking difference observed in the nauplii was incapability of grazing on larger size categories (Figs. 1 & 3). MULLIN & BROOKS (1967) and FERNÁNDEZ (1979a) observed the same difference of laboratory-reared *Calanus pacificus*, i.e. its nauplii could not consume larger diatoms fed upon by the adults. As great morphological changes occur by metamorphosis from nauplius to copepodite, the change of feeding behavior is convincing. On the contrary, in comparative feeding experiments for nauplii and copepodites of *Eurytemora affinis* and *Acartia* spp. on natural particles, ALLAN et al. (1977) did not observe any difference in their capability to consume particles of different sizes. The selective grazing by copepod nauplii was rejected by ALLAN et al. (1977), but this was supported by the present investigation since nauplii of *P. marinus* appeared to consume at disproportionately higher rates on certain size categories within the range capable to handle (Fig. 3). However, the biomass peaks were not always grazed most by them. Selective feeding was also reported by FERNÁNDEZ (1979b) for nauplii of *Calanus pacificus*, using cultured phytoplankton, plastic beads, pollen grains and detritus as food.

In natural conditions the particle distribution is heterogeneous, i.e. the size and concentration change in space and time. In such a dynamic system, copepods may adapt to the change of particle distribution. Obviously, the selective grazing on larger particles as well as biomass peaks may convey advantage in maximizing energy intake and lead to minimizing the dominance of certain size categories (POULET 1973, 1974). Since the copepod community

consists of various species and developmental stages, we should consider intra- and interspecific competition for the same food resources. POULET (1978) compared co-existing adult females of five copepod species (*Pseudocalanus minutus*, *Temora longicornis*, *Eurytemora herdmani*, *Acartia clausi* and *Oithona similis*) on natural particles. All these copepods reacted similarly and simultaneously to the change of particle size spectrum by shifting their grazing pressure from one size range to another, indicating severe interspecific competition. HARRIS (1982) also reported that the interspecific competition was important in resource partitioning, from the comparative examination of the grazing behavior of small-sized *Pseudocalanus minutus* and large-sized *Calanus pacificus*. The grazing behavior revealed in the present study (Figs. 1–3) and the data of POULET (1977) provide the evidence that feeding niches are separated between nauplii, copepodites and adults. Therefore, the natural food resources can be utilized effectively by reducing intraspecific competition.

*Ingestion Rates of Adult Females at Various Particle Concentrations*

In the present experiment, the seawater for food suspension and experimental grazers were not always taken from the same location. However, *P. marinus* from Fukuyama Harbor behaved similarly to *P. marinus* from Tomo and to the change of natural food environment at Tomo. Its ingestion rates were totally dependent on the particle concentration without any apparent indication of the threshold nor saturation response (Fig. 4). This was contradictory to our unpublished data that *P. marinus* showed a typical saturation-type functional response when fed with cultured *Thalassiosira* sp. and *Chattonella antiqua*. The reason for this inconsistency was given by CONOVER (1978b) and MAYZAUD & POULET (1978). They found a linear relationship between ingestion rate of five copepod species and naturally occurring particle concentration from a year-course investigations. They criticized the saturation-type of feeding, suggesting that it was perhaps an artifact resulting from too sudden exposure to increasing the amount of a single food source. The planktonic copepods were capable of adapting to the change of heterogeneous natural food by regulating their digestive enzyme activity. However, a short period of time (18–20 h) was not enough for acclimation of the digestive system (MAYZAUD & POULET 1978). Similarly, nonsaturated feeding was reported by REEVE & WALTER (1977) for *Acartia tonsa* and by HUNTLEY (1981) for three species of the genus *Calanus* on natural particles covering the whole range of the annual fluctuation. The particle concentration used in the present study did not cover the whole range encountered in nature by *P. marinus*. We therefore can not conclude that the saturated feeding never occurs in nature. However, the concept of a critical concentration may be ecologically meaningless at least within the range of the particle concentration between 0.66 and 5.02 ppm ($=166$ and $593 \,\mu\text{gC} \cdot \text{l}^{-1}$).

The present experiment demonstrated that the amount of carbon ingested by *P. marinus* rarely exceeded the requirement for predicted egg production (Fig. 6). On several occasions, the ingested carbon was not enough even for metabolic requirement (Fig. 6). These data suggest that the growth rate of *P. marinus* is dependent on food supply in nature. However, our previous findings did not support this. We found that in situ egg production rates were

temperature-dependent rather than food-dependent, since the rates were always higher for field populations than for laboratory populations fed with cultured phytoplankton ad libitum (UYE et al. 1982). There is no diel feeding periodicity for *P. marinus*, since they egested equal numbers of fecal pellets both in daytime (illuminated) and nighttime (darkened). Probably, *P. marinus* can ingest plentiful food deposited on the sea-bottom during a daytime epibenthic phase to attain the potential egg production.

## Acknowledgements

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