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Rates of ingestion and their variability between individual calanoid copepods: direct observations

G.-A. Paffenhöfer¹, M.H. Bundy^{1,3}, K.D. Lewis¹ and C. Metz²

¹Skidaway Institute of Oceanography, 10 Ocean Science Circle, Savannah, GA 31411, USA and ²Alfred-Wegener-Institut für Polar- und Meeresforschung, 2850 Bremerhaven, FRG

³Present Address: Great Lakes Environmental Research Laboratory, 2205 Commonwealth Boulevard, Ann Arbor, MI 48105, USA

Abstract. The goals of this study were to determine rates of ingestion and fecal pellet release, and their variability, for individual planktonic copepods over extended periods of time (>20 min). Ingestions and rejections of individual cells of the diatom *Thalassiosira eccentrica* by adult females of the calanoid *Paracalanus aculeatus* were directly quantified by observing individual copepods continuously at cell concentrations ranging from 0.1 to 1.2 mm³ l⁻¹. Average ingestion rates increased with increasing food concentration, but were not significantly different between 0.3 and 1.0 mm³ l⁻¹ (9.8 and 32.7 µg C l⁻¹) of *T. eccentrica*. Rates of cell rejections were low and similar at 0.1 and 0.3, but were significantly higher at 1.0 mm³ l⁻¹. The coefficients of variation for average ingestion rates of individual copepods hardly differed between food concentrations, ranging from 17 to 22%, and were close to those for average fecal pellet release intervals which ranged from 15 to 21%. A comparison between individuals at each food concentration found no significant differences at 1.0; at 0.1 and 0.3 mm³ l⁻¹, respectively, ingestion rates of four out of five females did not differ significantly from each other. Average intervals between fecal pellet releases were similar at 0.3 and 1.0 mm³ l⁻¹ of *T. eccentrica*, but significantly longer at 0.1 mm³ l⁻¹. Fecal pellet release intervals between individuals were significantly different at each food concentration; these significant differences were attributed to rather narrow ranges of pellet release intervals of each individual female. Potential sources/causes of variability in the sizes and rates of copepods in the ocean are evaluated.

Introduction

To exist and persist in an almost continuously food-limited and hostile environment, copepods have to find and capture food as well as avoid predators. These topics have been addressed repeatedly over decades in numerous publications (for references, see Ohman, 1988; Price, 1988). Despite these efforts, our understanding of the breadth of copepod behavioral ranges, the degrees of variability, and their causes, has advanced at a modest pace. This can partly be explained by the scarcity of interdisciplinary research, by the emphasis on larger scale (spatial and temporal) studies in the ocean, and by the lack of faith that behavioral observations would result in major advances in knowledge of copepod performances, i.e. emphasizing holistic and de-emphasizing mechanistic approaches.

The significance of observing freely moving zooplankters over time in larger volumes of water and eventually *in situ* has already been pointed out (e.g. Omori and Hamner, 1982; Marine Zooplankton colloquium 1, 1989) and the importance of observations on a copepod's temporal and spatial scales has been demonstrated (e.g. Price *et al.*, 1983). After short-term observations (several seconds) of restrained and free-swimming copepods (Strickler, 1982; Paffenhöfer and Lewis, 1989), we took the next step by following free-swimming copepods continuously for extended periods on their activity scales of micrometers and milliseconds. We

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intended to quantify ingestion and rejection of food particles by individuals as well as fecal pellet release frequency in relation to food concentration, and to improve our understanding of the interindividual variability of those variables.

Method

Adult fertilized females of the calanoid copepod *Paracalanus aculeatus*, which occurs abundantly on the middle and outer shelf off the southeastern USA (Bowman, 1971), were observed at 20°C in darkness. These animals were reared from hatching to adulthood at 0.1–0.3 mm³ l⁻¹ each of the flagellate *Rhodomonas* sp. (~300 µm³ cell volume, ~174 µg C mm⁻³) and the dinoflagellate *Gymnodinium nelsoni* (~25 000–45 000 µm³, ~130 µg C mm⁻³) in volumes of 960 and 1920 ml on a Ferris wheel rotating at 0.2 r.p.m. at 14 h light/10 h darkness. Within 1–2 days of reaching adulthood and being fertilized, the females were placed in 1920 ml jars and pre-conditioned at the respective food concentrations near 0.1, 0.3 and 1.0 mm³ l⁻¹ (3.3, 9.8 and 32.7 µg C l⁻¹, respectively; Strathmann, 1967) of the diatom *Thalassiosira eccentrica* (~20 000–35 000 µm³) for 24–48 h. One to three females were then gently placed into cuvettes filled with 1000 or 3000 ml of copepod pre-conditioned filtered seawater with the respective concentration of *T. eccentrica*. The activity of individual females was videotaped on S-VHS (60 frames s⁻¹) by following each copepod with a motorized three-dimensional stage made by DAE-DAL, Harrison City, PA, on which a laser diode (830 nm) and a Pulnix TM-745 camera were mounted with their respective optics. This instrument resembled closely the Critter Cam® designed by J.R. Strickler, as shown in Strickler (1985). The field of observation was ~16 × 10 mm, at which a resolution of ~15 µm was attained, allowing us to follow individual diatom cells as they were displaced towards the copepod, captured and at times rejected. The entire 21–73 min of observations of each copepod were analyzed. If a cell was captured and not rejected during the following seconds, it was assumed to have been ingested. Active rejection of a cell usually occurred within less than one to several seconds after capture. Also, fecal pellet releases were recorded. Analyses of the times of cell captures and rejections, and pellet releases, were made with motion-analysis software by Peak Performance, Inc., Boulder, CO.

Results

Comparison of Average Rates

We visually observed the ingestion of individual cells of *T. eccentrica* by five females at 0.10–0.14 mm³ l⁻¹, by five females at 0.30–0.34 mm³ l⁻¹ and by six females at 1.0–1.2 mm³ l⁻¹. Individual copepods were observed over a period of 21–73 min and each animal's mean ingestion rate (cells ingested min⁻¹) was calculated (Figure 1). The mean ingestion rates increased from 0.1 to 0.3 [significant at $P < 0.01$, Kruskal-Wallis Test, and Multiple Comparison Test (Conover, 1980)] and were not significantly different between 0.3 and 1.0 mm³ l⁻¹ (Figure 1). Maximum ingestion rates were reached near 0.3 mm³ l⁻¹ of *T. eccentrica* which equals 9.8 µg C l⁻¹. At this food level, a *P. aculeatus* female ingested daily 52.6% of its body carbon. The clearance rates decreased non-linearly with increasing food concentration (Figure

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Fig. 1. Average ingestion rates of individual adult females of *P. aculeatus* at different concentrations of the diatom *T. eccentrica*. Vertical bars represent ± 1 SE.

2). The average number of actively rejected cells, i.e. captured and then rejected, did not differ between 0.1 and 0.3 mm³ l⁻¹, but was significantly higher at 1.0 mm³ l⁻¹ ($P < 0.01$; Figure 3). The percentage of gathered cells which were ingested was 85.7 at 0.1 mm³ l⁻¹, 90.3% at 0.3 mm³ l⁻¹ and 39.1% near 1.0 mm³ l⁻¹.

We also included in our observations the average intervals at which fecal pellets were released because they (i) indicate whether an animal is feeding and (ii) can serve as a coarse indicator of feeding activity (Paffenhöfer 1994). The results showed significant differences in release intervals between 0.1 and 0.3 mm³ l⁻¹ ($P < 0.05$), but not between 0.3 and 1.0 mm³ l⁻¹ (Figure 4). The coefficients of variation between averages of ingestion rates and fecal pellet release rates were similar (Table I).

Table I. Individual *P. aculeatus* females feeding on *T. eccentrica*: coefficients of variability between averages (%)

	Food concentration (mm³ l⁻¹)		
	0.1	0.3	1.0
Ingestion rate	19.4	22.2	17.0
Pellet release rate	15.1	21.2	21.0

Comparison of Rates of Individuals

Next we conducted an analysis of variance of rates among individual females at each of the three food concentrations, again using the Kruskal-Wallis Test and, when needed, a Multiple Comparison Test (Conover, 1980). The number of cells ingested was quantified for each period between pellet releases and then normalized to cells ingested min⁻¹. For ingestion rates, the null hypothesis that the rates were identical was rejected for 0.1 and 0.3 mm³ l⁻¹ ($P < 0.05$), but not for 1.0 mm³ l⁻¹.

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Fig. 2. Average clearance rates of individual adult females of *P. aculeatus*.

Fig. 3. Average food particle rejection rates of individual adult females of *P. aculeatus*.

At $0.1 \text{ mm}^3 \text{ l}^{-1}$, the highest value was significantly different from the two lowest values ($P < 0.01$; Figure 1), and at $0.3 \text{ mm}^3 \text{ l}^{-1}$ the lowest value ($1.42 \text{ cells ingested min}^{-1}$) was significantly different from the other four values ($P < 0.05$). The ranges of the coefficients of variation were similar at all three food levels and ranged from 23 to 36% (0.1), 20 to 42% (0.3), and 22 to 38% ($1.0 \text{ mm}^3 \text{ l}^{-1}$). Comparing the intervals between pellet releases at each food concentration resulted in rejection of the null hypothesis that the intervals were identical (Kruskal-Wallis Test). We present these data in detail to illustrate the differences (Tables II–IV). The Multiple Comparison Test revealed significant differences between the three highest and two lowest values at $0.1 \text{ mm}^3 \text{ l}^{-1}$ ($P < 0.05$; Table II). At 0.3 , only two females had similar intervals (Table III) and at $1.0 \text{ mm}^3 \text{ l}^{-1}$ only females 1 and 2, and 4 and 5

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Fig. 4. Average fecal pellet release intervals of individual adult females of *P. aculeatus*.

Table II. Intervals between releases of fecal pellet(s) by individual adult females of *P. aculeatus* at $0.1 \text{ mm}^3 \text{ l}^{-1}$ of *T. eccentrica*

	Female no.				
	1	2	3	4	5
Mean	375	413	427	534	550
n	8	7	7	6	7
± SD	31	20	83	119	59
± SE	11	7.4	31	49	22
CV (%)	8.3	4.7	19.5	22.3	10.7
Range	330-419	385-440	322-598	366-691	446-647

n = number of intervals.
 SD = standard deviation.
 SE = standard error.
 CV = coefficient of variability.

Align column on dec 0, ten and hundreds

(Table IV). The coefficients of variation for the pellet release intervals were low, particularly at 0.3 and $1.0 \text{ mm}^3 \text{ l}^{-1}$, and may explain the significant differences found (see Discussion).

We did not compare rejection rates because they occurred only occasionally at 0.1 and $0.3 \text{ mm}^3 \text{ l}^{-1}$. To illustrate the course of events (ingestion, rejection and pellet release), we display for one female at $0.3 \text{ mm}^3 \text{ l}^{-1}$ (Figure 5, for 3200 s i.e. ~53 min) and another female at $1.0 \text{ mm}^3 \text{ l}^{-1}$ (Figure 6, 3600 s i.e. ~60 min) when ingestions,

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Table III. Intervals between releases of fecal pellet(s) by individual adult females of *P. aculeatus* at $0.3 \text{ mm}^3 \text{ l}^{-1}$ of *T. eccentrica*

	Female no.				
	1	2	3	4	5
Mean	271	278	290	338	447
n	12	6	13	8	7
± SD	19	22	28	24	68
± SE	5.6	9	7.8	8.6	26
CV (%)	7.1	8.0	9.7	7.2	15.2
Range	243-321	247-304	220-331	299-375	381-578

n = number of intervals.
 SD = standard deviation.
 SE = standard error.
 CV = coefficient of variability.

Table IV. Intervals between releases of fecal pellet(s) by individual adult females of *P. aculeatus* at $1.0 \text{ mm}^3 \text{ l}^{-1}$ of *T. eccentrica*

	Female no.					
	1	2	3	4	5	6
Mean	232	250	313	353	354	433
n	6	9	8	8	10	8
± SD	27	30	25	15	31	50
± SE	11	10	8.8	52	9.9	18
CV (%)	11.6	12.1	7.9	4.1	8.8	11.5
Range	178-265	182-281	286-359	332-380	311-408	369-532

n = number of intervals.
 SD = standard deviation.
 SE = standard error.
 CV = coefficient of variability.

Align table columns in dec, ten and hundreds

rejections and pellet releases occurred. The x-axis represents time and the y-axis each of the four periods which make up the entire observational period. When ingestions or rejections were close to each other, one or two of the data points were positioned above/below the respective line to separate each event from the following one. At 0.3 and $1.00 \text{ mm}^3 \text{ l}^{-1}$, ingestions sometimes occurred at irregular, at other times at fairly regular intervals: e.g. at 0.3 between 1600 and 1800 s (Figure 5), at 1.0 from ~2000 to 2200 s (Figure 6). At $0.3 \text{ mm}^3 \text{ l}^{-1}$, rejections were occasional and at irregular intervals, and pellet releases were at near regular intervals during the first 1200 s, becoming longer later. At $1.0 \text{ mm}^3 \text{ l}^{-1}$, rejections occurred

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frequently, and could not be related to preceding ingestions or pellet releases. Pellets were released at fairly regular intervals (Figure 6). The rejections presented are active rejections, i.e. the representative copepod had captured a cell and released/rejected it within ~1 s or less.

Discussion

Direct visual and continuous observations

This study was aimed at determining ingestion rates of individual copepods and the variables related to ingestion rates by using direct and continuous observations. This type of observation provides, in comparison to indirect observations, unequivocal evidence of what and how much has been eaten. Previously, almost all zooplankton feeding studies were based on quantifications integrated over time using a beginning and end point, e.g. (i) particle removal from a suspension, (ii) particle accumulation (e.g. radioisotopes) or (iii) decrease (e.g. gut fluorescence) in an animal's body. What actually happened between beginning and end points was unknown. Each of these methodologies was utilized assuming that constant conditions prevailed. Continuous uninterrupted coverage of individual copepods results in continuous observations of the process of ingestion, and increased statistical confidence in the data. Since each copepod was treated in a specific and

Fig. 5. Time course of ingestions and rejections of cells of *T. eccentrica* at a concentration of $0.3 \text{ mm}^3 \cdot \text{l}^{-1}$ by a female of *P. aculeatus* over a period of 3200 s. When ingestions or rejections were close to each other, the preceding or following one was positioned slightly above or below.

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Fig. 6. As Figure 5, but for a different female at $1.0 \text{ mm}^3 \cdot \text{l}^{-1}$ over 3600 s.

reproducible manner, observations on individual variability are strengthened statistically.

Paracalanus aculeatus is an offshore calanoid which usually encounters relatively low levels of particulate matter on the outer shelf and at the shelf break of the southeastern USA (e.g. Paffenhöfer and Lee, 1987). This species is found in other parts of the world's tropical and subtropical oceans (e.g. Gonzalez and Bowman 1965; Madhupratap and Haridas, 1986; Sameoto, 1986). Ingestion rates increased with increasing food concentration and reached a maximum near $0.3 \text{ mm}^3 \cdot \text{l}^{-1}$ of *T. eccentrica*, which amounted to a daily rate of 52.6% of its body carbon. These rates are relatively low when compared to those of adult females of *Paracalanus parvus/quasimodo* which ingested daily a maximum of nearly 160% of its body weight at 20°C feeding on the diatom *Thalassiosira weissflogii* at $80 \mu\text{g C l}^{-1}$ (Paffenhöfer, 1984). The relatively low level of satiation concentration for females of *P. aculeatus* may be characteristic of small offshore copepods which have evolved to exist at very low, hardly varying food concentrations. It may also be that diatoms are not this species' preferred food (Kleppel *et al.*, 1988a). Therefore, our observations should be considered as an initial effort to quantify ingestion rates of free-swimming individuals.

Clearance rates increased non-linearly with decreasing food concentration (Figure 2) as observed in numerous previous studies (e.g. Frost, 1980). These rates may change over a period of 24 h, and may differ with different types of food. Recalculating our data, the average clearance rate of a *P. aculeatus* female ($\sim 0.9 \text{ mm}^3$

cephalothorax length) per 24 h would have been 318 ml at $0.1 \text{ mm}^3 \text{ l}^{-1}$ ($3.3 \mu\text{g C l}^{-1}$) and 228 ml at $0.3 \text{ mm}^3 \text{ l}^{-1}$ of *T.eccentrica* ($9.8 \mu\text{g C l}^{-1}$). The latter rate is similar to that of females of *P.parvus*, feeding on large cells at 18°C , which was near 240 ml female $^{-1}$ per 24 h at $\sim 10 \mu\text{g C l}^{-1}$ (Bartram, 1981; his Figure 9). *Paracalanus* sp. females (most likely *P.quasimodo*, $\sim 0.7 \text{ mm}$ cephalothorax length) removed the small diatom *T.weissflogii* ($12 \mu\text{m}$ diameter) at average concentrations near $7 \mu\text{g C l}^{-1}$ at rates between 181 and 234 ml female $^{-1}$ per 24 h in the presence of $\sim 2 \mu\text{g C l}^{-1}$ of *Rhizosolenia alata* and $\sim 20 \mu\text{g C l}^{-1}$ of *Isochrysis galbana* (personal observation).

Our continuous observations not only provided rates, but a mechanism by which an individual copepod modifies its clearance rates: at both low concentrations $\sim 10\%$ of the cells captured were actively rejected, whereas at $1.2 \text{ mm}^3 \text{ l}^{-1}$ almost 60% were rejected (Figure 3). From these observations, one could assume that at low food levels nearly all cells perceived at a distance by *P.aculeatus* females were ingested, but not at higher food levels. The selection of cells for ingestion seemingly occurs at the mouth, i.e. by gustation (Paffenhöfer *et al.*, 1982). If such decisions indeed occur at the mouth, this could explain the overall lower ingestion rates, at similar food concentrations, when *Paracalanus* spp. was offered several phytoplankton species simultaneously as compared to feeding on only one species (Paffenhöfer, 1984). Decision making at the mouth with subsequent rejections requires time and effort, whereas deciding by olfaction, i.e. long distance, does not. For *Paracalanus* females, coarse decisions concerning food particles are probably made long distance, and fine-tuned ones at the mouth.

Variability

Our study was also designed to determine interindividual variability in the rates of feeding and fecal pellet release by changing food concentration, using animals of identical history. Here we will: (i) relate our findings to previous observations on feeding variability; (ii) evaluate possible causes for variability in copepod body size and physiological condition; and (iii) discuss the possibility of integrating environmental variability by copepods.

(i) The extent of individual variability among zooplankton and its causes have been addressed earlier, including feeding rates (e.g. Bamstedt, 1988; Paffenhöfer, 1994). We consider here only studies of actual cell ingestion or fecal pellet releases, and we do not include those of mouthpart activity because mouthpart activity cannot be used as an unequivocal indicator of feeding, as shown by our results on rejection and ingestion (0.3 versus $1.0 \text{ mm}^3 \text{ l}^{-1}$; Figures 1 and 3), with all adult females moving their mouthparts nearly continuously. Earlier obtained measurements of indices of feeding of individual copepods had coefficients of variation (CV) from 35 to 65% (Rodriguez and Durbin, 1992) and 60 to 170% (Kleppel *et al.*, 1988b). These data represent one-time measures of the gut contents of copepods of the genus *Acartia*. The authors attributed the variability to non-synchronous feeding of individuals. Intermittent, temporally enhanced or reduced feeding cannot be excluded as copepods *in situ* may (i) modify feeding rates over periods of several hours, as could be assumed from the observations of Stearns *et al.* (1989) whose results on changes in gut fullness of female *Acartia tonsa* suggest that these animals may have altered their feeding activity during their main feeding period, i.e. night-

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time (their Figure 1). This could be similar to dielly migrating *Calanus pacificus* whose ingestion rates decrease over hours after encountering high food levels (McAllister, 1970); (ii) reside only intermittently in thin vertical layers of abundant food (Cowles and Desiderio, 1993); and (iii) rapidly respond to changing food abundances by increasing or decreasing their mouthpart activity (female *Eucalanus hyalinus*; Price and Paffenhöfer, 1986).

CV between averages of ingestion rates and pellet release intervals of adult females of *P. aculeatus* were similar between food concentrations (Table I). These CV were close to those on average pellet release rates of tethered adult females of oceanic origin of the calanoid copepod *Eucalanus pileatus* which were 23.5, 27.5 and 24.2%, feeding on the diatom *T. weissflogii* at 0.1, 0.3 and 1.0 mm³ l⁻¹, respectively (Paffenhöfer, 1994).

We also compared rates of individuals to determine interindividual differences. Significant differences were few for ingestion rates, and pronounced for pellet release intervals (see Results). Why would that be? Our observations on cell ingestions and active rejections over time (Figures 5 and 6) suggest that the distribution of cells of *T. eccentrica* in the experimental vessels (which we considered to be even) and the swimming routes taken by each copepod determined cell captures. Sometimes several cells were close to each other, resulting in many captures in e.g. 60 s; at other times, individual cells were farther apart from each other. This led to considerable differences in the number of ingested cells from one period to the next (feeding period = time between pellet releases, normalized to cells ingested min⁻¹) as seen from the rather high CV for individual females. All females of *P. aculeatus* which we observed were moving continuously and at rather even velocities, seemingly creating a feeding current all the time. Therefore, differences in other activities should not be considered for causing the high variability for ingestion rates in this study. Our findings suggest that encounter rates/long-distance perception governed ingestion rates at 0.1 and 0.3 mm³ l⁻¹, but that at 1.0 mm³ l⁻¹ satiation through selection behavior at the mouth determined the rate of food consumption.

CV for pellet release intervals of individual *P. aculeatus* were relatively low (Tables II–IV), particularly at 0.3 and 1.0 mm³ l⁻¹. Variability of ingestion over several minutes will not immediately manifest itself in similar variability of pellet release rates. Rather, the latter should somehow integrate variability of ingestion frequency (Donaghay, 1988), resulting in lower variability of release intervals. As each animal, particularly at 0.3 and 1.0 mm³ l⁻¹, had a relatively narrow range of release intervals, the probability of significant differences was high. Certain females had a specific longer (females 4 and 5 at 0.3 mm³ l⁻¹) or shorter release period (females 1 and 2 at 1.0 mm³ l⁻¹) which we could not relate to lower or higher feeding rates. Each animal appears to possess its specific release rate at saturating food levels. Higher or lower release intervals could also be related to smaller or larger pellet size, respectively.

(ii) How can our findings on the variability of feeding between individual copepods be related to the influence of the variability of environmental variables on zooplankton feeding in the ocean? The history of a copepod will translate itself into size, weight and physiological condition. Among diverse variables, intermittent scarcity and lower quality of food during juvenile life will affect later stages.

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Variability in body weight of individual copepods, as observed by Bamstedt (1988) and Bamstedt *et al.* (1992), can be partly explained by the fact that not all juveniles of an identical stage of a species operate in the same vertical layer: e.g. field studies showed that a large percentage of copepodid stages I(CI) of *Temora turbinata* occupied the warm upper mixed layer (28°C) at low food abundance (with few diatoms), whereas another large fraction occurred in the cool (17–20°C) diatom-rich deep layer, and a third fraction was found in the thermocline (Paffenhöfer and Lee, 1987; Paffenhöfer *et al.*, 1987). In comparison, the vast majority of juveniles and adult females of *E. pileatus* remained in the cool, food-rich deep layer where food was usually evenly distributed (Paffenhöfer, 1983). Similarly, the vast majority of *Oncaea* spp. early copepodids remained together in the upper mixed layer, whereas the late copepodids and adults were almost exclusively found in the cold deep layer (Paffenhöfer, 1983). The latter two observations should result in small interindividual variability of feeding and therefore size, as was found for length of females of *E. pileatus* in summer (Paffenhöfer, 1994). If, however, a copepod shows a wide vertical distribution for each stage and, in addition, an extended juvenile life, then variability of size and physiological condition between individuals due to life history should be enhanced. The longer the juvenile life, the larger the number of environmental changes an individual will encounter, e.g. due to meteorological disturbances.

(iii) Copepods are thought to be able to integrate environmental variability through physiological and behavioral mechanisms (Donaghay, 1988). Here are some possible mechanisms. Decreases in food concentration are physiologically countered by increased perceptive ability, i.e. a decrease in food concentration from ~ 0.3 to $\sim 0.1 \text{ mm}^3 \text{ l}^{-1}$ of cells of *T. weissflogii* will result in only a small decrease of ingestion rate of adult females of *E. pileatus* (Paffenhöfer and Lewis, 1990). For early juvenile copepods which satiate at rather low food levels (e.g. Harris and Paffenhöfer, 1976; Ambler, 1986), wide variability in food concentrations should not be that important unless they reach levels at which these animals cannot cover their requirements for metabolism and slow growth. Older stages encountering low food levels can compensate not only physiologically (Paffenhöfer and Lewis, 1990), but behaviorally, by migrating vertically to find different food conditions. Females of the large calanoid *E. hyalinus* respond to decreasing food levels by increasing periods of inactivity between feeding bouts (Price and Paffenhöfer, 1986). Overall, copepods seem to have evolved behavioral mechanisms to limit the effects of varying food concentrations.

Our results for *P. aculeatus* females showed feeding rates similar to those found for congeneric females at low food levels. They revealed that above the satiation food level many cells are captured and soon afterwards rejected, indicating pronounced selectivity and energy expenditure when food is abundant. Considerable intraindividual variability of ingestion rates resulted in significant differences between only a few individuals at 0.1 and 0.3, and none at $1.0 \text{ mm}^3 \text{ l}^{-1}$. However, females at the two high food levels had rather narrow, individual-specific pellet release rates which resulted in significant differences between numerous individuals. These observations are an attempt to improve our understanding of the feeding behavior of calanoid copepods, particularly the variability between

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individuals, and to some extent within an animal. Our study was an initial effort using controlled conditions. We hope and expect that it will spawn wider-ranging efforts, revealing diel and short-term differences for different species and stages, leading to an understanding of previously environmentally observed variability. We feel that, ultimately, *in situ* observations on zooplankton individuals will be an essential component to comprehend how a pelagic community functions (U.S. GLOBEC, in press).

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