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Effect of temperature on lower feeding thresholds, gut evacuation rate, and diel feeding behavior in the copepod *Acartia hudsonica*

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ABSTRACT: Adult females of the marine copepod *Acartia hudsonica* Pinhey were fed the unicellular diatom *Thalassiosira constricta* (10.4 µm equivalent spherical diameter) at 4, 8, 12, and 16 °C, to determine whether there was a threshold food concentration below which feeding ceased or was sharply reduced. Field-collected copepods were acclimated for 24 h at 2000 cells ml^{-1} *T. constricta*, and then transferred to a range of low food concentrations (15 to 876 cells ml^{-1}). Gut pigments were determined fluorimetrically after a 5 h period of feeding, which was calculated to be sufficient for gut contents to equilibrate to the new food concentration. Experiments were carried out during the same phase of the diel cycle (05:00 to 10:00 h) and were terminated near midday, a time when feeding rate was relatively stable, in order to standardize the effects of the diel feeding rhythm. Lower feeding thresholds of 280, 127, 282, and 214 cells ml^{-1} respectively at 4, 8, 12, and 16 °C were indicated by segmented linear regression analysis of the relationship between gut pigments and phytoplankton concentration. These thresholds corresponded to carbon concentrations of 30.5, 11.6, 20.7, and 16.4 µg C l^{-1}, and were not significantly different at the 4 temperatures. Diel changes in gut pigment content were measured at 8 and 12 °C, at a *T. constricta* concentration of 2000 cells ml^{-1}. Highest gut contents occurred at night, and were ca 4-fold higher than the lowest measured gut contents. Total daily ingestion rates were respectively 11 460 and 14 430 cells d^{-1}, or 1.34 and 2.40 µg C and 0.24 and 0.42 µg N d^{-1}, and 33.4 and 56.5 % body C and 23.3 and 38.5 % body N d^{-1}. The instantaneous gut evacuation rates were also determined at the 4 temperatures, with mean values of 0.0239, 0.0494, 0.0518, and 0.0645 min^{-1} respectively at 4, 8, 12, and 16 °C, yielding a Q_{10} of 1.88.

INTRODUCTION

The existence of a lower feeding threshold in copepods (a food concentration below which they substantially decrease or cease feeding) is controversial. Feeding experiments with unialgal cultures under laboratory conditions give zero (Frost 1972) or very low values (Frost 1975, Deason 1980, Kiørboe et al. 1985a). However, studies in which the copepod were fed a natural assemblage of particulate matter indicate that feeding halts at threshold concentrations significantly greater than zero (Adams & Steele 1966, Parsons et al. 1967, Reeve & Walter 1977). A lower feeding threshold has been included in models of phytoplankton-herbivore interactions (Steele 1974) because it provides the phytoplankton with a refuge in low density so that they cannot be grazed to extinction (Steele & Mullin 1977). Modelling also indicates that a lower feeding threshold would reduce energy expenditures when food abundance is low (Lam & Frost 1976, Lehman 1988). Direct observations of individual copepods using high speed microcinematography have shown that activity is reduced when food is scarce or absent (Cowles & Strickler 1983, Price & Paffenhöfer 1986, Gill & Poulet 1988, Jonsson & Tiselius 1990), consistent with energy conservation under low food.

Lower feeding thresholds are difficult to quantify. When ingestion is estimated indirectly from the change in food abundance over time, both accuracy

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and precision decline at the low food concentrations of greatest interest in studies of lower feeding thresholds (Mullin et al. 1975). However gut fluorescence (Mackas & Bohrer 1976, Reeve & Walter 1977) provides a direct measure of recent feeding by the copepods, and is sufficiently sensitive for use at low food levels. Opinions differ as to whether gut pigments provide a quantitative estimate of feeding rate (see Kiørboe & Tiselius 1987, Dam & Peterson 1988, Peterson et al. 1990, Durbin et al. 1990 for a review, including methodological problems with these determinations). Present data indicate that gut pigments are conserved in *Acartia* spp. (Kiørboe & Tiselius 1987, Durbin et al. 1990).

Here we use measurements of gut fluorescence to investigate lower feeding thresholds in adult females of the copepod *Acartia hudsonica* Pinhey, fed the unicellular diatom *Thalassiosira constricta* at 4, 8, 12, and 16 °C. The present study is the first to quantify the effect of temperature upon lower feeding thresholds using direct measurements of gut contents. The diel feeding pattern in adult female *A. hudsonica* is also described at 8 and 12 °C. Diel feeding rhythms are known from other copepods (e.g. Mackas & Bohrer 1976, Nicolajsen et al. 1983, Kleppel et al. 1985, Simard et al. 1985, Stearns 1986, Durbin et al. 1990), but have not previously been investigated in *A. hudsonica*. Gut evacuation rates were determined at 4, 8, 12, and 16 °C to permit estimation of ingestion rate from gut contents (Elliott & Persson 1978).

We define the lower feeding threshold C_t as the food concentration at which gut contents increase significantly above background levels, indicating either the onset of, or a sharp increase in, feeding rate. Above C_t the clearance rate F increases until a second threshold concentration C_m, associated with the onset of maximum filtering effort, is reached (Frost 1975). At food concentrations above C_m, different feeding models predict different trajectories for clearance rate: In a rectilinear model, F is assumed to remain constant between C_m and the critical concentration C_c, above which ingestion rate stabilizes at a maximum rate, and clearance rate declines curvilinearly (e.g. *Calanus pacificus*; Frost 1972, 1975). In a curvilinear model F ascends curvilinearly to a sharp peak at C_m and immediately begins to decline, well below the critical concentration associated with maximum ingestion rate (e.g. *Acartia* spp.; Kiørboe et al. 1985a, Paffenhöfer & Stearns 1988, Durbin & Durbin 1992).

Acartia hudsonica (formerly called *Acartia clausi* Giesbrecht; Bradford 1976) is the dominant winter-spring copepod in Narragansett Bay, Rhode Island, USA (Hulsizer 1976, Durbin & Durbin 1981) where the phytoplankton population is dominated by diatoms (Pratt 1965, Smayda 1973, Durbin et al. 1975). The experimental temperatures and food therefore reflect the environmental conditions experienced by *A. hudsonica* in the field.

MATERIAL AND METHODS

Collection and acclimation of copepods. Zooplankton were collected during early morning, using a 50 cm mouth diameter net of 333 µm mesh, towed horizontally at 1 to 2 knots at a station in the lower West Passage of Narragansett Bay (see Fig. 1 in Durbin et al. 1990). Within 30 min of time of collection, copepods were transported to the laboratory in covered, 20 l polyethylene containers and incubated at the desired temperature, either 4, 8, 12, or 16 °C. Experimental temperatures were within ± 3 °C of the field temperature (Table 1), to provide seasonally acclimated copepods for the investigation of temperature effects upon feeding behavior. Diel feeding experiments were carried out during spring 1985, and the lower feeding threshold experiments during spring 1986.

Sorting and acclimation. For the threshold experiments 800 to 2000 adult female *Acartia hudsonica* were isolated by pipetting into a clean, 20 l polyethylene container with *Thalassiosira constricta* at a concentration of 2000 cells ml^{-1} filtered seawater. Sorting was done under a dissecting microscope in subdued light, with care taken to avoid a thermal shock to the copepods, and was completed within 3 to 4 h after the copepods were collected in the field. Copepods used for the diel feeding studies and evacuation rate measurements were not presorted. Based upon a preliminary count, volumes of zooplankton containing ca 1000 female *A. hudsonica* were dispensed into two 20 l containers with *T. constricta* at 2000 cells ml^{-1}.

For all experiments, the containers were placed into a water bath to maintain a constant temperature. The contents were stirred for 1 min every 3 min with a Plexiglas paddle (similar to one described by Frost 1972) to avoid settling of the phytoplankton. Copepods were allowed to acclimate to the laboratory conditions for ca 24 h. Food level was monitored with a Model ZM Coulter Counter, and additional culture added as needed to maintain an approximately constant concentration of 2000 cells ml^{-1}. A light : dark cycle appropriate to the time of year was maintained during the acclimation and experimental periods. The light period in the diel experiments was 05:00 to 18:00 h at 8 °C and 05:00 to 20:00 h at 12 °C; and in the threshold experiments, 06:00 to 18:00 h, 05:30 to 18:15 h, 04:30 to 19:00 h, and 04:15 to 19:15 h respectively at 4, 8, 12, and 16 °C.

Table 1. Field collection dates, field and experimental temperatures, and mean carbon and nitrogen contents of adult *Acartia hudsonica* in the experiments. Carbon and nitrogen determinations were made on groups of 10 to 20 copepods

Date	Expt	Temperature (°C) Field	Lab	Carbon (µg copepod^{-1}) Mean ± SE	Nitrogen (µg copepod^{-1}) Mean ± SE	No. of copepods
Diel experiments						
22 Apr 1985		10.0	8.0	4.01 ± 0.70	1.03 ± 0.09	45
13 May 1985		14.0	12.0	4.25 ± 0.69	1.09 ± 0.16	45
Threshold experiments						
10 Mar 1986	A	1.5	4.0	6.97 ± 0.06	1.74 ± 0.06	45
17 Mar 1986	B	4.5	4.0	6.08 ± 0.69	1.54 ± 0.22	45
24 Mar 1986	C	4.0	4.0	7.73 ± 0.32	1.86 ± 0.03	45
2 Apr 1986	A	7.5	8.0	7.29 ± 0.63	1.66 ± 0.11	30
7 Apr 1986	B	7.5	8.0	7.19 ± 0.43	1.70 ± 0.06	30
8 May 1986	A	10.5	12.0	3.31 ± 0.20	0.67 ± 0.07	45
14 May 1986	B	12.0	12.0	5.14 ± 0.20	1.18 ± 0.16	45
6 Jun 1986	A	18.0	16.0	3.18 ± 0.07	0.77 ± 0.03	45
9 Jun 1986	B	17.5	16.0	3.61 ± 0.33	0.88 ± 0.09	45

The unicellular diatom *Thalassiosira constricta* was used as food during the experiments, and was cultured in f/2 media (Guillard & Ryther 1962) under a 12:12 h light:dark cycle. Phytoplankton were temperature acclimated to match the experimental temperature, and cultures were monitored with frequent visual cell counts to check cell viability and to ensure cultures were used while in the log phase of growth. The same clone (isolated from Narragansett Bay) was used throughout; cell size, pigment, carbon and nitrogen content in the different experiments and temperatures are presented in Table 2.

Diel feeding studies. After the 24 h acclimation the copepods were transferred to a clean 20 l container with fresh media of 2000 cells of *Thalassiosira constricta* ml^{-1}. Cells were kept in suspension with the Plexiglas paddle, as before. Nine samples were collected every 3 h during the ensuing 24 h, starting at 11:10 h and ending at 11:10 h next day. The container was gently stirred, and a volume of media containing ca 100 adult female *Acartia hudsonica* was removed with 1.5 l beakers. The sample was concentrated in a submerged, 7 cm diameter Plexiglas cylinder with 153 µm mesh on the sides and bottom, the copepods immediately transferred to an anesthetic solution of 0.58 g MS-222 (3-aminobenzoic acid ethyl ester) l^{-1} of chilled filtered seawater (4 to 7 °C), and placed over crushed ice in the dark until they could be sorted (Durbin et al. 1990). Anesthesia was necessary in order to prevent evacuation of gut contents during sorting; the stability of gut pigments under this procedure was confirmed and is described in a later section. Within 30 to 60 min, 3 replicates of 10 to 32 females (usually 30) were sorted microscopically under subdued light onto Whatman GF/F glass fiber filters, which were folded, wrapped in aluminium foil, and frozen until further analysis. Frozen samples were analyzed within 24 h. A 300 ml subsample of the media was retained for determination of phytoplankton pigment and cell numbers, and the remainder was returned to the experimental container to keep the total volume approximately constant. On each sampling occasion, 3 replicate subsamples were filtered onto Whatman GF/F 2.4 cm glass fiber filters for chlorophyll pigment analysis, and 100 ml of the media was preserved with Lugol's solution for cell counts.

Threshold feeding experiments. After acclimation the presorted adult female *Acartia hudsonica* were gently siphoned into a clean container, concentrated onto a submerged 153 µm screen, and dispensed into a beaker with filtered seawater. The females were split into groups of 100 to 120 individuals, and dispensed into 4 l glass jars containing *Thalassiosira constricta* at concentrations ranging from 15 to 876 cells ml^{-1}. The jars were closed tightly and placed on a 1 rpm plankton wheel enclosed in a water bath to maintain temperature control. The jars were attached at right angles to the axis of rotation so that they turned end-over-end.

Several factors influenced the duration of the experiment and the time of day chosen for the final gut content measurement. The experiments needed to be of rather short duration to prevent the copepods from depleting the phytoplankton, especially at the lower concentrations. On the other hand an interval of time was required for gut contents to equilibrate to the change in food concentration after transfer from the

Table 2. *Thalassiosira constricta*. Chemical composition, pigment content and size of diatoms fed to *Acartia hudsonica* in the diel feeding and lower feeding threshold experiments

Temp (°C)	Expt	Pigments cell^{-1} pg chl *a* Mean ± SE	Pigments cell^{-1} pg total Mean ± SE	Carbon (ng cell^{-1}) Mean	Nitrogen (ng cell^{-1}) Mean	Cell size Volume (µm^3)	Cell size Diameter (µm)
			Diel experiments				
8		2.67 ± 0.16	4.64 ± 0.20	0.117[a]	0.021[a]		
12		3.77 ± 0.29	5.62 ± 0.25	0.166[a]	0.029[a]		
			Threshold experiments				
4	A	2.11 ± 0.32	2.21 ± 0.33	0.135	0.018	–	–
4	B	2.42 ± 0.10	2.67 ± 0.11	0.096	0.018	744	11.2
4	C	2.57 ± 0.09	2.80 ± 0.10	0.096	0.020	665	10.8
8	A	1.60 ± 0.04	1.77 ± 0.04	0.088	0.017	596	10.4
8	B	2.43 ± 0.08	2.56 ± 0.09	0.095	0.018	625	10.6
12	A	2.50 ± 0.16	2.61 ± 0.17	0.077	0.013	442	9.5
12	B	1.86 ± 0.08	2.06 ± 0.08	0.070	0.014	–	–
16	A	2.27 ± 0.15	2.40 ± 0.16	0.076	0.011	518	10.0
16	B	1.32 ± 0.05	1.49 ± 0.06	0.077	0.013	–	–

[a] Estimated from relationships in threshold experiments, where overall mean C/chl *a* = 43.9 and N/chla *a* = 7.7

acclimation media to the experimental food level (Elliott & Persson 1978, Dam et al. 1991). When feeding rate is constant gut contents approach the equilibrium value asymptotically, at a rate determined by the instantaneous gut evacuation rate R. For present purposes the time to gut equilibrium may be approximately by the time to reach 90 % of the equilibrium value, and in our experiments ranged from about 125 min for R = 0.0183 min^{-1} at 4 °C, to 30 min for R = 0.0826 min^{-1} at 16 °C. Based on these considerations an experimental duration of 5 h was chosen for the threshold experiments. The diel periodicity in the feeding behavior of the copepods made it desirable to make the measurements of gut content at a time of day when the feeding behavior and gut contents were not changing rapidly. The most suitable time was between 10:00 and 11:00 h, when the gut contents had reached their daytime minimum and would remain fairly stable for the next several hours. In the threshold experiments, therefore, the copepods were transferred from the acclimation medium to the experimental concentrations during the time interval from 05:00 to 06:00 h, and collected for gut content analysis exactly 5 h later, during 10:00 to 11:00 h.

Copepods were processed as before to obtain 3 replicate measurements of (usually) 30 adult females at each food concentration. Each jar was subsampled for determination of phytoplankton pigments (3 replicates filtered onto Whatman GF/F glass fiber filters) and cell counts (2 replicate 100 ml bottles preserved in Lugol's for later subsampling and enumeration).

Gut evacuation rate. During acclimation the copepods were contained in a 16 l acrylic chamber with 153 µm Nitex mesh on the bottom, set inside a 20 l polyethylene container. The mesh permitted sinking of eggs and feces to the bottom of the container, and rapid transfer of the copepods from food into filtered seawater for the measurement of gut evacuation rate. At the beginning of the experiment the chamber was lifted slowly from the media, dipped briefly into a filtered seawater rinse, and transferred to a clean container of filtered seawater at the appropriate temperature. Samples were collected with a 1.5 l beaker at 3 to 4 min intervals for 45 min, and the copepods processed as described before. Three replicates of 10 to 30 (usually 25) adult female *Acartia hudsonica* were collected for each sample. The chamber containing the animals was transferred into fresh filtered seawater after 12 to 16 min to prevent reingestion of fecal pellets by the copepods.

The instantaneous gut evacuation rate R min^{-1} was determined by regression of gut contents vs time during the experiment, using a nonlinear least squares estimation procedure on nontransformed data [Statistical Analysis System (SAS) Procedure NLIN, DUD method of computation (Ralston & Jennrich 1979) on an IBM 4381 computer]. R was estimated from data corresponding to the period between 0 to 75 % of gut evacuation. Data from the final 25 % of gut evacuation were excluded from the analysis because inclusion of data from the late stage of gut evacuation in filtered seawater may underestimate R in actively feeding copepods (Kiørboe & Tiselius 1987, Durbin et al. 1990).

Ingestion rate was computed from gut contents and the evacuation rate using the model of Elliott & Persson (1978) where:

$$C_t = R S_t$$

where C_t = consumption over the interval $t_{0,t}$, and S_t = gut content at time t.

Stabilization of gut pigments. Tests were carried out to determine the lowest concentration of anesthetic that would immobilize the copepods but would not cause an involuntary gut clearance. The anesthetic solution was made up with chilled filtered seawater (4 to 7 °C); the optimum concentration was found to be 0.58 g of MS-222 l^{-1} of seawater (Durbin et al. 1990). Copepods treated with this concentration of MS-222 did not show any mechanical activity but would recover and resume swimming if transferred to filtered seawater. Recovery has been observed even after exposure for 24 h at 5 °C.

After determining the optimum concentration of anesthetic to immobilize the copepods, a test was carried out to determine the stability of gut pigments over time. Copepods were collected from one of the 15 m^3 MERL mesocosm tanks, rinsed into a beaker and anesthetized in MS-222/seawater at a temperature of 4 to 7 °C. Zooplankton were transferred to small culture dishes over crushed ice, covered with a light-tight cover and stored in a refrigerator at 7 °C. At intervals during the first and third hour following collection, adult female *Acartia hudsonica* were sorted in groups of 10 onto glass fiber filters for analysis of gut pigments. The sequential measurements are shown in Table 3; the mean values of the samples collected during the first and third hours were 0.34 and 0.36 ng total pigments copepod^{-1} respectively, and were not significantly different ($p < 0.05$). The regression slope of gut pigments vs time (0.0001) was nonsignificantly different from zero. These results indicate that gut pigments remain stable for at least 197 min after the copepods are anesthetized. Based on these experiments, all copepods in this study were treated with MS-222 at 0.58 g l^{-1} of chilled filtered seawater, stored over crushed ice in the dark, and sorted onto glass fibers and frozen within 60 min of collection.

Sample analysis. Frozen zooplankton samples were processed within 24 h after collection. Both zooplankton and phytoplankton samples were ground in 90 % aqueous acetone, transferred to a freezer for a minimum of 1 h for extraction, centrifuged at 90 rpm for 5 min, and the fluorescence of the supernatant before and after acidification measured on a Turner Designs Model 10 fluorometer. Analyses were conducted in subdued light. Because chlorophyll *a* (chl *a*) is rapidly converted to phaeopigments after ingestion, the copepod gut pigments and phytoplankton pigments are reported here as weight of total pigments (chl *a* plus phaeopigments expressed as chl *a* equivalents), using the equations of Parsons et al. (1984).

Table 3. *Acartia hudsonica*. Sequential measurements of gut pigments during storage in an anesthetic solution of 0.58 g MS-222 l^{-1} chilled filtered seawater Samples were kept in the dark over crushed ice. Determinations were made on groups of 10 adult females

Elapsed time (min)	Total pigments (ng copepod^{-1})
8	0.38
15	0.21
28	0.52
35	0.18
41	0.39
47	0.28
52	0.42
59	0.31
	mean ± SE = 0.34 ± 0.11
151	0.39
159	0.20
169	0.35
174	0.51
181	0.40
187	0.20
192	0.41
197	0.38
	mean ± SE = 0.36 ± 0.11

Carbon and nitrogen determinations were made with a Hewlett-Packard Model 185B Carbon Hydrogen Nitrogen Analyzer.

Phytoplankton enumeration was done by microscopic counting using a light microscope. Subsample volumes ranged from 1 to 10 ml (drawn from 100 ml of sample) and were chosen to obtain a minimum of 200 cells per count. Not more than 10 ml were taken for any one subsample, however, yielding counts as low as 80 cells at the lowest concentrations. Subsamples were filtered at 5 psi (3.3×10^4 Pa) onto Millipore filters. The circular yellow area of filtration was marked with a pen, and the filters allowed to dry on paper towel. The next step was to transfer the dry filter to a glass slide, apply a drop of immersion oil and press a cover slip on the top. The entire area of filtration was counted, and 4 such replicate filters were counted for each cell concentration. Cell volume and diameter were determined using a Coulter Model ZM particle counter.

Data analysis. In order to test for the presence of a lower feeding threshold, the gut contents (ng total pigments and number of cells copepod^{-1}) were plotted against cell concentration to determine whether an abrupt change in slope, indicating a lower feeding threshold, was present (see Fig. 2). We used segmented linear regression to provide an objective test for a lower feeding threshold, below which *Acartia*

hudsonica sharply decreased or ceased feeding. Replicate experiments within each temperature were pooled for this analysis.

Somerton (1980) proposed the use of segmented linear regression for crustacean growth data when there is an apparent change in slope within the same data set. The data are partitioned into 2 segments at the break point where the slope changes, and curves are fit to each segment. The objective selection of the break point is a critical part of the statistical analysis, and Somerton presented an iterative method whereby the data are subdivided into 2 segments, and a break point is determined to minimize the residual sum of squares pooled over both segments. In a series of trials, the X, Y pairs of data are divided into 2 segments, one for which X values were less than or equal to the chosen breakpoint value X_b, and the other for which X values were greater than X_b. The initial X_b value is selected arbitrarily. A linear regression is fit to each segment, and the total residual sum of squares for both segments computed. The value of X_b is then incremented and the process repeated for all values of X_b until a value of X_b is found that minimizes the RSS pooled over both segments. The segmented regression is then compared to the null hypothesis of no breakpoint, i.e. all data fit to a single linear regression.

In the present study, at all 4 temperatures the segmented regression produced a lower RSS than the simple regression of all data combined, thus rejecting the null hypothesis of no threshold. Therefore, after finding the best segmented linear fit, the data points in the left-hand segment were treated as 'background' fluorescence due to factors other than phytoplankton pigments from feeding in the experimental media. The threshold was calculated by finding the intersection between the regression line from the right-hand segment, and the line $y = b$, where b was the mean value of the data points in the left-hand segment (see Figs. 2, 3 & 4).

The linear model used here appeared to be suitable over the restricted range of cell concentrations tested, but is not meant to imply linearity in the relationship between ingestion and food concentration over the full range between C_t and C_c. Previous work indicates this relationship to be curvilinear in *Acartia* spp. (Kiørboe et al. 1985a, Durbin & Durbin 1992).

RESULTS

Diel feeding behavior

Adult female *Acartia hudsonica* showed diel feeding rhythmicity, with about a 4-fold amplitude in feeding rate (Fig. 1, Table 4). Maximum gut content occurred at night, and the minimum during the day. Gut contents were converted to cells copepod^{-1} from the total

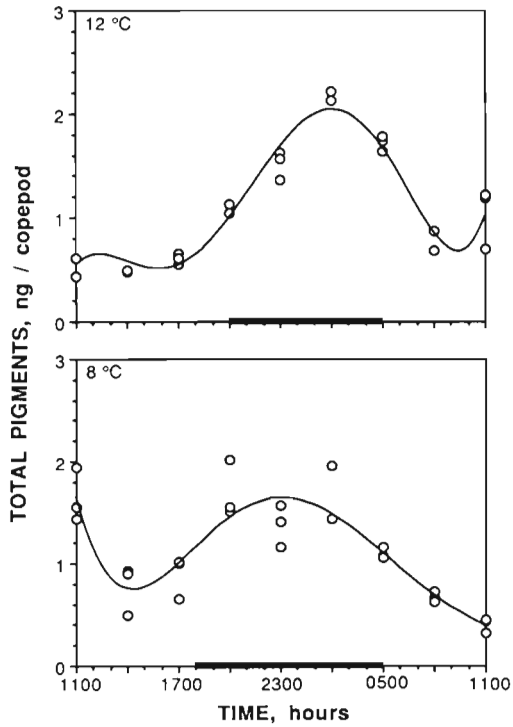

Fig. 1. *Acartia hudsonica*. Diel feeding behavior of adult females fed *Thalassiosira constricta* at 8 and 12 °C. Black bar denotes dark period

pigment content cell^{-1} (Table 2); carbon and nitrogen contents were estimated using mean values from the threshold feeding studies where C:chl *a* = 43.9 and N:chl *a* = 7.7, respectively (Table 2). Total daily ingestion at 8 and 12 °C were respectively: 52.4 and 81.0 ng total pigments copepod^{-1} d^{-1}; or 11 460 and 14 430 cells d^{-1}; 1.34 and 2.40 µg C d^{-1} and 0.24 and 0.42 µg N d^{-1} (Table 4). Ingestion as a percentage of copepod carbon and nitrogen (Table 1) corresponded to 33.4 and 56.5 % body C, or 23.3 and 38.5 % body N d^{-1} respectively at the 2 temperatures.

Lower feeding threshold

The mean cell size in *Thalassiosira constricta* was similar at all 4 temperatures, ranging from 9.5 to 11.2 µm diameter and 442 to 744 µm^3 (Table 2). With increasing temperature, carbon and nitrogen contents declined from ca 0.109 µg C and 0.019 µg N at 4 °C to ca 0.076 µg C and 0.012 µg N cell^{-1} at 16 °C (Table 2). However the C:N ratio did not change significantly with temperature [mean (range) = 5.8 (4.8 to 7.5)].

The lower feeding thresholds varied slightly according to the units from which they were computed, but were similar at the 4 temperatures. When estimated from the total pigment copepod^{-1}, thresholds at 4, 8,

Table 4. *Acartia hudsonica*. Diel feeding rhythm in adult females fed the diatom *Thalassiosira constricta* in the laboratory. Maximum and minimum gut contents and corresponding ingestion rates (I d^{-1}), where I = contents × R min^{-1} × 1440 min d^{-1} Total daily ingestion rate computed by integration under curve in Fig. 1 on an hourly basis, where I = integrated gut contents × R h^{-1} Instantaneous gut evacuation rates (R) from Fig. 5; ingestion can be expressed as µg C and N, and % body C and N, using relationship in Tables 1 & 2

Temp (°C)	Index	Gut content copepod^{-1} ng pigments	Cells	R	Ingestion copepod^{-1} d^{-1} ng pigments	Cells
8	Max	1.71	368	0.0312 min^{-1}	76.6	16530
	Min	0.42	91	0.0312 min^{-1}	19.0	4090
	Max:min	4.0	4.0		4.0	4.0
	Total daily	28.40	6120	1.872 h^{-1}	52.4	11460
12	Max	2.17	386	0.0466 min^{-1}	145.7	25970
	Min	0.49	87	0.0466 min^{-1}	32.7	5840
	Max:min	4.5	4.4		4.5	4.4
	Total daily	28.98	5160	2.796 h^{-1}	81.0	14430

12, and 16 °C were respectively 280, 127, 282, and 214 cells ml^{-1}, or 30.5, 11.6, 20.7, and 16.4 µg C l^{-1} (Fig. 2, Table 5). Converting gut pigments to cells copepod^{-1}, to correct for differences in the chlorophyll pigments cell^{-1} in different experiments, yields slightly different threshold estimates of 258, 130, 280, and 223 cells ml^{-1}, or 28.1, 11.9, 20.6, and 17.1 µg C l^{-1} respectively at the 4 temperatures (Fig. 3, Table 5). Finally, conversion of gut contents to ingestion rate, to correct for differences in gut evacuation rate in experiments, yields estimates of 304, 129, 285, and 212 cells ml^{-1}, or 33.1, 11.8, 20.9, and 16.2 µg C l^{-1} (Fig. 4, Table 5).

A regression of threshold vs temperature yielded a nonsignificant slope, indicating no trend in lower feeding thresholds with increasing temperature. The significance of differences among the thresholds was initially tested using covariance analysis of the segmented regressions. However regression slopes for the right-hand segments of the data were found to increase significantly with temperature ($p < 0.001$; Figs. 2, 3 & 4), rejecting the hypothesis of the equality of slopes, a requirement for further covariance analysis. The thresholds were therefore compared using pairwise t-tests, where the value of α in the t statistic is corrected for the number of pairwise comparisons according to: $\alpha = \alpha/(2n)$ where n = 6 in the present study (C. Hanumara pers. comm.). To test for differences at the 5 % significance level, α was adjusted to $\alpha = 0.05/(2 \times 6) = 0.004$. Differences among thresholds

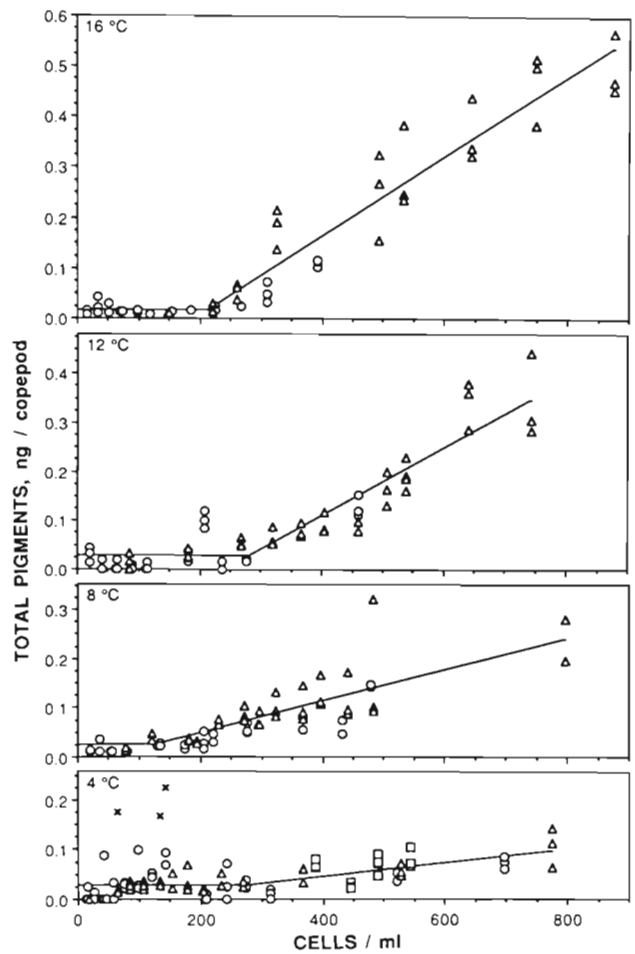

Fig. 2. *Acartia hudsonica*. Gut contents (µg total pigments copepod^{-1}) of adult females fed different concentrations of *Thalassiosira constricta* at 4 temperatures. Segmented linear regression fit to data indicate a lower feeding threshold at the junction of the 2 segments. Left-hand segment represents 'background' gut contents, which may include residual gut contents from high pre-experimental food concentration, or represent occasional feeding at low experimental food concentration. Right-hand segment represents actively feeding copepods. Replicate experiments: A (○), B (△) and C (□, 4 °C only). Three data points at 4 °C marked as X's were omitted from the analysis; further explanation in text

Table 5. *Acartia hudsonica*. Lower feeding thresholds for adult females fed *Thalassiosira constricta* at 4 temperatures. Thresholds (cells ml^{-1}) converted to $\mu g\ C\ l^{-1}$ and $\mu g\ N\ l^{-1}$ from mean relationships in Table 2. Also shown are the mean 'background' values corresponding to the left hand segment of the segmented regressions

Temp (°C)	Background gut contents (ng pigment copepod^{-1}) Mean ± SE	Lower feeding thresholds Cells ml^{-1} Mean ± SE	$\mu g\ C\ l^{-1}$ Mean ± SE	$\mu g\ N\ l^{-1}$ Mean ± SE
	Threshold computed from gut contents (total pigments copepod^{-1})			
4	0.028 ± 0.004	280 ± 29	30.5 ± 3.2	5.2 ± 0.5
8	0.026 ± 0.002	127 ± 52	11.6 ± 4.8	2.2 ± 0.9
12	0.026 ± 0.006	282 ± 15	20.7 ± 1.1	3.8 ± 0.2
16	0.016 ± 0.002	214 ± 18	16.4 ± 1.4	2.6 ± 0.2
	Threshold computed from gut contents (cells copepod^{-1})			
4	11.4 ± 2.1	258 ± 31	28.1 ± 3.4	4.8 ± 0.6
8	12.6 ± 1.1	130 ± 50	11.9 ± 4.6	2.3 ± 0.9
12	10.6 ± 2.5	280 ± 16	20.6 ± 1.2	3.8 ± 0.2
16	7.9 ± 1.1	223 ± 21	17.1 ± 1.6	2.7 ± 0.3
	Threshold computed from ingestion (cells copepod^{-1} min^{-1})			
4	0.28 ± 0.04	304 ± 31	33.1 ± 3.4	5.7 ± 0.6
8	0.73 ± 0.06	129 ± 50	11.8 ± 4.6	2.3 ± 0.9
12	0.61 ± 0.16	285 ± 17	20.9 ± 1.2	3.8 ± 0.2
16	0.54 ± 0.08	212 ± 17	16.2 ± 1.2	2.5 ± 0.2

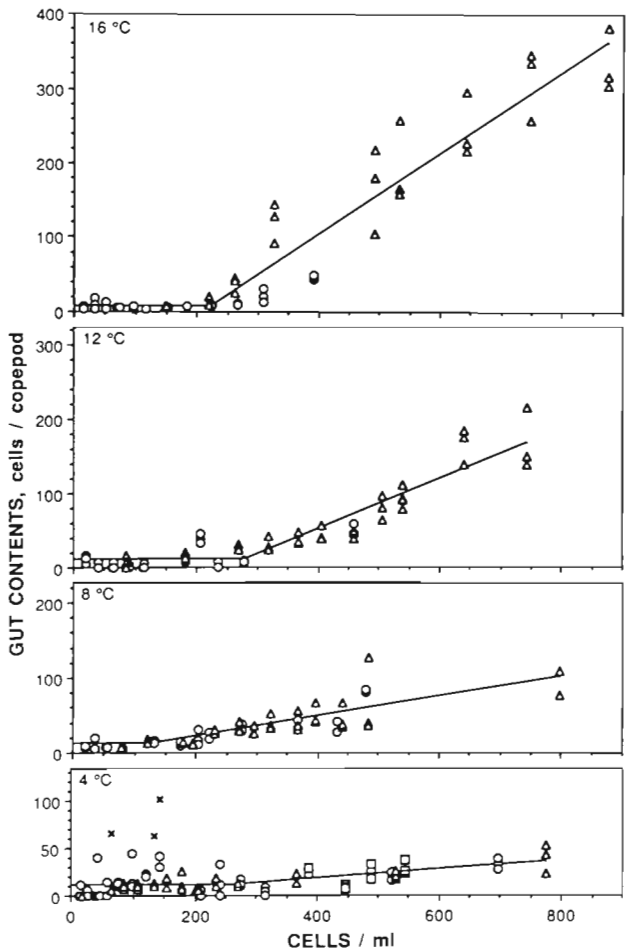

Fig. 3. *Acartia hudsonica*. Gut contents (cell copepod^{-1}) in copepods fed different concentration of *Thalassiosira constricta* at 4 temperatures, showing segmented linear regressions and lower feeding thresholds. Symbols as in Fig. 2; note different scale for 4 °C

were nonsignificant in all combinations but two (4, 8 °C and 12, 16 °C for thresholds estimated from ingestion min^{-1}). These differences were only marginally significant: $t > t_{79,\ 0.004} = 3.11 > 2.99$, and $t > t_{66,\ 0.004} = 3.04 > 3.01$, respectively. From the pairwise comparisons we conclude that differences among lower feeding thresholds were nonsignificant, and showed no trend with temperature.

The increase in the regression slopes of the right-hand segments indicated that, above an approximately constant lower feeding threshold, the rate at which ingestion increased with food level accelerated with temperature (Figs. 2, 3 & 4).

The mean 'background' gut contents and ingestion rates corresponding to the left-hand segment were low, and similar at all 4 temperatures (Table 5). The mean 'background' fluorescence ranged from 0.016 to 0.028 ng pigments copepod^{-1}, or 7.9 to 12.6 cells copepod^{-1}. If these gut contents were derived from feeding they represented very low ingestion rates, where mean ± SE = 0.28 ± 0.04, 0.73 ± 0.06, 0.61 ± 0.16, and 0.54 ± 0.08 cells min^{-1} respectively at 4, 8, 12, and 16 °C, corresponding to 0.7, 1.3, 1.9, and 1.8 % body C d^{-1}.

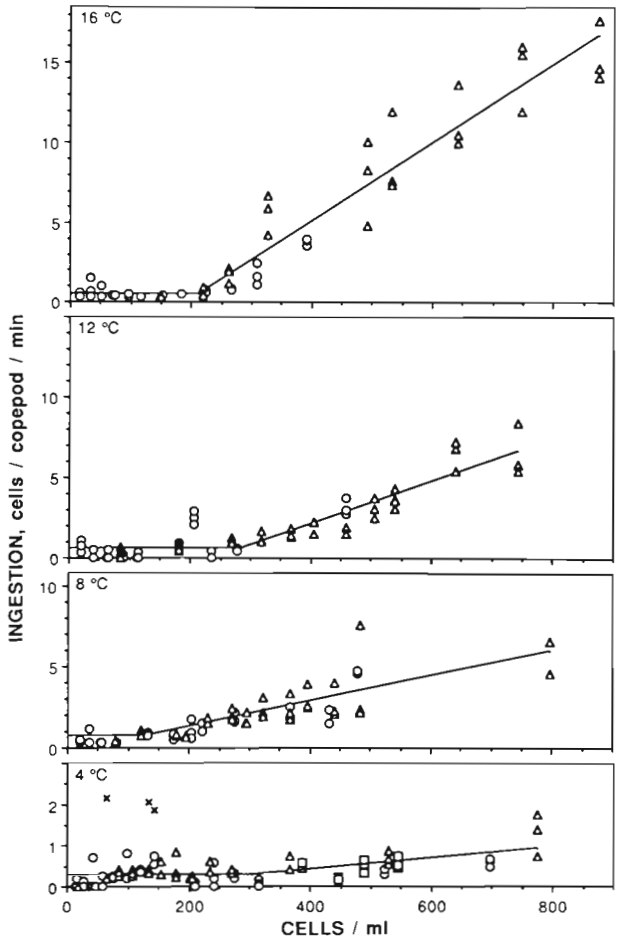

Fig. 4. *Acartia hudsonica*. Ingestion rates in adult females fed different concentrations of *Thalassiosira constricta* at 4 temperatures, as estimated by multiplying the gut contents in Fig. 3 by the corresponding instantaneous gut evacuation rates in Fig. 5. Symbols as in Fig. 2; note different scale for 4 °C

The data at 4 °C were more variable than at the other temperatures, for reasons which cannot be explained. In particular, 3 very high values (the data points shown as X's in Figs. 2, 3 & 4) were several times greater than replicate measurements at the same food concentrations, and fell outside the range of all other observations at low food. Because these 3 data points greatly affected the threshold estimate at 4 °C, a test was performed to determine whether they might be statistical outliers, due to experimental error or some unusual condition of the copepods. According to Grubbs' test (Sokal & Rohlf 1981, p. 413) the 3 points were found to be outliers ($p < 0.05$), and the data were removed before calculation of the segmented linear regressions.

The instantaneous gut evacuation rate R min^{-1} increased with temperature (Fig. 5), with mean values of 0.0239, 0.0494, 0.0518, and 0.0645 min^{-1} respectively at 4, 8, 12, and 16 °C, yielding a Q_{10} of 1.88.

DISCUSSION

Gut fluorescence measurements have revealed diel feeding rhythms in many copepods (Mackas & Bohrer 1976, Hayward 1980, Head et al. 1985, Batchelder 1986, Daro 1988, Ohman 1988, Peterson et al. 1990 and others), including *Acartia* spp. (Kleppel et al. 1985, Stearns 1986, Stearns et al. 1987, Durbin et al. 1990), supporting Petipa's (1958) hypothesis of a diel variation in filtering rate. Diel variation in feeding rate appears to be controlled independently of diel vertical migration to and from the chlorophyll-rich surface layer (Stearns & Forward 1984a, b, Head et al. 1985, Stearns 1986, Dagg et al. 1989). Field studies have suggested that diel feeding rhythms are reduced under low food availability (Boyd et al. 1980, Dagg 1985, Dagg & Walser 1987, Daro 1988), but in the laboratory Durbin et al. (1990) found that the diel feeding rhythm in *A. tonsa* persisted under both high and low food conditions. The stability of the behavior provided indirect evidence that diel feeding rhythms, like diel vertical migration, may reduce vulnerability of the copepods to visual predators (Frost 1988, Haney 1988, Bollens & Frost 1989, Dagg et al. 1989).

In this study the ca 4-fold amplitude of the feeding rhythm in *Acartia hudsonica* was comparable with the 3 to 4-fold amplitude observed in *A. tonsa* (Stearns 1986, Stearns et al. 1987, Kleppel et al. 1988, Durbin et al. 1990). The total daily food consumption at 8 and 12 °C (33.4 and 56.5 % body C respectively) was similar to values obtained at those temperatures (37.2 and 67.9 % body C) in an earlier study with *A. hudsonica* females also fed *Thalassiosira constricta*, where ingestion was determined from the change in the abundance of cells over 24 h (Durbin & Durbin 1992).

The present study demonstrates that a lower feeding threshold exists in *Acartia hudsonica*, consistent with earlier reports of reduced clearance and ingestion rates in other copepod species at low food abundance (Frost 1975, Kiørboe et al. 1985a, Paffenhöfer & Stearns 1988), and direct observations of reduced swimming and feeding activity in copepods when food was absent or of low abundance [Piontkovskii & Petipa 1976 (cited in Paffenhöfer & Stearns 1988), Cowles & Strickler 1983, Price & Paffenhöfer 1986, Gill & Poulet 1988, Jonsson & Tiselius 1990]. Although a lower feeding threshold may be a widespread phenomenon, the response over the same food concentration range differs markedly among copepod species. For example, as food concentration declined below 0.22 µg C l^{-1}, the clearance rate in *Eucalanus pileatus* and *Paracalanus* sp. increased, whereas that in *A. tonsa* sharply declined (Paffenhöfer & Stearns 1988). Thus there will be no single absolute feeding threshold that is generally applicable to different copepod species.

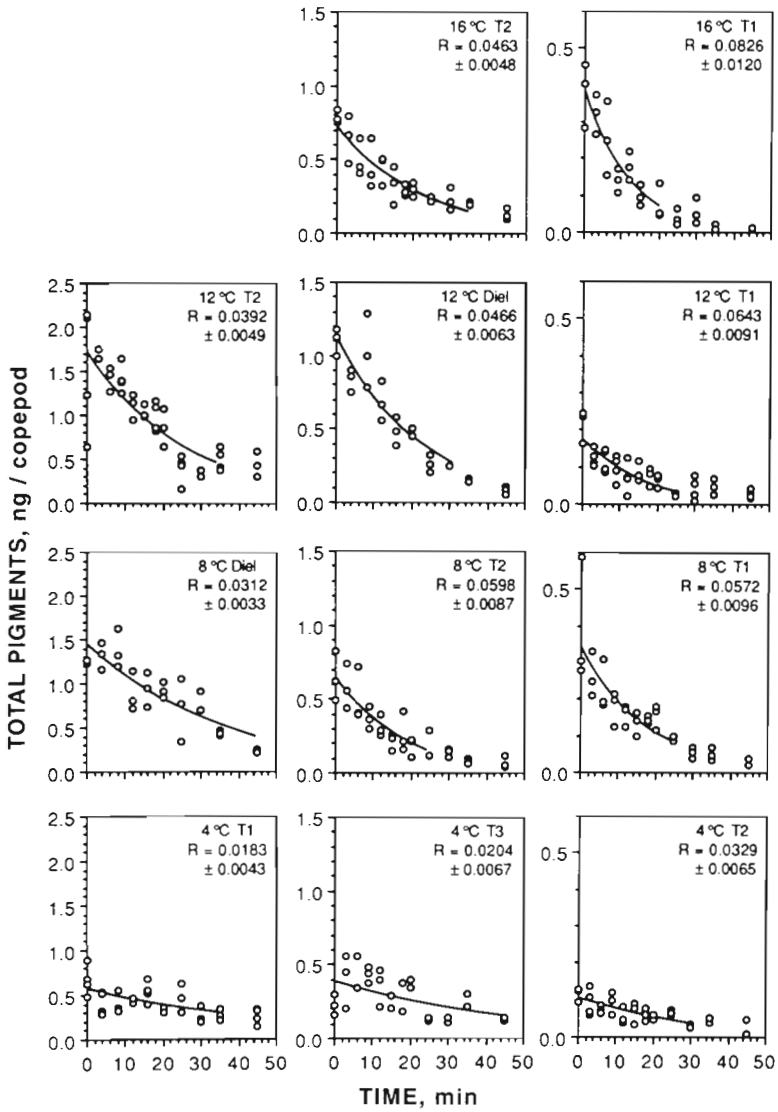

Fig. 5. *Acartia hudsonica*. Gut evacuation at 4 temperatures in adult females fed *Thalassiosira constricta*, and transferred to filtered seawater. The instantaneous gut evacuation rate (R min^{-1} ± SE) was estimated from a curve fit to data up to ca 75 % gut evacuation

Frost (1975) showed that in *Calanus pacificus* the threshold for maximum clearance rate C_m was inversely related to food particle size, reflecting the increased capture efficiency for larger particles. Evidence from *Acartia* spp. suggests that C_t is likewise an inverse function of food size (Table 6). In the present study where the mean *Thalassiosira constricta* cell size was 9.5 to 11.0 µm, C_t was higher than in Durbin & Durbin (1992), who used the same clone of *T. constricta* but of a larger mean cell size (16 to 17 µm) (Table 6). However C_t expressed as µg C l^{-1} was similar in both studies. Similarly, values of C_t and C_m were comparatively high in *A. tonsa* fed the small alga *Rhodomonas baltica* (8 µm), and low for large species like the dinoflagellate *Gymnodinium fissum* (44.4 × 30.6 µm) and the ciliate *Favella* sp. (65 to 75 × 100 to 200 µm) (Table 6). Paffenhöfer & Stearns (1988) found a sharp reduction in clearance rate corresponding to C_m at ca 22 µg C l^{-1} in *A. tonsa* fed *Thalassiosira weissflogii* (12 to 15 µm). In that study feeding continued at a reduced rate through the lowest food concentrations tested (ca 8 µg C l^{-1}), and a true lower feeding threshold C_t was not observed.

Two studies provide information concerning lower thresholds in *Acartia tonsa* fed natural assemblages. Reeve & Walter (1977) fed mixed stages of *A. tonsa* 2 species of cultured algae (*Phaeodactylum tricornutum* and *Dunaliella tertiolecta*), and a natural assemblage dominated by *Skeletonema* sp. at 21 °C and found lower thresholds in the range of about 7 to 18 µg C l^{-1}. Turner & Tester (1989) made extensive measurements of feeding by *A. tonsa* females upon natural assemblages dominated by diatoms and dinoflagellates. Although these investigators did not analyze their data for the existence of lower feeding thresholds, their figures suggest thresholds at about 10^4 cells ml^{-1} and 5 to 10 µg C l^{-1}.

In the present study the lower feeding thresholds varied slightly, depending upon the units of measurement. Correcting gut pigments for the pigment content per cell and gut evacuation rate did not materially change the estimates of lower feeding threshold. Such a correction becomes more important when more than one type of food is given, because both cellular composition and gut evacuation rate may differ considerably.

The small amount of gut fluorescence in copepods at food concentrations below the feeding threshold could have been due to several factors, including copepod body pigments, epiphytic algal growth on the copepod, or residual gut content (there is often some partially digested food present in the gut, unless the animals are starved for a biologically unreasonable long time; see also Baars & Helling 1985). Because zero values were obtained both in filtered seawater and at low food, however, the true background fluorescence for *Acartia hudsonica* was nondetectable and the observed 'background' probably due to residual gut content from the last meal, to reingested fecal pellets, to a low rate of feeding, or to some combination of these. The mean

Table 6. *Acartia* spp. Comparison of lower feeding thresholds

Species	Temp (°C)	Food	Size (µm)	Lower feeding threshold Cells ml^{-1}	µgC l^{-1}	Source
A. tonsa	18	*Rhodomonas baltica*	8[a]	1250	45	Kiørboe et al. (1985a)
A. hudsonica	4	*Thalassiosira constricta*	11.0	280	30.5	This study, from pigment copepod^{-1}
	8		10.5	127	11.6	
	12		9.5	282	20.7	
	16		10.0	214	16.4	
A. hudsonica	4	*Thalassiosira constricta*	17.2	46	9.2	Durbin & Durbin (1992)
	8		17.2	127	19.5	
	12		16.2	95	14.2	
	16		16.4	121	16.9	
A. clausi	20	*Gymnodinium fissum*	44.4 × 30.6	0.05–0.5	0.2–22	Piontkovskii & Petipa (1976)
A. tonsa	20	*Favella* sp.	65–75 × 100–200	0.01–0.1	0.02–2	Stoecker & Sanders (1985)

[a] The length of 18 µm given in the text of Kiørboe et al. (1985) was an error; T. Kiørboe pers. comm.

gut contents represented only a few cells copepod^{-1}, much less than the contents of a single fecal pellet (0.19 ng total pigments pellet^{-1} in *A. hudsonica* fed 2000 cells ml^{-1} *Thalassiosira constricta* at 16 °C; Wlodarczyk unpubl.), and corresponded to an ingestion rate of < 2 % body C d^{-1}.

If the gut contents at food concentration $< C_t$ represent feeding, rather than incomplete gut evacuation, does this indicate active feeding or incidental food intake during swimming? Piontkovskii & Petipa (1976, cited in Paffenhöfer & Stearns 1988), made visual observations of feeding behavior by *Acartia clausi* fed the dinoflagellate *Gymnodinium fissum* (44.4 × 30.6 µm) at 20 °C. The behavior of copepods at the lowest food level (0.05 cells ml^{-1}, or ca 0.2 µg C l^{-1}) was comparable to that of copepods with no food: both groups swam actively searching for food, but made few grasping movements with their feeding appendages (5.0 and 4.4 movements min^{-1}) respectively. In 6 feeding trials at 0.05 cells ml^{-1} only 1 cell was ingested, indicating that the capture efficiency, or percentage of cells encountered that were ingested, was about 16 %. At higher food concentrations (0.5 to 15 cells ml^{-1}), the number of grasping movements increased from 13 to 49 min^{-1}; the capture efficiency ranged from 16 to 26 %, and seemed to be not greatly affected by food concentration. In our study, the mean ingestion rate that would correspond to the observed gut contents ranged from about 0.3 to 0.7 cells copepod^{-1} min^{-1}. With an assumed efficiency of 16 %, these feeding rates would still only constitute 1.9 to 4.4 grasping movements min^{-1}. Thus the low ingestion rates computed for *A. hudsonica* below the threshold do not suggest an activity level above that which, as shown by Piontkovskii & Petipa, occurs even in the absence of food.

Vidal (1980a, b, c) has shown that the minimum food concentrations required for *Calanus pacificus* and *Pseudocalanus* sp. to achieve maximum body size, development and production rates increase with temperature, because of the increasing cost of metabolism. The present study indicates, however, that the lower feeding threshold C_t in *Acartia hudsonica* does not change significantly with temperature. Durbin & Durbin (1992), using another method, also found that C_t, C_m, and C_c in *A. hudsonica* were not significantly different between 4.5 and 16 °C. In contrast clearance and ingestion rates per unit body weight increased significantly with temperature. These relationships are summarized in Fig. 6.

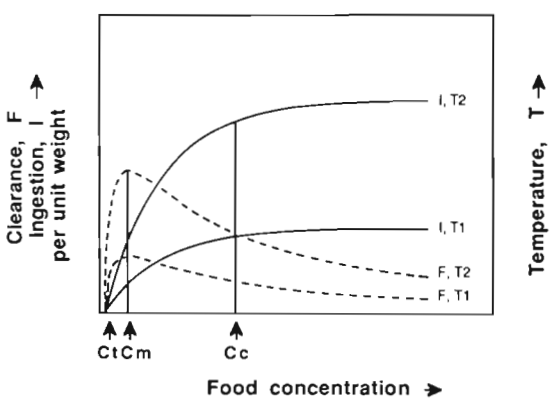

Fig. 6. *Acartia hudsonica*. Effect of temperature upon clearance (- - -) and ingestion (——) curves. Clearance and ingestion rates per unit weight increase with temperature, but the food concentrations associated with the lower feeding threshold C_t, the maximum clearance rate C_m, and the critical concentration C_c (here assumed to correspond to ingestion at 90 % of I_{max}) remain approximately constant

Gut evacuation rates at the same temperature were somewhat variable (Fig. 5). Experimental conditions were carefully standardized, and measurements taken at closely spaced intervals to describe the principal period of gut evacuation. Differences among replicate experiments remain unexplained, but may be attributed in part to the highly variable nature of individual gut contents (e.g. 50 to 100-fold in *Acartia tonsa*; Kleppel et al. 1988, Durbin et al. 1990), which remains significant even in pooled samples, and contributes to uncertainty in gut evacuation estimates.

Temperature strongly affected gut evacuation rates. Instantaneous rates measured in the present study were comparable to those reported by Kiørboe & Tiselius (1987) and Durbin et al. (1990) for *Acartia tonsa*. However Stearns et al. (1987) reported a much slower gut passage time of 30 min (equivalent to R = 0.033 min^{-1}) for *A. tonsa* at 25 °C fed *Thalassiosira weissflogii* 2 h prior to the experiment. The rate of gut evacuation in copepods has been shown to be temperature dependent, but the reported Q_{10} values differ widely [3.8 for *Centropages hamatus*, Kiørboe et al. (1982); 5.4 for *Neocalanus plumchrus*, Dagg & Wyman (1983); 4.1 for *Eudiaptomus graciliodes*, Christofferson & Jespersen (1986); 2.4 for *Temora longicornis*, and 2.2 for pooled data from several species, Dam & Peterson (1988). These values compare with the present Q_{10} of 1.88 for gut evacuation in *A. hudsonica*.

The lower feeding thresholds reflect the sensory and physical capabilities of each copepod species, and prey characteristics including size, motility, chemistry, and escape response, that affect its vulnerability to the copepod. In an evolutionary sense the lower thresholds are an expression of the bioenergetic cost of feeding in relation to food availability in those environments to which copepod species have become adapted. The study by Paffenhöfer & Stearns (1988) indicates that copepods from food-poor environments (e.g. *Paracalanus*) should have lower feeding thresholds than those from food-rich environments (*Acartia*). While on the time scale of an individual copepod, thresholds appear invariant with temperature, the effect of temperature upon the thresholds may well have been 'built in' over evolutionary time as part of the overall physical and behavioral development of a species.

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