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Seasonal changes in maximum ingestion rate of *Acartia tonsa* in Narragansett Bay, Rhode Island, USA

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ABSTRACT: Maximum ingestion rate (I_{max}) in *Acartia tonsa* females from Narragansett Bay, Rhode Island, USA, when measured under standardized conditions of temperature (20 °C) and food (the diatom *Thalassiosira weissflogii*), varied by a factor of 2 to 3 (22 000 to 50 320 cells copepod^{-1} d^{-1}, 6.00 to 18.6 µg C copepod^{-1} d^{-1}, and 1.33 to 3.32 µg N copepod^{-1} d^{-1}, or 121 to 376 % final body C d^{-1}, and 90 to 245 % final body N d^{-1}). Overall mean values were 38 200 cells copepod^{-1} d^{-1}, 10.3 µg C copepod^{-1} d^{-1}, 1.96 µg N copepod^{-1} d^{-1}, 203 % final body C d^{-1}, and 146 % final body N d^{-1}. Copepods gained weight during laboratory incubations, and consequently I_{max} averaged 25.6 % and 19.9 % higher as a percentage of initial, than of final, body C and N. I_{max} was most strongly related to the residual effects of field temperature, and secondarily to *in situ* food level, and initial body weight and condition factor (CF: weight per unit length). Weight and CF were strongly affected by the degree of food limitation. I_{max} was highest in copepods with low initial body weight and CF, and from the poorest food conditions in the field. This compensatory increase in I_{max} resembles the hunger response described for other copepods, and would enable food-limited *A. tonsa* to more effectively exploit transient plankton blooms. Copepods increased significantly in both weight and CF during the 24 h laboratory incubations, demonstrating that body size was food limited even during plankton blooms. Mean weight increments over 24 h were 27.8 % C, 20.3 % N, and 22.6 % dry weight. The amount of growth, and the growth efficiency, were inversely related to initial CF. Thus copepods that were most severely food limited in the field not only exhibited higher I_{max} and higher growth rates, but also allotted a greater fraction of ingested energy to growth, when provided with excess food in the laboratory.

KEY WORDS: *Acartia* · Zooplankton · Copepod

INTRODUCTION

In copepods the relationship between food concentration and grazing rate typically follows a saturation curve, of which the parameters of greatest interest are the maximum feeding rate I_{max}, the maximum clearance rate F_{max}, a possible lower feeding threshold C_t, and the food concentrations corresponding to I_{max} and F_{max} (C_c and C_m, respectively) (Parsons et al. 1967, Frost 1972, Mullin et al. 1975). Among these I_{max} is perhaps most important, because it establishes an upper limit to grazing rate. In contrast to F_{max}, I_{max} occurs over a broad range of food concentrations and can be determined relatively easily.

I_{max} and F_{max} in field-collected copepods have been shown to vary significantly when measured under standardized conditions of temperature and food in the laboratory (Runge 1980, Hassett & Landry 1990a). Such variation has been attributed to seasonal changes in the behavioral and physiological acclimation of zooplankton to variation in food supply (Mayzaud & Poulet 1978, Hassett & Landry 1983, 1990b, Landry & Hassett 1985, Mayzaud & Mayzaud 1985, Roche-Mayzaud et al. 1991), to the onset of the spring bloom and development of the digestive system after diapause (Runge 1980, Hassett & Landry 1990a), to seasonal change in body size (Runge 1980) or temperature (Deason 1980), or to other, unknown causes (Checkley 1980). In natural populations, however, the extent to which I_{max} and F_{max} vary in response to the interactive effects of

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changing environmental conditions, body size, and physiological condition remains poorly known.

In Narragansett Bay food and temperature conditions during summer and fall show short-term variability (Durbin et al. 1983) that may influence the ingestion capabilities of the dominant copepod *Acartia tonsa*. Here we investigate variation in the maximum ingestion rate of field-collected *A. tonsa* females, measured under constant conditions in the laboratory, in relation to changing field temperature, food availability, and body size.

MATERIAL AND METHODS

Plankton were collected twice weekly at about 09:00 h from a station in lower Narragansett Bay (Fig. 1 in Durbin et al. 1992), during a 2 mo period from 11 August to 6 October 1988. The water column depth was 8 m. Whole water samples for phytoplankton analysis were collected from surface, middle and bottom depths using a diaphragm pump, and the temperature measured at each depth. Equal volumes of approximately 1 l from each depth were pooled in a 4 l plastic bottle and returned to the laboratory. Live zooplankton for the laboratory grazing experiments were collected using gentle vertical hauls of a 0.5 m diameter, 250 µm mesh net, transferred to a 20 l bucket containing surface seawater, and returned to the laboratory within 1 h of collection.

In the laboratory duplicate 100 ml subsamples of bay water were filtered onto pre-combusted 2.5 mm Gelman AE glass fiber filters for determination of particulate C and N content. Bay water was size-fractionated with 10 µm Nitex screen, and triplicate samples of the total and <10 µm size fraction were filtered onto GF/F 2.5 cm diameter glass fiber filters for chlorophyll *a* (chl *a*) analysis.

The initial size of adult female *Acartia tonsa* was estimated from a subset of copepods immediately after the grazing experiments were set up (within 4 h of collection). Copepods were anesthetized in a solution of 0.576 g ethyl 3-aminobenzoate (MS-222) l^{-1} in chilled, filtered seawater (Durbin et al. 1990). Triplicate groups of 20 adult females were sorted and their images recorded on videotape for later length determination. Copepods from each group were briefly rinsed in deionized water to remove the salt, and placed on a preweighed aluminum pan for a pooled determination of dry wt and C and N contents. Samples were stored in a dessicator at room temperature. The same procedure was repeated with the copepods at the end of the feeding experiments.

The experimental food, the unicellular diatom *Thalassiosira weissflogii*, was a new large-cell isolate obtained from a culture containing post-auxospore cells shortly before the experiments began. Batch cultures were grown in f/2 nutrient media (Guillard & Ryther 1962) at 20°C, and illuminated with cool white fluorescent light at an irradiance of 180 µE $m^{-2} s^{-1}$. A light:dark cycle of 14:10 h approximated field conditions at the time. Cell concentrations in these cultures were monitored with a Model ZM Coulter Counter fitted with a 140 µm diameter aperture. Cells were used for experiments during the early log phase of growth.

Ingestion was measured at 8 concentrations of *Thalassiosira weissflogii* (200, 600, 1000, 2000, 3000, 4000, 5000, 6000 cells ml^{-1}), during 24 h experimental incubations. At each food concentration, 2 jars containing *Acartia tonsa* females provided replicate measurements of feeding rate, while 2 jars without grazers served as controls to estimate phytoplankton growth during the experiment. Experimental containers were widemouth glass jars, with lids fitted with a liner made of 3 mm thick closed-cell polyethylene foam to provide a tight seal. Jar size and the number of grazers were manipulated to ensure that the instantaneous grazing coefficient remained near 0.2 d^{-1}. Experimental jar volumes were 2 l for the 200 and 600 cell ml^{-1} concentrations, 1 l for 1000 to 3000 cells ml^{-1}, and 500 ml for 4000 to 6000 cells ml^{-1}. Control jars containing only phytoplankton were all 1 l volume. The 3 lowest food concentrations contained 20 grazers per jar, while the rest of the treatments had 30 *A. tonsa* each.

Prior to each experiment the concentration of cells in the stock culture was determined, and the experimental food concentrations obtained by adding known volumes of culture to 5 l containers of filtered seawater. Jars were filled with the experimental media, and a 50 ml sample taken from each jar and preserved in dilute Lugol's iodine solution for determination of the initial phytoplankton concentration. Once the jars were ready (approximately 2 h), groups of either 20 or 30 adult female *Acartia tonsa* were sorted and transferred to them.

Jars were topped off with media of the appropriate concentration, closed carefully to prevent loss of copepods, and placed on a 1 rpm plankton wheel. Jars were attached normal to the axis of rotation, to turn end-over-end. The plankton wheel was mounted inside a clear acrylic box through which temperature conditioned water was circulated; temperature control was ±0.1°C. The temperature for all experiments was 20°C and the irradiance level 125 µE $m^{-2} s^{-1}$, on a 14:10 h light:dark cycle.

After 24 h the jars were taken from the plankton wheel, mixed and a subsample preserved in dilute Lugol's iodine solution for later determination of cell concentration. Copepods were collected on a 200 µm screen, rinsed into a Petri dish and anesthetized in MS-222, and processed for length and weight determination as described above.

At the end of each experiment duplicate subsamples of 50 ml were taken from one of the 1000 cell ml^{-1} control jars for determination of *Thalassiosira weissflogii* chl *a*, C and N content.

Copepod dry wt was measured with a Cahn electrobalance. A Hewlett-Packard Model 185B and a Carlo Erba NA 1500 were used for analysis of plankton C and N contents. Phytoplankton chl *a* was determined by fluorescence (Parsons et al. 1984). Phytoplankton cell concentrations were counted with a Coulter model ZM-C1000 Accucomp System particle counter calibrated with 18.8 µm microspheres. Five 0.5 ml subsamples were counted, and the mean value used to calculate rates of ingestion and phytoplankton cell growth.

Video images were recorded with an MTI Dage video camera interfaced with a Wild M5 dissecting microscope and a Panasonic NV 8950 video recorder. Cephalothorax length was measured from the video images using an IBM compatible ImageMeasure program. The system was calibrated before each series of measurements with a video image of a micrometer scale, taken at the same microscope magnification (16×) as used for the copepods.

Copepod condition factor (CF), a measure of weight per unit length, was calculated according to Durbin et al. (1992) as:

$$CF = aW/L^3 \quad (1)$$

where a is a dimensionless constant equal to 0.1, 0.2 and 0.8 for D-CF (dry-weight CF), C-CF, or N-CF respectively, W is the dry wt, or C or N content (µg female^{-1}), and L is the cephalothorax length (mm).

Ingestion rates and the instantaneous rates of phytoplankton growth in each treatment were calculated according to the equations of Frost (1972). The relationships between ingestion and food concentration (see Fig. 8) indicated that the critical concentration C_c, above which ingestion saturated, varied from <200 cells ml^{-1} (Expts 7 & 11) to ~1000 cells ml^{-1} (Expts 3 & 9). I_{max} was therefore calculated as the mean of all ingestion values for food concentrations ≥2000 cells ml^{-1}. Mean final body size (Table 2) was also computed from treatments ≥2000 cells ml^{-1} to conform with I_{max}.

Empirical models were fit using a nonlinear least squares estimation procedure on nontransformed data (Procedure NLIN, DUD method of computation) from the Statistical Analysis System (SAS) Version 5, on an IBM 4381 computer (Ralston & Jenrich 1979). For statistical analysis of copepod length, weight, and C and N contents a parametric *t*-test for unpaired samples was used. The data set was tested for normality using the Kolmogorov Smirnov test. The significance level used was $p < 0.05$. Average values reported in the text are the means ± standard error.

RESULTS

Environmental conditions

Temperature at the field station declined from 23.3 to 16.2°C during the period of study (Table 1). Phytoplankton exhibited several short blooms, with peaks

Table 1. Field temperature and food level, and size, chemical composition and mean instantaneous daily growth rate (k) of the *Thalassiosira weissflogii* culture

Expt	Field						*Thalassiosira weissflogii*			
	Date 1988	Temp. (°C)	Chl *a* (µg l^{-1}) Total	Chl *a* (µg l^{-1}) >10 µm	C (µg l^{-1})	N (µg l^{-1})	Chl *a* (pg $cell^{-1}$)	C (pg $cell^{-1}$)	N (pg $cell^{-1}$)	k (d^{-1})
1	Aug 11	23.3	4.4	2.8	607	81.7	13.6	369.8	64.1	0.50
2	Aug 15	23.6	6.0	2.5	674	149.8	11.7	337.5	81.1	0.60
3	Aug 18	22.5	4.4	2.7	550	98.1	10.0	246.0	53.1	0.59
4	Aug 22	21.3	11.0	8.5	1036	148.3	13.6	293.3	59.2	0.42
5	Aug 25	19.8	6.9	6.2	699	126.7	12.4	223.6	37.8	0.52
6	Aug 29	20.5	3.1	1.9	526	89.2	11.0	295.0	53.3	0.30
7	Sep 1	20.5	3.0	1.8	486	80.3	11.1	250.6	47.6	0.55
8	Sep 6	20.0	10.0	6.9	818	161.0	12.2	283.5	53.1	0.50
9	Sep 12	19.3	2.9	1.5	536	121.9	12.1	233.5	41.7	0.43
10	Sep 15	18.5	2.7	0.8	464	77.1	13.6	272.5	61.2	0.52
11	Sep 19	18.6	3.9	0.6	439	–	13.8	247.6	53.3	0.54
12	Sep 26	18.0	2.9	0.8	672	81.6	10.0	247.5	42.6	0.47
13	Sep 29	17.5	4.4	1.2	426	88.9	8.8	222.6	37.6	0.61
14	Oct 3	17.8	8.8	5.3	742	130.6	12.0	222.3	40.4	0.41
15	Oct 6	16.2	5.1	3.5	424	80.1	12.4	261.4	44.7	0.35
Mean		19.8	5.3	3.1	607	108.2	11.9	267.1	51.4	0.49
SE		0.6	0.7	0.6	44	8.1	0.4	11.1	3.0	0.02

(8.8 to 11.0 µg chl *a* l^{-1}) in late August, early September and early October (Fig. 1A; Table 1). Chlorophyll minima (2.7 to 3.1 µg chl *a* l^{-1}) occurred during late August and mid-/late September. The >10 µm size fraction, the size class most available to *Acartia tonsa* females (Bartram 1980, Berggreen et al. 1988), ranged between 0.6 and 8.5 µg chl *a* l^{-1}, and averaged 54% of total chl *a* (Fig. 1A; Table 1). Chlorophyll peaks were associated with increases in the >10 µm size fraction, causing total and >10 µm chl *a* to follow the same temporal trend. Algal blooms on 11 and 22 August and 6 September were produced by the chain-forming diatom *Skeletonema costatum*. In contrast the bloom on 3 October was due to *Coscinodiscus* sp., and the increased chl *a* reflected large cell size (approximately 300 µm valve diameter) rather than high cell abundance (P. Fofonoff & T. Smayda, University of Rhode Island, pers. comm.). Particulate C and N (Fig. 1B) were positively correlated with chl *a* (Fig. 1C) and followed a similar temporal trend. The positive *y*-intercepts in Fig. 1C indicate non-phytoplankton concentrations of 326 µg C and 61 µg N l^{-1}. The C:N ratio ranged from 4.4 to 8.2 (mean = 5.8 ± 0.3; Table 1) and was unrelated to phytoplankton biomass as measured by total chl *a*.

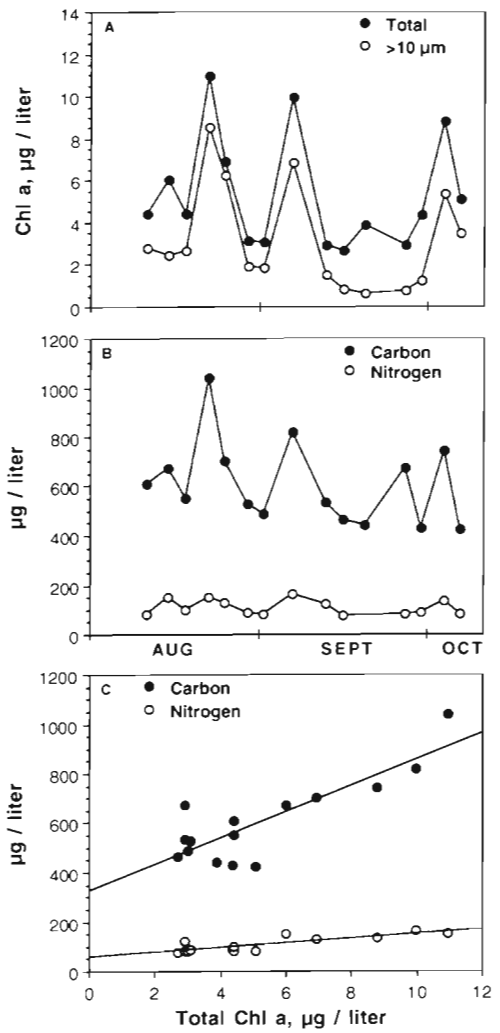

Fig. 1. Environmental conditions in Narragansett Bay during the study period. Field chl *a* (µg l^{-1}), total and >10 µm size fractions, particulate C and N (µg l^{-1}), and C vs chl *a* and N vs chl *a*, where: C (µg l^{-1}) = 326 + 53.1chl *a* (µg l^{-1}), R^2 = 0.71; and N (µg l^{-1}) = 61 + 8.9chl *a* (µg l^{-1}), R^2 = 0.66

Laboratory food

Thalassiosira weissflogii cellular C and N declined during the first 2 experiments, but afterward stabilized and showed only slight variation during the remainder of the study (Table 1). Mean cell diameter was 18 to 23 µm. Mean cellular composition was 11.9 ± 0.4 pg chl *a* $cell^{-1}$, 267.1 ± 11.1 pg C $cell^{-1}$, 51.4 ± 3.0 pg N $cell^{-1}$, and 5.3 ± 0.2 C:N ratio (Table 1). The instantaneous daily growth rate *k* was similar at the different cell concentrations in each experiment, and showed no trend with increasing cell concentration as found by Durbin & Durbin (1992a). The overall mean *k* was 0.49 ± 0.02 d^{-1} (Table 1).

Acartia tonsa body size

Cephalothorax length varied considerably during the study period (Fig. 2A), indicating a continual influx of new females into the population. The most pronounced changes were observed between 1 and 6 September, when mean initial size decreased from 932 to 860 µm, and 26 and 29 September, when it increased from 905 to 949 µm. The mean initial length was 924 ± 9 µm (range 860 to 987 µm) (Table 2).

Initial body C, N, dry wt and CF followed similar trends, with a peak in late August, low values in September, and an increase in late September-early October (Fig. 2). Overall individual mean weights were 4.07 ± 0.16 (range 3.15 to 5.05) µg C, 1.14 ± 0.05 (range 0.87 to 1.43) µg N, and 11.2 ± 0.5 (range 8.5 to 14.5) µg dry wt (Table 2). Mean copepod initial C:N ratio was 3.6 ± 0.03 (range 3.3 to 3.8). Comparable CF values were 1.04 ± 0.03 (range 0.81 to 1.24) for C-CF, 1.17 ± 0.03 (range 0.93 to 1.37) for N-CF, and 1.43 ± 0.04 (range 1.19 to 1.69) for D-CF (Table 2). Low weight and CF during September coincided with the lowest observed food levels during the study. The variable CF meant that seasonal changes in body weight were due to changes in copepod nutritional status as well as body length.

Initial cephalothorax length showed only a weak correlation with environmental temperature (*T*, °C) and

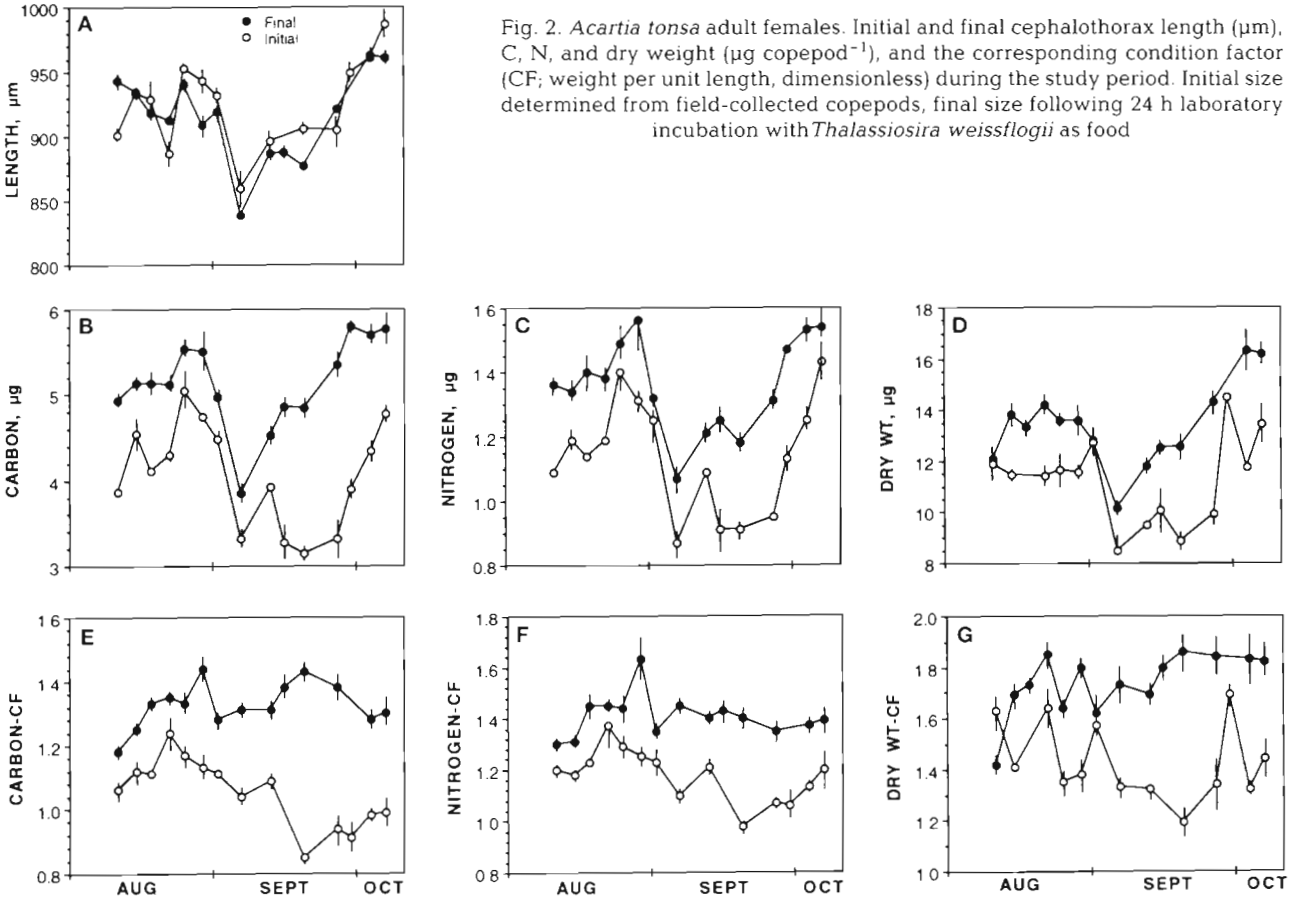

Fig. 2. *Acartia tonsa* adult females. Initial and final cephalothorax length (µm), C, N, and dry weight (µg copepod^{-1}), and the corresponding condition factor (CF; weight per unit length, dimensionless) during the study period. Initial size determined from field-collected copepods, final size following 24 h laboratory incubation with *Thalassiosira weissflogii* as food

Table 2. *Acartia tonsa* adult females. Initial and final cephalothorax length, C, N, dry weight, and the corresponding condition factors. Significant differences between initial and final size marked by •

Expt	Length (µm)		C (µg)		N (µg)		Dry wt (µg)		C-CF		N-CF		D-CF	
	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final
1	901	943•	3.87	4.93•	1.09	1.36•	11.9	12.1	1.06	1.17•	1.20	1.28•	1.63	1.43•
2	933	935	4.54	5.14•	1.19	1.34•	11.5	13.8•	1.12	1.26•	1.18	1.31•	1.41	1.68•
3	929	918	4.11	5.13•	1.14	1.40•	-	13.4	1.11	1.33•	1.23	1.44•	–	1.72•
4	887	913•	4.30	5.12•	1.19	1.38•	11.4	14.2•	1.24	1.34•	1.37	1.45	1.64	1.88•
5	953	941	5.05	5.54•	1.40	1.49	11.7	13.6•	1.17	1.34•	1.29	1.44	1.35	1.64•
6	943	908	4.75	5.51•	1.31	1.56	11.6	13.6•	1.13	1.46•	1.25	1.64•	1.38	1.80•
7	932	920	4.49	4.97•	1.25	1.32	12.7	12.8	1.11	1.29•	1.23	1.36	1.57	1.64
8	860	838	3.32	3.85•	0.87	1.07•	8.5	10.1•	1.04	1.30•	1.10	1.44•	1.33	1.68•
9	896	886	3.92	4.53•	1.09	1.21•	9.5	11.8•	1.09	1.31•	1.21	1.42•	1.32	1.71•
10	–	888	3.27	4.86•	0.91	1.25•	10.1	12.5•	–	1.39	–	1.43	–	1.78
11	906	877•	3.15	4.84•	0.91	1.18•	8.9	12.6•	0.85	1.43•	0.98	1.40•	1.19	1.90•
12	905	921	3.32	5.35•	0.95	1.31•	9.9	14.3•	0.81	1.37•	0.93	1.35•	1.34	1.92•
13	949	–	3.90	5.80•	1.13	1.47•	14.5	–	0.91	–	1.06	–	1.69	–
14	961	963	4.34	5.70•	1.25	1.53•	11.7	16.3•	0.98	1.30•	1.13	1.38•	1.32	1.82•
15	987	961	4.77	5.77•	1.43	1.54	13.5	16.2•	0.99	1.30•	1.20	1.38	1.44	1.81•
Mean	924	915	4.07	5.14	1.14	1.36	11.2	13.4	1.04	1.33	1.17	1.41	1.43	1.74
SE	9	9	0.16	0.13	0.05	0.04	0.5	0.4	0.03	0.02	0.03	0.02	0.04	0.03

food level (P, µg chl a l^{-1}), according to the following empirical relationship:

$$\text{Initial length (µm)} = 1100\,[e^{-0.0083\,T}(1 - e^{-4.94\,P})] \quad (2)$$
$$R^2 = 0.27$$

In contrast initial C, N, C-CF and N-CF were strongly dependent upon food level (Fig. 3), but not temperature. Dry wt and D-CF exhibited similar patterns, although the coefficients of determination were lower (Fig. 3).

During the 24 h experimental incubations, copepod body weight and CF increased, while length remained approximately constant. Growth increments averaged 27.8 ± 4.4 % (range 9.7 to 61.1 %) body C, 20.3 ± 2.7 %

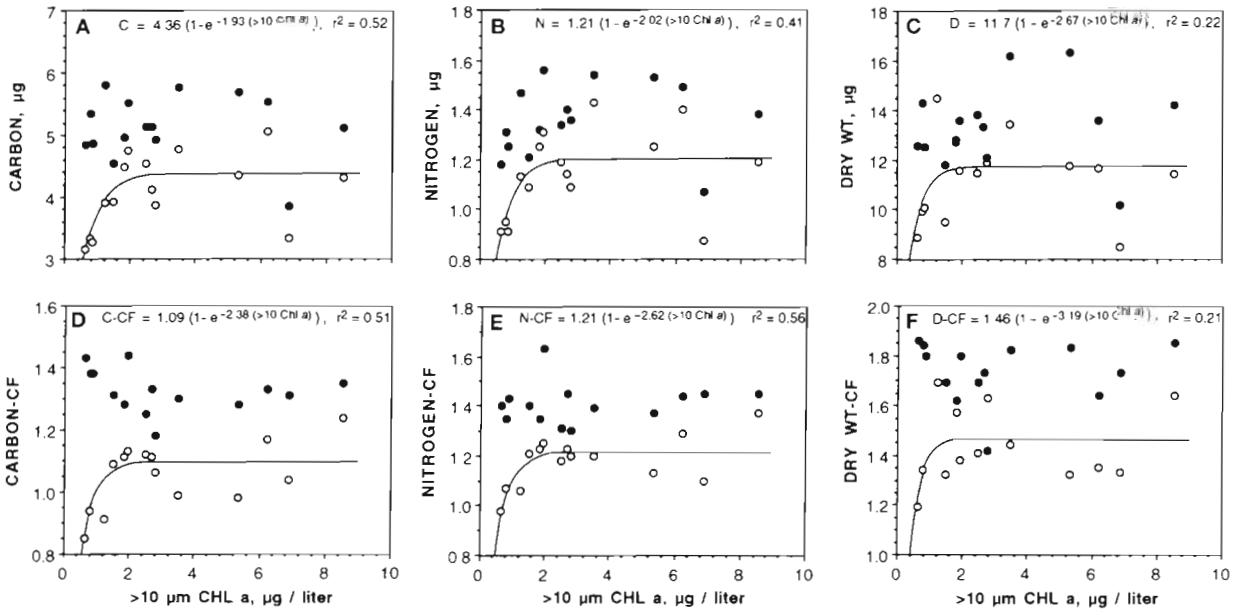

Fig. 3. *Acartia tonsa* adult females. Body C, N, dry weight (µg copepod^{-1}), and the corresponding condition factor (CF), in relation to the >10 µm chl a in the field. (○) initial weight and CF; (●) final weight and CF

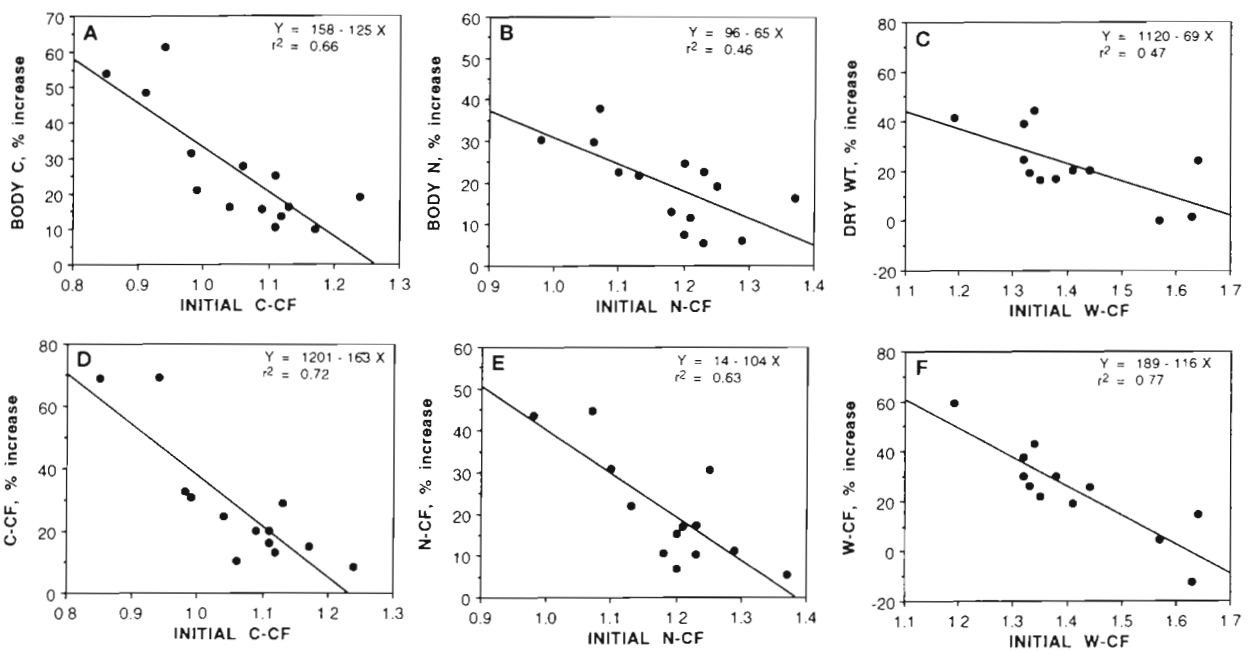

Fig. 4. *Acartia tonsa* adult females. Percent increase in body mass and condition factor (CF) during 24 h laboratory incubation with *Thalassiosira weissflogii*, in relation to initial CF

(range 5.5 to 37.8 %) body N, and 22.6 ± 3.7 % (range 0.4 to 44.2 %) dry wt, respectively (Table 2, Fig. 2). Increases were significant in all cases for C and C-CF, and in most cases for N, dry wt, and their corresponding CF. Changes in cephalothorax length, though sometimes significant, were small and averaged −0.6 ± 0.7 % (range −3.8 to 4.8 %) (Table 2). These results demonstrate that body weight and CF were food limited in the field, even during plankton blooms. The amount of laboratory growth was greatest during September during the seasonal minima in food level, copepod weight and CF, indicating that food limitation was most intense during this interval.

The amount of growth in the laboratory was negatively correlated with initial CF (Fig. 4). Thus copepods with the lowest initial CF, corresponding to the poorest food conditions in the field, grew the most when provided with excess food in the laboratory.

The final size of the copepods did not differ significantly at the different experimental food concentrations (Fig. 5), although ingestion rates were sometimes reduced at the lowest food levels (see Fig. 8). A similar final body size at all levels of feeding implies that a larger fraction of the ingested energy was allocated to body growth at the lowest food concentrations.

The seasonal change in the allocation of ingested food to body growth was examined with a partial growth efficiency pK_1 (Growth/Ingestion, neglecting egg production). pK_1 remained fairly stable between 11 August and 12 September (mean = 0.061 ± 0.005 for C and 0.078 ± 0.008 for N) in spite of widely fluctuating food levels in the field, but increased abruptly on 15 September and remained elevated through the end of the study (mean = 0.21 for both C and N) (Fig. 6A). Growth efficiency, like growth rate, was negatively correlated with initial CF (Fig. 6B, C) and food level in the field. Thus copepods that were most severely food limited in the field not only exhibited higher growth rates, but also allotted a greater fraction of ingested energy to growth, when provided with excess food in the laboratory.

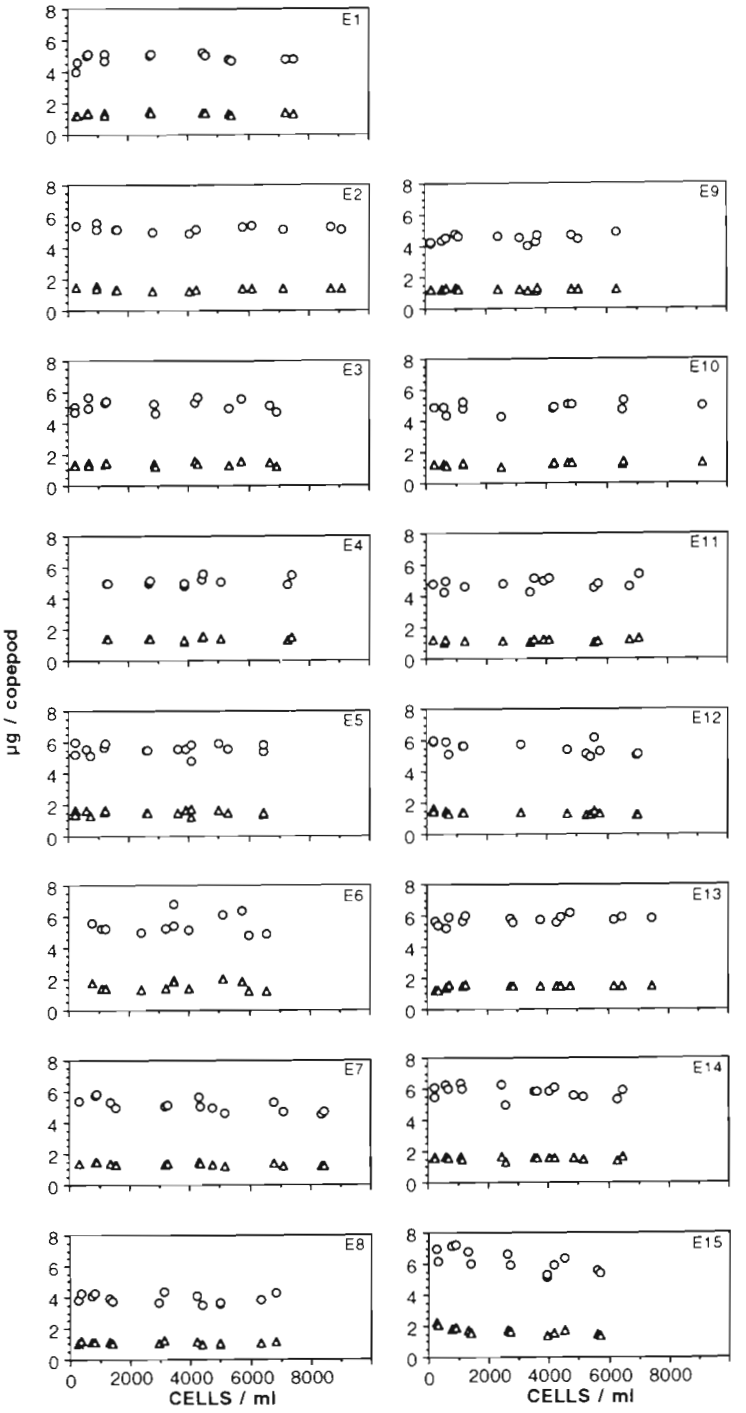

Fig. 5. *Acartia tonsa* adult females. Final body C (o) and N (Δ) in each experiment (E1 to E15), after 24 h incubation with different concentrations of *Thalassiosira weissflogii* as food

Final body C, N, dry wt, and CF were not correlated with field chl *a*, indicating that the residual effects of *in situ* food level were eliminated during 24 h feeding at high food levels (Fig. 3). Final CF was less variable than initial CF (Fig. 3), suggesting that copepods provided with excess food approach a similar weight per unit length, despite initial differences in body size and degree of food limitation.

Copepod C, N, and dry wt increased exponentially with cephalothorax length (Fig. 7). Because of growth

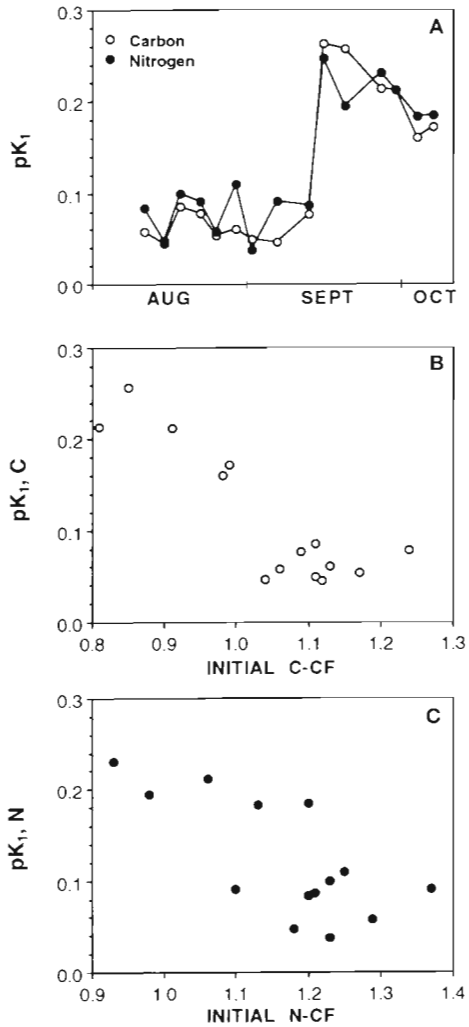

Fig. 6. *Acartia tonsa* adult females. Mean gross growth efficiency, pK_1 (neglecting egg production) during 24 h incubations with *Thalassiosira weissflogii* as food, for all food levels >1000 cells ml^{-1} Seasonal change in pK_1, and pK_1 in relation to initial condition factor (CF) are shown

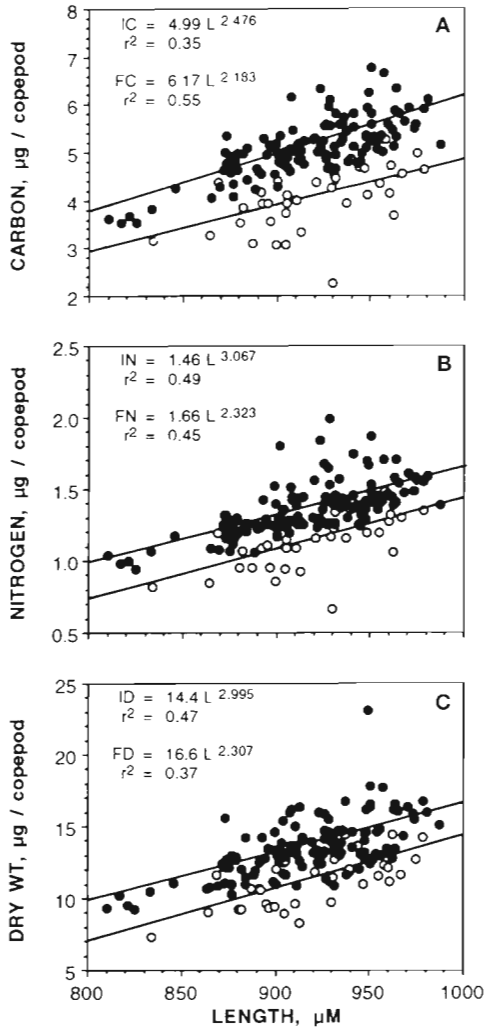

Fig. 7. *Acartia tonsa* adult females. Relationship between cephalothorax length (µm) and body C, N, and dry weight (µg copepod^{-1}) before (o) and after (•) 24 h laboratory incubation with *Thalassiosira weissflogii* as food. I: initial; F: final

in the laboratory, the elevation of the length-weight relationship at the end of the experiments was higher than in the field-collected copepods.

Ingestion rates

The critical concentration, C_c, for this relatively large clone of *Thalassiosira weissflogii* appeared to vary from <200 cells ml^{-1} to ~1000 cells ml^{-1} (Fig. 8). The few observations at low food concentrations did not allow C_c to be accurately determined, however, and the relationship between C_c and other variables was not examined.

I_{max} was highest at the beginning of the study and declined through 22 August, then exhibited a secondary peak in late August/early September and a precipitous decline in mid-September, followed by a recovery towards higher values (Fig. 9). The range in I_{max} was 2- to 3-fold, depending upon the units of computation (Table 3). I_{max} for cells ranged from 22 000 to 50 320 cells copepod^{-1} d^{-1}, with an overall mean of 38 200 ± 2000 cells copepod^{-1} d^{-1}. Comparable I_{max} values for C and N were 6.00 to 18.6 (mean 10.3 ± 0.8) µg C copepod^{-1} d^{-1} and 1.33 to 3.32 (mean 1.96 ± 0.17) µg N copepod^{-1} d^{-1}.

Ingestion as a percentage of body C and N was higher when normalized to initial than to final weight (Fig. 9D, E), because of growth that occurred during the experiments. Thus mean I_{max} was 255 ± 21% (range 171 to 481%) initial body C d^{-1} but 203 ± 18%

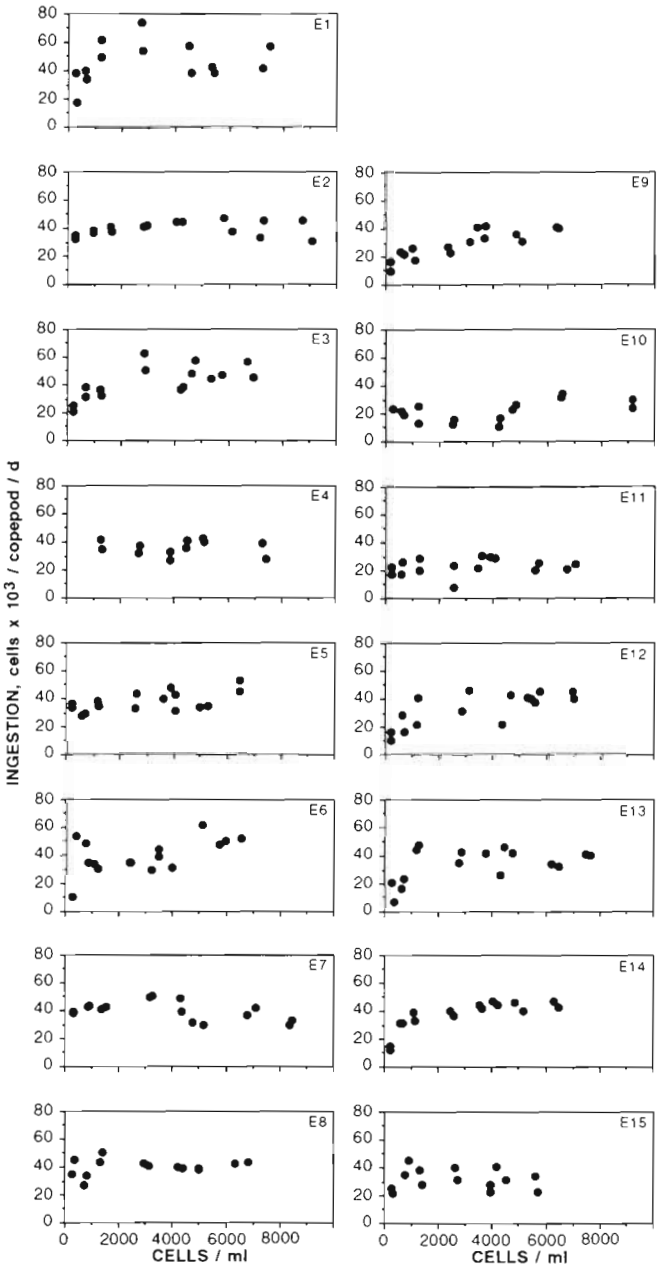

Fig. 8. *Acartia tonsa* adult females. Ingestion rate (cells × 10^3 copepod^{-1} d^{-1}) on different concentrations of *Thalassiosira weissflogii*

(range 121 to 376%) final body C d^{-1}; and 175 ± 16% (range 98 to 296%) initial body N d^{-1} but 146 ± 13% (range 90 to 245%) final body N d^{-1} (Table 3).

The relationships between I_{max} and field temperature, food level, and copepod body size were described by an empirical regression equation as:

$$I_{max} = A[e^{BT} W^C (1 - e^{-DP})] \quad (3)$$

where T (°C) is the field temperature; W is the initial or final C or N content (µg female^{-1}) or the corresponding CF (dimensionless); P is field food abundance, as total chl *a*, >10 µm chl *a*, or total particulate C or N (µg l^{-1}); and A, B, C, and D are fitted constants. Cephalothorax length did not contribute significantly to the fit of the regression, and was not used in the final formulation.

The best fits as indicated by the regression R^2 were for I_{max} expressed in units of nitrogen; carbon was intermediate, and cells yielded the poorest fits (Table 4). Field temperature was the dominant variable in all regressions, explaining 32% of the variation in I_{max} as cells, 63% and 59% for I_{max} as C and % final body C d^{-1}, and 86% and 79% for I_{max} as N and % final body N d^{-1}. I_{max} for cells was significantly related only to temperature and food level. I_{max} as µg C and N was significantly related to temperature, food level and initial CF. I_{max} as % final body C and N was significantly related to temperature, food level, and initial body C, N, and CF. Empirical models of best fit are shown with the experimental data in Fig. 10.

Because all experiments were carried out at 20°C, the temperature term represented a residual effect of the recent thermal history in the field. According to the equations of best fit in Table 4 (Eqs. I2, I4, I8, I10 & I16), using mean values for >10 µm chl *a* and body C, N, C-CF and N-CF from Tables 1 & 2, we find that the Q_{10} for this residual effect was least for ingestion as cells d^{-1} (1.4), intermediate for C and % body C d^{-1} (3.2 and 2.7), and highest for N and % body N d^{-1} (3.9 and 3.5).

I_{max} was negatively related to initial CF. Thus copepods with low weight per unit length fed at an elevated rate, possibly to replenish low body reserves. After restoration of weight and CF during 24 h at high food level, the effect of CF upon I_{max} became nonsignificant. The negative correlation between I_{max} as % final body C or N, and initial body C, N, and CF indicated that smaller copepods from the field ate more, as a percentage of their final body weight, than larger copepods.

Food may have been limiting in quality as well as quantity, but food quality is difficult to measure in natural assemblages of plankton. The R^2 for regressions relating I_{max} to food abundance was significantly higher for >10 µm chl *a* than for total chl *a*, indicating that the larger size fraction was a better measure of food availability than total phytoplankton biomass. Regressions relating I_{max} to total food biomass as chl *a*, C and N yielded nearly identical R^2, however, indicating that chl *a* was as useful a measure of food quality as the more laborious measurements of C and N. The C:N ratio did not change greatly during the study period, and was not significantly related to I_{max}. Microzooplankton were a potential food source not measured by chl *a*, but at

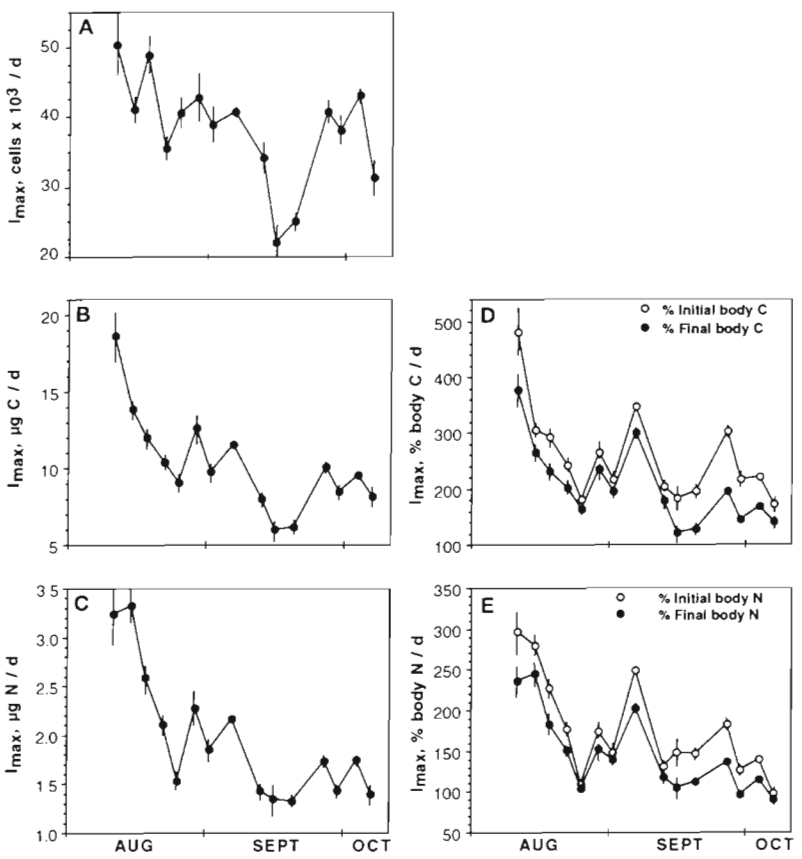

Fig. 9. Seasonal change in maximum ingestion rate, I_{max}, of *Acartia tonsa* adult females fed *Thalassiosira weissflogii*

least partially included in the C and N determinations. A better measure of microzooplankton abundance might have strengthened the correlation between I_{max} and food quantity. Thus while I_{max} was influenced by food size, other food quality effects were not detectable from our measurements of total C, N or C:N ratio.

DISCUSSION

Food limitation of *Acartia tonsa* in Narragansett Bay

This study demonstrated that the maximum ingestion rate of *Acartia tonsa* females collected from Narragansett Bay, and measured under standardized conditions, showed significant temporal variation over a 2 mo period in late summer. These variations in I_{max} were most strongly related to the residual effects of field temperature, and secondarily to *in situ* food level, body weight and CF. I_{max} was highest in copepods with initially low body weight and CF, and from the poorest food conditions in the field. Weight and CF were food limited throughout the period of

Table 3. *Acartia tonsa* females fed *Thalassiosira weissflogii*. Maximum ingestion rate as cells, C, and N copepod^{-1} d^{-1}, and percent initial and final body C and N copepod^{-1} d^{-1}

Expt	Cells (cop.$^{-1}$ d^{-1})	C (µg cop.$^{-1}$ d^{-1})	N (µg cop.$^{-1}$ d^{-1})	% Initial body C d^{-1}	% Final body C d^{-1}	% Initial body N d^{-1}	% Final body N d^{-1}
1	50320	18.6	3.23	481	376	296	236
2	41030	13.9	3.32	305	266	279	245
3	48760	12.0	2.59	292	231	227	183
4	35480	10.4	2.10	242	200	177	150
5	40580	9.1	1.53	180	164	110	103
6	42750	12.6	2.28	265	235	174	152
7	38910	9.8	1.85	217	195	148	140
8	40750	11.6	2.16	348	301	248	203
9	34180	8.0	1.43	204	178	131	118
10	22000	6.0	1.35	183	121	148	105
11	24980	6.2	1.33	195	128	146	112
12	40780	10.1	1.73	304	195	183	137
13	38060	8.5	1.43	217	145	127	97
14	43040	9.6	1.74	220	168	139	114
15	31300	8.1	1.40	171	141	98	90
Mean	38200	10.3	1.96	255	203	175	146
SE	2000	0.8	0.17	21	18	16	13

Table 4. *Acartia tonsa* females fed *Thalassiosira weissflogii*. Maximum ingestion rate (I_{max}), in relation to field temperature (°C), *A. tonsa* weight (C or N content, µg copepod^{-1}) or the corresponding condition factor (dimensionless), and >10 µm field chl *a* (µg l^{-1}), where: $I_{max} = A[e^{BT} W^{C} (1 - e^{-DP})]$ (see text for definition of variables)

I_{max}	Wt or CF term	*A*	*B*	*C*	*D*	R^2	Eq.
Cells d^{-1}		13450 ± 5710	0.0523 ± 0.0208			0.32	I1
		20710 ± 8740	0.0336 ± 0.0200		2.03 ± 0.63	0.50	I2
µg C d^{-1}		1.06 ± 0.52	0.1131 ± 0.0232			0.63	I3
	Init. C-CF	1.23 ± 0.58	0.1149 ± 0.0233	−1.514 ± 0.747	1.50 ± 0.53	0.76	I4
	Init. N-CF	1.83 ± 0.95	0.0994 ± 0.0243	−1.136 ± 0.913	1.75 ± 0.78	0.70	I5
µg N d^{-1}		0.115 ± 0.038	0.1406 ± 0.0154			0.86	I6
	Init. C-CF	0.127 ± 0.042	0.1427 ± 0.0159	−1.260 ± 0.521	1.84 ± 0.56	0.91	I7
	Init. N-CF	0.173 ± 0.059	0.1352 ± 0.0155	−1.391 ± 0.585	1.87 ± 0.58	0.91	I8
% Final body C d^{-1}		18.98 ± 10.84	0.1179 ± 0.0272			0.59	I9
	Init. C	160.5 ± 111.5	0.1006 ± 0.0235	−1.188 ± 0.372	1.29 ± 0.36	0.78	I10
	Init. N	39.93 ± 21.57	0.0926 ± 0.0248	−1.021 ± 0.351	1.38 ± 0.42	0.76	I11
	Init. C-CF	20.28 ± 11.92	0.1259 ± 0.0290	−1.868 ± 0.938	1.30 ± 0.52	0.70	I12
	Init. N-CF	34.99 ± 19.03	0.1112 ± 0.0265	−2.134 ± 0.971	1.30 ± 0.49	0.71	I13
% Final body N d^{-1}		9.36 ± 3.81	0.1363 ± 0.0192			0.79	I14
	Init. C	44.50 ± 27.1	0.1295 ± 0.0192	−0.974 ± 0.308	1.97 ± 0.64	0.88	I15
	Init. N	13.87 ± 5.49	0.1251 ± 0.0180	−0.969 ± 0.258	2.07 ± 0.62	0.90	I16
	Init. C-CF	8.25 ± 3.85	0.1489 ± 0.0223	−1.441 ± 0.743	2.17 ± 1.07	0.84	I17
	Init. N-CF	13.44 ± 4.93	0.1419 ± 0.0159	−2.404 ± 0.624	1.62 ± 0.41	0.90	I18

study, but were not significantly correlated with field temperature.

In Narragansett Bay the levels of chl *a*, C and N were relatively high, often comparable to our laboratory incubations (Table 1). The laboratory food was high quality with regard to nutritional value and size (cells of that size are retained with nearly 100% efficiency by *Acartia tonsa* females; Bartram 1980). The natural assemblage in Narragansett Bay contained a mixture of high and low quality food particles, and the available food was therefore lower than total food biomass would indicate.

Food limitation seems to be characteristic of the environment in which *Acartia tonsa* lives (Durbin et al. 1983,

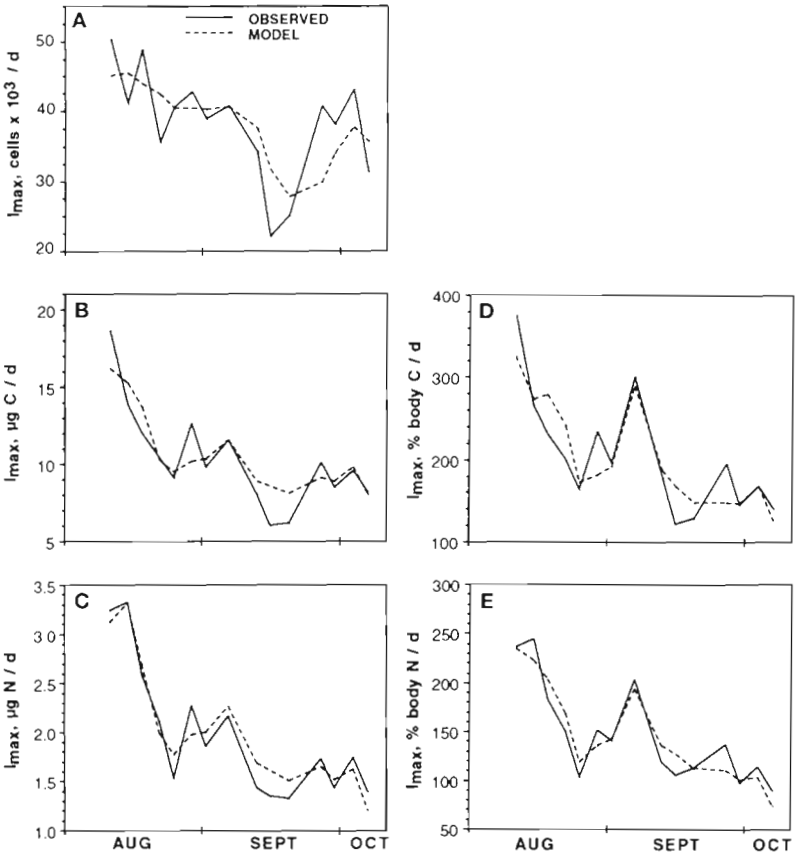

Fig. 10. Seasonal change in maximum ingestion rate, I_{max}, of *Acartia tonsa* adult females fed *Thalassiosira weissflogii*. Observed values and the best fit from an empirical regression relating I_{max} to >10 µm chl *a* and body weight or CF (Eqs. I2, I4, I8, I10 & I16 in Table 4) are shown

Ambler 1985, 1986, Sullivan & Ritacco 1985, Beckman & Peterson 1986, Bellantoni & Peterson 1987, Paffenhöfer & Stearns 1988, Durbin & Durbin 1989). In our study I_{max} was better correlated with the >10 µm size fraction than with total chl *a*, indicating that food particle size was limiting. Microzooplankton represent an additional food source that, though not quantified in the present study, was apparently insufficient to eliminate food limitation of *A. tonsa* in Narragansett Bay. Food quality, especially food particle size, has previously been shown to limit *A. tonsa* egg production and body size even when total food quantity is relatively high (Durbin et al. 1983, Bellantoni & Peterson 1987, Durbin & Durbin 1989). In contrast *Acartia hudsonica*, the winter/spring dominant in Narragansett Bay, was not food limited except near the end of the spring bloom (Durbin et al. 1992).

Acartia tonsa responded quickly to improved feeding conditions in the laboratory, and grew by as much as 61.1% body C, 37.8% body N, and 44.2% dry wt within 24 h. These growth rates are comparable to earlier observations on *A. tonsa* from Narragansett Bay (Durbin et al. 1983, Durbin & Durbin 1989). Laboratory growth was negatively correlated with initial CF, which in turn reflected food availability in nature. Copepods with the lowest CF showed the strongest growth response, and the highest partial growth efficiency, in the laboratory. These results indicate that previous feeding history controls the partitioning of energy within adult *A. tonsa*. If *A. tonsa* must replenish its body reserves after being exposed to limiting food conditions, the available energy for other purposes like egg production will be temporarily reduced (Durbin et al. 1983, Donaghay 1985).

In the past many investigators have assumed that body weight in adult copepods is constant, or can be accurately estimated from measurements of length without regard to possible differences in copepod CF. Neither assumption can be justified for *Acartia* spp., because of the potentially large variation in weight per unit length, and significant short-term weight changes that occur during experimental incubations (Durbin & Durbin 1978, 1989, 1992b, Durbin et al. 1983, 1990, present study).

Seasonal changes in maximum ingestion rate

I_{max} in field-collected *Acartia tonsa* varied 2- to 3-fold when measured under standard conditions in the laboratory. Overall mean values of 38 200 cells copepod^{-1} d^{-1}, 10.3 µg C copepod^{-1} d^{-1}, and 1.96 µg N copepod^{-1} d^{-1}, and 203% final body C d^{-1} and 146% final body N d^{-1} compare with an estimate of 148% body C d^{-1} and 104% body N d^{-1} in *A. tonsa* females fed *Thalassiosira weissflogii* at 20°C (Durbin et al. 1990). Other investigators also reported ingestion rates >100% body wt d^{-1} in *Acartia* spp. (Deason 1980, Kiørboe et al. 1985, Støttrup & Jensen 1990), although body weight in those studies was estimated and not measured.

The 24 h interval over which we measured I_{max} included an unknown period for behavioral and physiological adjustment to the changed food level. Our results indicated compensation for the effects of initial body weight and CF within the 24 h experiment, but the time required for thermal adaptation remains unknown. Field conditions in Narragansett Bay are such that *Acartia tonsa* could experience temperature differences of several degrees over relatively short time and space scales. We therefore expect that physiological rate processes in *A. tonsa* will be in a continual state of thermal adaptation, and are seldom fully acclimated to the current temperature *in situ*.

Temperature effects

The residual effects of temperature upon I_{max} reflected the underlying positive relationship between temperature and physiological rate processes in poikilotherms (e.g. Conover 1956, Mullin & Brooks 1970, Vidal 1980). The residual Q_{10} ranged between 1.4 and 3.9 for different expressions of I_{max}. The Q_{10} for I_{max} as % final body C and N for the equations of best fit (2.7 and 3.5: Eqs. I10 & I16 in Table 4) compare with values of 2.3 and 2.4 for I_{max} in *Acartia hudsonica* over 4.5 to 16°C (Durbin & Durbin 1992b). These *A. hudsonica* were also field collected, but had been preadapted to the experimental temperature for 72 h, and may have been in a more complete state of thermal acclimation than *A. tonsa* in the present study. By comparison the Q_{10} for I_{max} as % body C in *Centropages hamatus* was about 3.9 over 5 to 15°C (Kiørboe et al. 1982).

Persistent effects of previous thermal acclimation have been shown to influence development time in *Acartia hudsonica* (Landry 1975) and egg hatching time in *A. tonsa* (Tester 1985). Tester (1985) showed that *A. tonsa* adapted more quickly to a temperature increase than a decrease, but the time required depended both upon the actual temperatures involved, and the interval over which temperatures were changed. For example, acclimation from 20 to 25°C required about 24 h, but from 20 to 15°C about 48 h.

Initial body weight and CF

I_{max} was inversely related to initial body weight and CF, as shown by the negative sign for W in the empirical regressions (Table 4). The negative relationship

suggests that food-limited copepods increase I_{max} to compensate for low body weight and CF. After 24 h at high food levels the relationship between I_{max} and final CF was nonsignificant, indicating that I_{max} in food-replete copepods is not affected by weight per unit length.

Changes in body weight and CF during the course of an experiment confound the relationship between weight and ingestion. In the present study I_{max} for % body C and N averaged 25.6% and 19.9% higher when normalized to initial, as compared with final, weight. The amount of weight change depends upon the initial state of the copepods and experimental conditions, and can vary greatly between experiments. *Calanus pacificus*, for example, lost about 36% dry wt over 10 d in one starvation experiment, but about 20% over 2 d in another (Hassett & Landry 1990b). Such weight changes will materially affect ingestion calculations, and must be experimentally measured in order to obtain meaningful feeding rate estimates.

Feeding prehistory

Seasonal variation in copepod clearance and ingestion rates has been attributed to previous feeding history (Mayzaud & Poulet 1978, Runge 1980), possibly through alteration of gut enzyme levels (Hassett & Landry 1990a, b and references therein, Roche-Mayzaud et al. 1991). The acclimation hypothesis of Mayzaud & Poulet (1978) predicts that ingestion rate and gut enzyme level should vary directly with food abundance in the field. I_{max} is viewed as an artifact of the saturation of gut enzymes in food-limited copepods, which are unable to immediately synthesize enough enzymes to fully exploit higher food levels. Under this hypothesis, copepods acclimated to high food in the field should exhibit a higher I_{max} than those acclimated to low food.

In our experiments natural food levels in Narragansett Bay were limiting, to a variable degree, throughout the period of study. High I_{max} was associated with low food level and correspondingly low body weight and CF, the reverse of what would be predicted by the acclimation hypothesis of Mayzaud & Poulet (1978). Since the most strongly food-limited copepods exhibited the highest I_{max}, it appeared that ingestion in the field was not limited by the availability of gut enzymes. Thus our results do not support the acclimation hypothesis of Mayzaud & Poulet (1978).

In subsequent investigations by Mayzaud and colleagues (Roche-Mayzaud et al. 1991, Mayzaud et al. 1992), 'acclimation' was defined differently, to mean that in food-limited copepods, feeding rate is positively correlated with food abundance (as would be expected), and that gut enzyme levels are positively related to feeding rate. However, the availability of gut enzymes was not shown to restrict feeding rate, especially the maximum feeding rate (not determined in those studies), as might be expected in a true acclimation. Therefore we conclude that, while gut enzymes do reflect current feeding levels, they are a *consequence* of feeding behavior, not a *regulator* of feeding, and do not have predictive value for the ingestion potential of *Acartia* spp.

The compensatory increase in I_{max} in *Acartia tonsa* with low initial weight and CF resembled the hunger response in *Calanus* spp. (Mullin 1963, McAllister 1970, Runge 1980). Although the hunger response may be transient, our results are consistent with observations of elevated I_{max} and clearance rates in *Calanus pacificus* during long-term acclimation to low food (Hassett & Landry 1983, 1990b). Landry & Hassett (1985) observed increased gut enzymes, assimilation efficiency, and I_{max} in *C. pacificus* at low food and suggested that this represents an adaptation to more effectively exploit food resources during periods of shortage, and to enable the copepods to anticipate future encounters with higher food abundance. Thus, as pointed out by Roche-Mayzaud et al. (1991), the ingestion process is regulated both by food availability and by feedback mechanisms reflecting the nutritional status of the copepod.

Our results suggest that I_{max} in *Acartia tonsa* is dependent upon recent thermal history, food level *in situ*, and copepod weight and CF which are in turn influenced by the degree of food limitation. Additional factors that may influence I_{max} include the type and size of food (Mullin 1963, Frost 1972, 1975), the size and developmental stage of the copepods (Paffenhöfer 1971, Paffenhöfer & Knowles 1978), diel changes in behavior (Gauld 1953, Mackas & Bohrer 1976, Stearns 1986, Durbin et al. 1990), the presence of predators (Ohman et al. 1983, Dagg et al. 1989), and the age distribution of the adults (Ohman 1985, Durbin & Durbin 1992a). Ecosystem models typically represent I_{max} as a more or less fixed element of an ingestion curve dependent mainly upon temperature and food type (e.g. Kremer & Nixon 1978). Present results indicate that as these models are further refined, I_{max} would be more realistically modelled as variable by a factor of 2 or 3, and subject to behavioral and physiological as well as environmental control.

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