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Effects of food quality on the functional ingestion response of the copepod *Acartia tonsa*

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ABSTRACT: Effects of food quality on the functional ingestion response of the copepod *Acartia tonsa* were determined using 3 algal species 6 to 12 μm in diameter (dinoflagellate *Amphidinium carteri*, coccolithophorid *Hymenomonas carterae*, senescent and actively growing diatom *Thalassiosira weissflogii*), over a wide range of concentrations. The algal cells were characterized by their contents of carbon, nitrogen, protein, carbohydrate, lipid and chlorophyll *a*, and by dry weight. *A. tonsa* ingestion rates increased to an asymptote and were fit to the Ivlev model without a feeding threshold at low algal concentrations. Maximum ingestion rates of algal cells were inversely proportional to their protein, nitrogen, and carbon content. Maximum ingestion rates of protein and nitrogen increased with increasing cell content of these variables. In contrast, maximum ingestion rates of algal carbon were generally constant with increasing cellular carbon content. The effects of cellular carbohydrate, lipid, and chlorophyll *a* content on maximum ingestion rates were variable. The rate at which the ingestion of phytoplankton cells approached the maximum ingestion rate increased with greater protein and nitrogen content. Our results suggest that cellular protein and nitrogen content (or factors related to them) are important in regulating *A. tonsa* ingestion rates.

INTRODUCTION

Ingestion rates of copepods are determined by their reaction to ambient particle concentrations, sizes, and biochemical properties. Most research has focussed on the effects of food concentration and size on copepod ingestion rates (see review by Conover 1981) with less emphasis on possible effects of food quality. Copepods can discriminate and selectively ingest phytoplankton over plastic beads (Donaghay & Small 1979, Huntley et al. 1983, Paffenhöfer & Van Sant 1985); phytoplankton over detritus (Roman 1977, Roman 1984); and they can differentiate between similar size phytoplankton species (Huntley et al. 1983) as well as phytoplankton of the same species but in different growth states (Ryther 1954, Mullin 1963, Cowles et al. 1987). This ability to discriminate and selectively ingest food particles of greater nutritional quality fits general theories of optimal foraging behavior (Pyke et al. 1977) and can enhance copepod growth rates. For example, ingestion of algal species highest in protein and lipid supported maximum growth and reproduction of *Acartia tonsa* and the brine shrimp *Artemia salina* (Cahoon 1981, Sick 1976, respectively). This suggests that the amount and quality of food ingested may be a good indicator of zooplankton production rates.

The purpose of this study was to examine the effects of food quality on the functional ingestion response of the euryhaline copepod *Acartia tonsa*, the dominant copepod species in many temperate and subtropical coastal marine environments (Reeve & Walter 1977). *A. tonsa* egg production and ingestion rates respond rapidly to changes in food abundance and food quality (Dagg 1977, Cahoon 1981, Durbin et al. 1983). We conducted short-term ingestion experiments using 3 phytoplankton species of similar size over a wide range of concentrations and food quality. The rate at which ingestion reached saturation levels and the maximum amount of phytoplankton ingested were related to selected biochemical components of the algae in order to examine how food quality affects copepod feeding behavior.

METHODS

Culture conditions. *Acartia tonsa* cultures were initiated from copepods collected in the Chesapeake Bay during May and July, 1984. Copepods were main-

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tained at 30 ppt, 20 °C seawater on a 16:8 light:dark cycle in a constant temperature chamber. For 1 wk prior to an ingestion experiment, copepods were fed the highest concentration of food to be tested to ensure digestive enzyme induction (Mayzaud & Poulet 1978).

The phytoplankton species *Amphidinium carteri (A.c.)*, a dinoflagellate; *Hymenomonas carterae (H.c.)*, a coccolithophorid; senescent and actively growing *Thalassiosira weissflogii* (s.*T.w.* and *T.w.*, respectively), a diatom, were used in ingestion experiments. The dinoflagellate ingestion experiment was conducted twice (*A.c.* #1 and *A.c.* #2). Algae were grown at 30 ppt and 20 °C in continuous culture (Goldman et al. 1974) on f/2 media (Guillard 1975) except senescent *T w.* which was grown in f/4 media in batch cultures. Daily cell counts were made to determine when cultures became senescent. Silica was excluded from the dinoflagellate media because it may inhibit growth (Guillard & Keller 1984).

Table 1. Food quality measurements conducted on phytoplankton

Carbon, Nitrogen[1]	CHN Analyzer
Chlorophyll *a*	Yentsch & Menzel 1963
Protein	Hartree 1972
Carbohydrate[2]	Dubois et al. 1956
Lipid[3]	Barnes & Blackstock 1973

[1] Carbon and nitrogen samples of *H.c.* were fumed over HCl to remove carbonates
[2] The carbohydrate assay may have underestimated the amount of carbohydrate in the algal cell wall due to TCA extraction prior to the assay
[3] Species-specific gravimetric algal lipid standards were used with the Sulphovanillan method instead of cholesterol standards because sterols constitute a low percentage of total algal lipid

Biochemical analyses. The algae produced during the previous day were collected 24 h prior to an experiment and sampled for carbon and dry weight. The remaining culture was split into duplicate flasks and the volume doubled with f/2 media. One flask was inoculated with 125 μCi $NaH^{14}CO_3$ l^{-1}. The next day, samples of the non-labeled algae were filtered in triplicate onto precombusted GF/C filters for biochemical measurements (Table 1).

In terms of biochemical content per cell, *A.c.* #1 had the most carbon, nitrogen, protein, carbohydrate, and lipid, while *T.w.* had more of all biochemical components than s.*T.w.*, except chlorophyll *a* (Table 2). Samples of the non-labeled algae were counted on a Coulter Counter (Model ZB) to determine cell volumes which were converted to cell size classes. Over 60 % of

Table 2. Concentrations in pg $cell^{-1}$ of carbon (C), nitrogen (N), protein (PRO), carbohydrate (CHO), lipid (LIP), chlorophyll *a* (chl-*a*), dry weight (dw); and dpm. Means are given with standard error; N = 3 s.*T.W.* = senescent *Thalassiosira weissflogii*; *T.w.* = exponential *T weissflogii*; *A.c.*#1 = *Amphidinium carteri* Expt 1; *A.c.*#2 = *A. carteri* Expt 2; *H.c.* = *Hymenomonas carterae*

	s.*T.w.*	*T.w.*	*A.c.*#1	*A.c.*#2	*H.c.*
C	122.0 (4.9)	154.4 (4.3)	540.5 (3.2)	80.2 (4.3)	81.7 (3.4)
N	16.1 (1.0)	28.7 (0.9)	114.6 (0.8)	13.6 (1.9)	9.4 (0.5)
PRO	51.6 (1.6)	105.0 (1.6)	381.4 (18.7)	45.1 (2.1)	33.6 (2.1)
CHO	16.3 (2.0)	40.2 (1.0)	57.0 (9.6)	10.5 (3.3)	25.6 (2.0)
LIP	120.4 (11.8)	202.2 (13.9)	311.3 (17.5)	36.3 (14.2)	130.1 (10.5)
Chl-*a*	4.0 (0.4)	3.7 (0.1)	3.1 (0.3)	1.7 (0.2)	1.6 (0.1)
Dw	670.3 (107.1)	503.9 (15.8)	942.6 (54.7)	408.8 (16.8)	284.1 (16.0)
Dpm	1.12(0.01)	0.32(0.01)	0.40(0.01)	0.41(0.01)	0.33(0.02)

Table 3. Algal cell volumes measured with Coulter Counter Values expressed as % of total cells in each volume range. Algae as in Table 1

Volume	283–503 μm^3	503–785 μm^3	785–1131 μm^3	1131–1357 μm^3	1357–1810 μm^3
Diameter (ESD)*	4–6 μm	6–8 μm	8–10 μm	10–12 μm	> 12 μm
s.*T.w.*	–	36.29	44.27	14.53	4.91
T.w.	3.34	44.33	35.35	11.89	5.10
A.c.#1	–	47.70	36.18	12.28	3.84
A.c.#2	41.70	51.15	5.82	0.98	0.35
H.c.	38.40	54.68	5.87	0.88	0.17

* ESD: equivalent spherical diameter calculated from cell volume estimates

the algal cells were between 6 and 10 µm. *A.c.* #1 had a markedly higher proportion of larger cells relative to *A.c.* #2 (Table 3).

Ingestion experiments. Labeled phytoplankton was harvested by gentle filtration over a 3.0 µm Nuclepore filter, rinsed and resuspended in filtered seawater. Triplicate samples of labeled algae were filtered onto preweighed, pre-dried 3.0 µm membra-fil (Nuclepore) filters, rinsed with ammonium formate, dried and weighed. Fluorescence measurements and microscope counts were taken on both labeled and non-labeled algae. Dry weight and carbon of the non-labeled algae were also measured and compared to the fluorescence and dry weight concentrations of the labeled algae the day of the experiment to calculate test concentrations as µg C l^{-1}. Each experiment had 7 or 8 food concentrations (ranging from 7 to 2400 µg C l^{-1}) with 4 to 6 replicates and 3 zero time controls (to correct for adsorption of label to copepods and filters) per treatment.

Ingestion experiments were conducted in 0.5 l jars on a rotating wheel (end over end) in the dark for 45 min with 25 *Acartia tonsa* (adult and Stage V) per jar. These feeding times are less than the gut retention times of *A. tonsa* determined in dye experiments (Gottfried & Roman 1983). After incubation, the copepods were collected on 333 µm sieves, rinsed with filtered seawater onto preweighed 12 µm Nuclepore filters, rinsed with 10 % HCl, and the dry weight and number of copepods determined before isotope analysis. The mean dry weight of *A. tonsa* was 11.14 µg (SE = 0.23) individual^{-1}. Ingestion rates were converted to µg or cells ingested mg copepod dw^{-1} h^{-1} from algal specific activities and the amount of carbon (C), nitrogen (N), protein (PRO), lipid (LIP), carbohydrate (CHO), chlorophyll *a* (chl-*a*), and number of cells ml^{-1} of labeled algae (Eq. 1) by calculating:

$$\text{dpm} \cdot \text{ml algae}^{-1} \div \mu\text{g algae or \# of cells} \cdot \text{ml algae}^{-1} \div \text{dpm} \cdot \text{mg dry weight copepods}^{-1} \div \text{time} = \text{\# of cells or µg algae ingested} \cdot \text{mg copepods dw}^{-1}\,\text{h}^{-1} \quad (1)$$

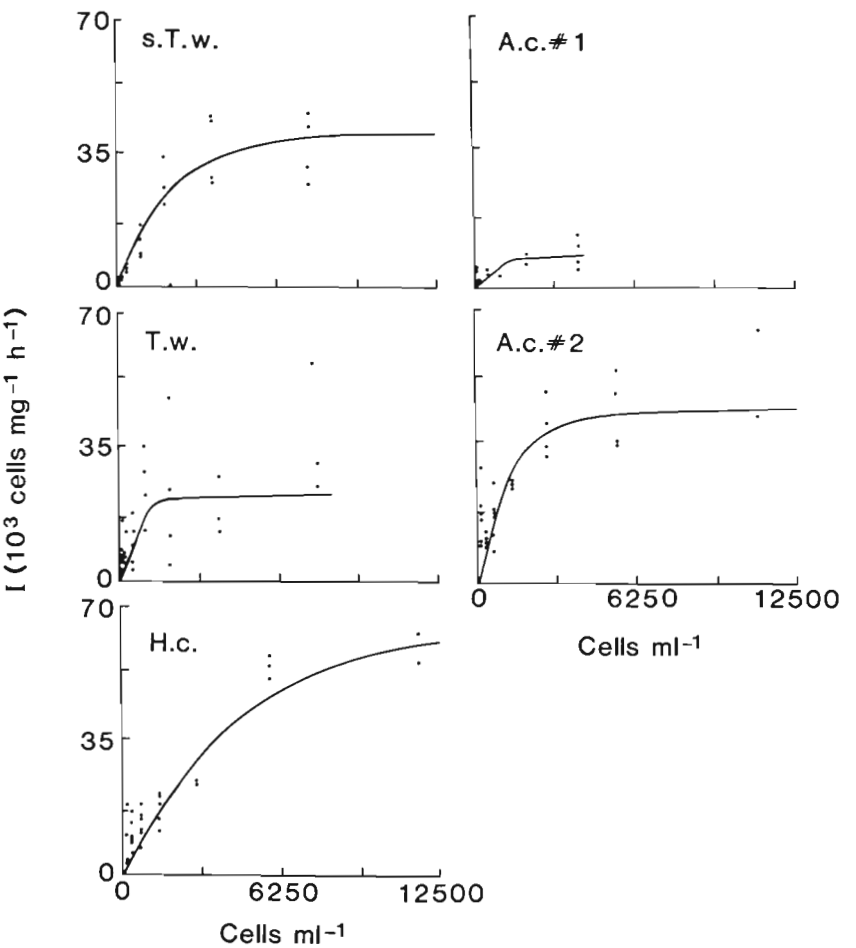

Fig. 1 *Acartia tonsa*. Functional ingestion response to algal cell density. s.*T.w.* = senescent *Thalassiosira weissflogii*, *T.w.* = actively growing *T. weissflogii*, *H.c.* = *Hymenomonas carterae*, *A.c.* #1 = *Amphidinium carteri* Expt 1, *A.c.* #2 = *A. carteri* Expt 2

Acartia tonsa in this study was 27.73 % PRO dw^{-1}, 25.38 % CHO dw^{-1}, and 19.46 % LIP dw^{-1}. Based on these values and 40 % C dw^{-1} and 10 % N dw^{-1} for *A. hudsonica*, which is similar in weight to *A. tonsa* (Deason 1980), ingestion rates at saturation concentrations were extrapolated to daily rations of C, N, PRO, CHO, LIP, and dw copepod^{-1} d^{-1}.

We used the Ivlev equation to fit the ingestion dates:

$$I = I_{max} \times (1 - e^{(-alpha \times C)}) \quad (2)$$

where I = ingestion rate (µg mg dw^{-1} h^{-1} or cells mg dw^{-1} h^{-1}); I_{max} = maximum ingestion rate; C = food concentration (µg l^{-1} or cells ml^{-1}); alpha = rate at which ingestion approaches the maximum ingestion rate. The lower threshold term was excluded from analysis because ingestion was measured at the lowest food concentrations tested. Iteration of the Ivlev equation by the Gauss-Newton method (Hartley 1961) led to convergence of the equation parameters, I_{max} and alpha, for all food types and biochemical components tested. The model was fit using the NLIN procedure of SAS (Statistical Analysis System).

RESULTS AND DISCUSSION

The Holling type 2 feeding response (Holling 1965) was observed for all variables of ingestion for all foods tested and was fit well by the Ivlev (1955) equation (Fig. 1 & 2, Table 4). The ingestion curves with the highest I_{max} typically had the lowest alpha and the highest food saturation density (food concentration where ingestion rates were within 95 % of I_{max}, Table 4). Conversely, ingestion curves with the highest alpha had the lowest I_{max}. Fits to the Ivlev model were calculated as r^2 and ranged from 0.82 *(T.w.)* to 0.97 *(H.c.)*. However, the Ivlev model underestimated ingestion rates at the lowest particle concentrations that were tested: from 7 to 37 µg Cl^{-1}, 2 to 5 µg Nl^{-1}, 4 to 15 µg PRO l^{-1}, 3 to 31 µg LIP l^{-1}, 2 to 5 µg CHO l^{-1}, 0.1 to 1.2 µg chl-*a* l^{-1}, and 32 to 187 cells ml^{-1}. This underestimate may be a function of the large error associated with alpha (Table 4) and because the model heavily weights data at high food levels relative to low levels. However, in coastal areas where *Acartia tonsa* is abundant from early summer through fall, ambient

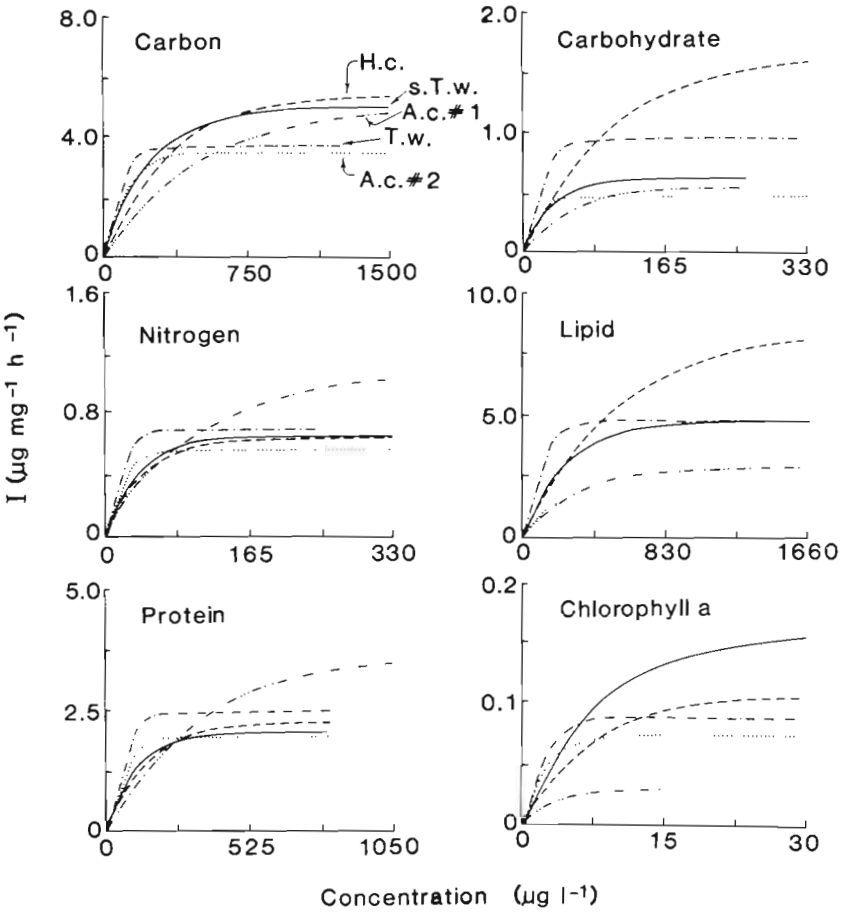

Fig. 2. *Acartia tonsa*. Functional ingestion response to algal carbon, nitrogen, protein, carbohydrate, lipid and chlorophyll *a*. Algae as in Fig. 1. Ingestion rates at the highest concentrations for some food types and biochemical components are not plotted, so that the scale on X-axis could be expanded to more easily examine ingestion at the lowest food concentration

Table 4. *Acartia tonsa* ingestion rates calculated from Eq. (2). I_{max} = µg or cells $mg^{-1}\ h^{-1}$ (± asymptotic 95 % confidence interval); alpha = $mg^{-1}\ h^{-1}$ (± 95 % confidence interval); r^2 = coefficient of determination; S = saturation concentration in µg l^{-1} or cells ml^{-1}. Numbers of samples were 38, 36, 38, 43 and 35 for s.*T.w.*, *T.w.*, *A.c.*#1, *A.c.*#2, and *H.c.*, respectively

	Component	I_{max} (± 95 % CI)	alpha (± 95 % CI)	r^2	S
s.*T.w.*	C	5.0456 (.6615)	.0041 (.0014)	.9283	731
T.w.		3.6654 (.7856)	.0122 (.0076)	.8205	245
A.c.#1		5.1379 (1.2135)	.0020 (.0012)	.8294	1490
A.c.#2		3.5185 (.3909)	.0090 (.0031)	.9260	332
H.c.		5.4088 (.5326)	.0029 (.0007)	.9661	1032
s.*T.w.*	N	.6399 (.0758)	.0302 (.0096)	.9415	99
T.w.		.6812 (.1461)	.0657 (.0409)	.8201	46
A.c.#1		1.0867 (.2568)	.0095 (.0058)	.8292	315
A.c.#2		.5971 (.0679)	.0523 (.0186)	.9231	57
H.c.		.6217 (.0707)	.0250 (.0062)	.9657	120
s.*T.w.*	PRO	2.0546 (.2437)	.0094 (.0030)	.9413	319
T.w.		2.4931 (.5342)	.0180 (0.111)	.8206	166
A.c.#1		3.6210 (.8516)	.0029 (.0018)	.8301	1044
A.c.#2		1.9776 (.2194)	.0160 (.0056)	.9262	187
H.c.		2.2320 (.2194)	.0070 (.0017)	.9659	427
s.*T.w.*	CHO	.6501 (.0770)	.0297 (.0094)	.9415	101
T.w.		.9548 (.2044)	.0469 (.0289)	.8205	64
A.c.#1		.5418 (.1267)	.0193 (.0118)	.8308	155
A.c.#2		.4573 (.0499)	.0705 (.0238)	.9278	42
H.c.		1.6973 (.1672)	.0092 (.0023)	.9659	325
s.*T.w.*	LIP	4.7978 (.5685)	.0040 (.0013)	.9415	749
T.w.		4.8000 (1.0297)	.0093 (.0058)	.8205	321
A.c.#1		2.9598 (.6994)	.0035 (.0021)	.8292	858
A.c.#2		1.5902 (.1718)	.0199 (.0070)	.9251	151
H.c.		8.6145 (.8499)	.0018 (.0004)	.9659	1655
s.*T.w.*	Chl-*a*	.1595 (.0189)	1211 (.0383)	.9417	25
T.w.		.0882 (.0189)	.5100 (.3105)	.8205	6
A.c.#1		.0292 (.0068)	.3612 (.2205)	.8236	8
A.c.#2		.0731 (.0081)	.4287 (.1515)	.9237	7
H.c.		1059 (.0104)	.1466 (.0364)	.9665	20
s.*T.w.*	Cells	39861 (4713)	.0005 (.0002)	.9417	6241
T.w.		23515 (5142)	.0020 (.0013)	.8229	1468
A.c.#1		8976 (2120)	.0012 (.0007)	.8294	2598
A.c.#2		43884 (4886)	.0007 (.0002)	.9258	4160
H.c.		66175 (6547)	.0002 (.0001)	.9657	12482

concentrations generally exceed these low values. For example, summer and fall particulate concentrations range from 722 to 4621 µg Cl^{-1} and 62 to 545 µg Nl^{-1} in the upper Chesapeake Bay, Maryland, USA (Malone et al. 1986) and from 450 to 3388 µg Cl^{-1}, 50 to 200 µg Nl^{-1}, and 2 to 52 µg chl-*a* l^{-1} in Narragansett Bay, Rhode Island, USA (Durbin et al. 1983).

The 2 experiments using the dinoflagellates had large differences in both the biochemical content of the algae and ingestion parameters by *Acartia tonsa*. For each feeding experiment, filtrations for biochemical analysis were done from 1300 to 1400 h and experiments were conducted between 1400 and 1730 h. Thus, it was assumed that *A. c.* #1 and *A. c.* #2, both grown under identical conditions, would have similar cell characteristics. However, *A. c.* #1 cells were larger than *A. c.* #2 (Table 3) and thus hat higher cellular concentrations of carbon, nitrogen, protein, lipid and carbohydrate (Table 2). Olson & Chisholm (1983) have shown that nutrient-replete cultures of *A. c.* grown on a 14:10 light:dark cycle have synchronized cell division that begins at the beginning of the dark period. It is possible that the cell cycle of *A. c.* became increasingly offset while acclimating to the culture conditions used in this study or that culture dilution rates differed between experiments, causing cell division to occur later in the dark cycle. This may have resulted in more small cells (or fewer doublet cells) being present when the *A. c.* #2 experiment was conducted. It is also possible that *A. c.* #2 exhibited periods of no division as observed by Olson & Chisholm (1983).

Maximum cell ingestion rates were inversely proportional (i.e. a negative exponential relation) to cellular protein, nitrogen, and carbon content, while the

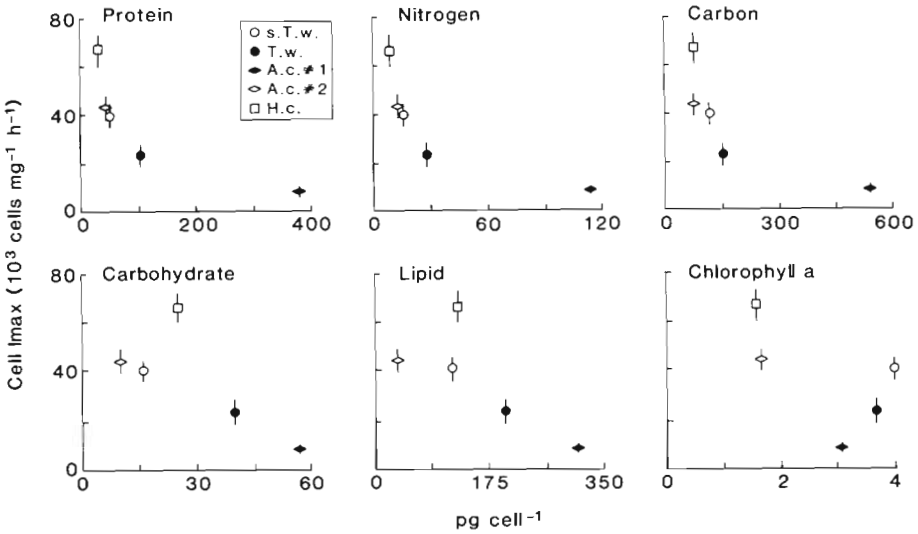

Fig. 3. Relation between maximum cell ingestion rates and cellular biochemical content. Maximum ingestion rates plotted with 95 % confidence limits

relations between cell I_{max} and carbohydrate, lipid, and chlorophyll-*a* cellular content were unclear (Fig. 3). Ingestion of *H.c.* and *A. c.* #2, which were lowest in nitrogen and protein, resulted in the highest maximum ingestion rates of cells while ingestion of *A. c.* #1, which was highest in N and protein, resulted in the lowest maximum cell ingestion rate. However, the particle capture efficiency of *Acartia* (based on intersetule distances) is greater on particles larger then 8 µm in diameter relative to smaller particles (Nival & Nival 1976, Donaghay & Small 1979, Bartram 1980). Thus, *A. c.* #1 may have been captured more efficiently than *A. c.* #2 because of its larger cell size (Table 3), which may explain the higher alpha observed for *A. c.* #1 cell ingestion compared to *A. c.* #2 (Table 4). Maximum cell ingestion of *A. c.* #1 occurred at a lower cell density than *A. c.* #2. This agrees with Frost (1972) who found that maximum ration is attained at lower concentrations of larger cells compared to smaller cells.

It has been shown that zooplankton ingest actively growing cells at a faster rate than senescent or slowly growing cells (Rhyther 1954, Mullin 1963, Cowles et al. 1987). In this study, *T.w.* had a higher cellular content of all measured biochemical components except chl-*a* than *s.T.w.* Maximum ingestion rates of *s.T.w.* C, chl-*a*, and cells were higher than *T.w.* (Table 4). Maximum ingestion rates of all biochemical components of *T.w.* always occurred at lower concentrations that the same components of *s.T.w.* because at cell concentrations lower than the critical or saturation concentration, *Acartia tonsa* ingested more actively growing *T.w.* than *s.T.W.* cells (Fig. 1). For example, at 750 cells ml^{-1}, *A. tonsa* ingested 2035 cells $copepod^{-1}$ h^{-1} of *T.w.* and 1389 cells $copepod^{-1}$ h^{-1} of *s.T.w.*

If protein and amino acids act as phagostimulants as suggested by Poulet & Ouellet (1978) and Cowles et al. (1987), one would expect that the algal cells highest in protein and N (or those leaking the most amino acids) would be ingested at a rate which rapidly approaches I_{max} (i.e. high alpha values). Our data show that the alphas for cell ingestion increased with greater cellular protein, nitrogen, and carbon content while the relationships between alpha and cellular carbohydrate, lipid, and chlorophyll *a* content were not clear (Fig. 4). If we exclude *A. c.* #1, which was significantly larger than other algae (Table 3), the correlations (r^2) of cell alpha to the biochemical composition of the cells were protein = 0.96, nitrogen = 0.98, carbon = 0.68, carbohydrate = 0.52, lipid = 0.38, chlorophyll *a* = 0.26. Thus for cells of similar size (or equal capture efficiency), protein content may be the best 'predictor' of cell ingestion rate below I_{max}. Because of this higher ingestion the density of cells required by the copepod to attain I_{max} was inversely proportional to the nitrogen and protein content of the algae (r^2 = 0.71 and 0.61 respectively); less for carbon (r^2 = 0.42), bur not for carbohydrate or cellular lipid composition (r^2 = 0.05 and 0.02, respectively).

The maximum ingestion rates of algal nitrogen and protein increased with increasing cellular nitrogen and protein, respectively, while maximum carbon ingestion rates were generally constant with increasing cellular carbon content (Fig. 2, Table 4). the specific daily rations which *Acartia tonsa* consumed (at I_{max}) of the various biochemical constituents appear low in comparison to previously published ingestion rates. For example, *A. hudsonica* feeding on *Skeletonema costatum* consumed a maximum daily ration of 660 % C and 250 % N (Deason 1980). The small copepod species *Paracalanus parvus* feeding on *Thalassiosira weiss-*

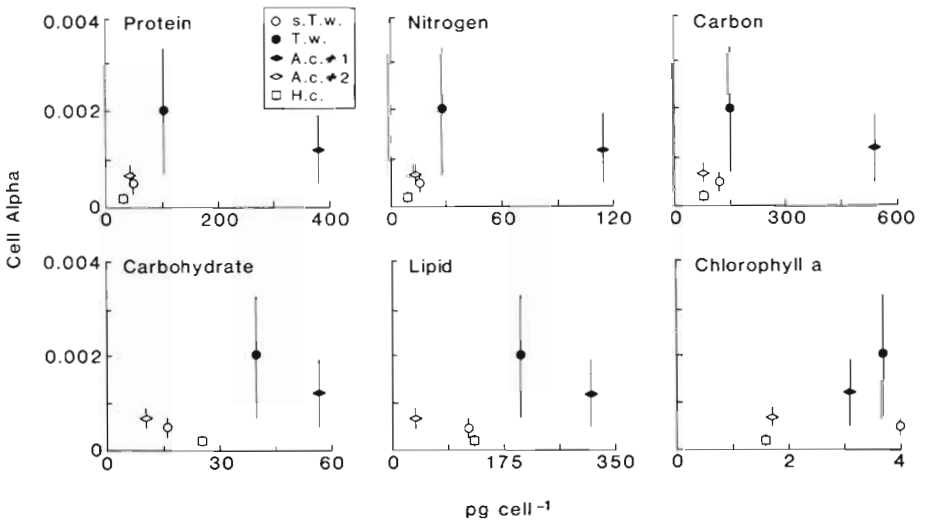

Fig. 4. Relation between alpha from cell ingestion and cellular biochemical content. Maximum ingestion rates plotted with 95 % confidence limits

flogii had daily rations of 360 % C and 150 % N (Checkley 1980). Generally, however, maximum daily carbon-specific ration of *Acartia* species is < 100 % (Petipa 1966, Vargo 1976, Roman 1977). The low values we obtained may be characteristic of the species or may be the result of extrapolation of our short-term ingestion measurements to daily rates. *A. tonsa* may show enhanced feeding rates in the dark (Stearns 1986). Although our grazing measurements were run in opaque jars, they were conducted during the day. Thus if *A. tonsa* exhibits an endogenous feeding behavior cued to photoperiod, extrapolated short-term feeding experiments, even though they were conducted in the dark, would underestimate daily rations. In addition, because the algae fed to *A. tonsa* were < 12 µm, their filtration efficiency may be < 60 % (Bartram 1980). Thus, their daily rations might be expected to be lower than found in studies using larger cells (i.e. *S. costatum* in Deason 1980) and for the same size algal cells fed to copepods which are more efficient at capturing smaller cells than *A. tonsa* (i.e. *P. parvus* in Checkley 1980).

A unique aspect of this study ist that ingestion rates of the various algae were measured not only in terms of carbon, chlorophyll *a*, and cells but also in terms of nitrogen, protein, carbohydrate, and lipid. Our results suggest that *Acartia tonsa* may regulate its maximum ingestion rate of cellular protein, nitrogen, and carbon. Note that I_{max} for protein, nitrogen and carbon for the 5 algal treatments varied by less than a factor of 2 whereas I_{max} of carbohydrate, lipid and chlorophyll *a* varied by more than 3-fold (Table 4). *A. tonsa* might detect differences in cellular protein and nitrogen levels before ingestion by the amount of amino acids in the zone around the algae. This behavior may have resulted in the higher alphas for cell-ingestion which we observed for algae which had higher cellular contents of protein and nitrogen. Then copepods may also respond to differences in algal biochemistry after ingestion by becoming satiated sooner on protein and nitrogen-rich algae. It ist interesting to note that the copepod *Eucalaus pileatus* became saturated at 10 to 20 µg N l^{-1} when feeding on the diatom *Rhizosolenia alta*, but not a similar nitrogen concentrations of fecal pellets (Paffenhöfer & Van Sant 1985). In our experiments, *A. tonsa* ingested more algal cells which were low in protein, nitrogen, and carbon in order to maximize its intake of these variables. Thus I_{max} was inversely proportional to the protein content of the algae (log I_{max} = 4.7440 − 0.0022 protein $cell^{-1}$, r^2 = 0.90). High and variable maximum ingestion rates of carbohydrate, lipid, and chlorophyll *a* may be a consequence of *A. tonsa* ingesting more of the cells lowest in protein and nitrogen in order to satisfy ist nutritional requirements.

There have been several attempts to model the feeding behavior of copepods (e.g. Steele & Frost 1977, Lehman 1976, Bartram 1980). These models estimate copepod ingestion rates from the concentration and size composition of the phytoplankton community. Our results demonstrate that the biochemical composition of the algae also can regulate copepod ingestion rates. Thus parameters such as C/N and protein/carbon ratio or data on protein $cell^{-1}$ or nitrogen $cell^{-1}$ obtained using flow-cytometry (i.e. Cowles et al. 1987) in conjunction with copepod feeding experiments may be used to better predict the utilization rate of phytoplankton *in situ*.

Algal protein and nitrogen may be the most important 'cues' that regulate copepod ingestion rate (Roman 1983). One might speculate that at the beginning of a

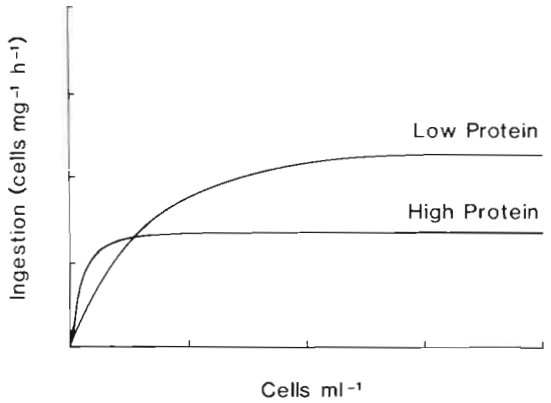

Fig. 5. *Acartia tonsa*. Idealized functional response curve for cell ingestion: low *vs* high protein algae

Table 5. *Acartia tonsa*. Daily ration at I_{max}. Values expressed as % body C, N, PRO, CHO, LIP, and dw d^{-1}

	s.*T.w.*	*T.w.*	*A.c.*#1	*A.c.*#2	*H.c.*
C	30.27	21.99	30.83	21.11	32.45
N	15.36	16.35	26.08	14.33	14.92
PRO	17.78	21.58	31.34	17.12	19.32
CHO	6.15	9.02	5.12	4.32	16.05
LIP	59.17	59.20	36.50	19.61	106.24
dw	64.10	28.44	20.31	43.08	45.10

phytoplankton bloom, when algae are high in protein due to the availability of inorganic nutrients, copepods would reach their maximum ingestion rate at low cell concentrations but at a fast rate, i.e. with a high alpha (Fig. 5). As inorganic nutrients are depleted and the phytoplankton have less protein $cell^{-1}$, maximum copepod ingestion rate would occur at a higher cell concentration but with a lower alpha than earlier in the bloom. Therefore, during the early bloom less cells are eaten per copepod and more cells are left to divide and grow. Later in the bloom when algal cells are lower in protein, the copepods may ingest more algal cells per individual to satisfy their protein requirements. A reduction in phytoplankton abundance may reduce competition between algae for the remaining nutrients. Enhanced grazing on low protein algae might also result in less phytoplankton in the water column allowing light to penetrate deeper, extending primary production in the water column. By responding to the protein or nitrogen content of algae, copepod feeding could thus regulate or contribute to fluctuations in phytoplankton productivity and standing stock.

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