

# Omnivory by the coastal marine copepods *Centropages hamatus* and *Labidocera aestiva*

Walter J. Conley\* and Jefferson T. Turner

Biology Department, Southeastern Massachusetts University, North Dartmouth, Massachusetts 02747, USA

**ABSTRACT:** Omnivory by the 2 coastal marine copepods *Centropages hamatus* (Lilljeborg) and *Labidocera aestiva* Wheeler was examined in laboratory grazing and predation experiments. Co-occurring food items were utilized. *C. hamatus* ingested more carbon in the form of plant material ( $\bar{x} = 2.05 \mu\text{gC copepod}^{-1} \text{d}^{-1}$ ) than did *L. aestiva* ( $\bar{x} = 0.66 \mu\text{gC copepod}^{-1} \text{d}^{-1}$ ). Conversely, *L. aestiva* ingested more carbon in the form of animal food ( $\bar{x} = 3.35 \mu\text{gC copepod}^{-1} \text{d}^{-1}$ ) than did *C. hamatus* ( $\bar{x} = 0.98 \mu\text{gC copepod}^{-1} \text{d}^{-1}$ ). Rates of ingestion of copepod nauplii and phytoplankton by both *C. hamatus* and *L. aestiva* increased significantly with increasing food concentrations and temperatures. Average grazing and predation rates of *C. hamatus* and *L. aestiva* upon natural phytoplankton assemblages and nauplii appeared to follow biomass peaks. The maximum field concentration of *C. hamatus* ( $722 \text{ m}^{-3}$ ) appeared capable of daily ingesting means of 0.85 % of phytoplankton carbon and 8.23 % of the copepod nauplii present. Maximum field concentration of adult *L. aestiva* ( $8 \text{ m}^{-3}$ ) appeared capable of ingesting means of only 0.01 % of phytoplankton carbon and 0.29 % of the copepod nauplii present.

## INTRODUCTION

Knowledge of copepod feeding habits is necessary for understanding marine ecosystem trophodynamics. Analyses of copepod gut contents, feeding appendages, and results of feeding experiments have revealed that various copepods eat both phytoplankton and animal food and hence are omnivores (Marshall, 1924, 1973; Wickstead, 1962; Anraku and Omori, 1963; Mullin, 1966; Haq, 1967; Robertson and Frost, 1977; Turner, 1978, 1984a, b, in press; Paffenhöfer and Knowles, 1980). However, the natural diets of most marine planktonic copepods are so ill defined that it is still impossible to assign them realistically to proper trophic levels. Further, there is little information on the relative roles of phytoplankton and animal food in the diets of omnivorous marine copepods.

The present study addresses the relative importance of carnivory and herbivory for 2 species of inshore copepods, *Centropages hamatus* (Lilljeborg) and *Labidocera aestiva* Wheeler. There is little information on the feeding habits of these species. *C. hamatus* has been shown to feed upon unialgal cultures (Klein Breteler, 1980; Kiørboe et al., 1982) and unnatural prey

items (*Artemia* nauplii) in the laboratory (Anraku and Omori, 1963). Members of the genus *Labidocera* (and the entire family Pontellidae) have often been assumed to be primarily carnivorous (Anraku and Omori, 1963; Gauld, 1966; Itoh, 1970; Landry, 1978). However, there is evidence of herbivory by several pontellid species, including *L. aestiva* (Lebour, 1922; Turner, 1977, 1978, in press).

The relative importance of phytoplankton and animal food has been examined by several investigators but rarely on naturally co-occurring foods. Wickstead (1962) and Itoh (1970) separated various copepods into 3 categories on the basis of gut analysis: herbivores, mixed feeders, and carnivores. Robertson and Frost (1977) offered cultured diatoms or *Artemia* nauplii to the omnivorous copepod *Aetideus divergens*. Mono-specific cultures of a diatom (*Thalassiosira fluviatilis*) and unnatural prey items (*Artemia* nauplii) were offered to 6 species of neritic copepods by Anraku and Omori (1963), and the results were discussed with regard to mouthpart morphology. All of these techniques (gut analyses, mouthpart morphology, and feeding experiments using unialgal cultures and *Artemia* nauplii as food) were utilized by Mullin (1966) to determine the feeding habits of various copepods from the Indian Ocean. The continental shelf copepods *Centropages velificatus* (reported as *C. furcatus*) and

\* Present address: Department of Marine Science, University of South Florida, 140 Seventh Avenue South, St. Petersburg, Florida 33701, USA

*Temora stylifera* also proved omnivorous when allowed to feed upon unialgal cultures and laboratory reared nauplii (Paffenhöfer and Knowles, 1980).

Various omnivory experiments have offered animal and plant food types in the same container (Landry, 1981), separately (Robertson and Frost, 1977; Paffenhöfer and Knowles, 1980), or together (Anraku and Omori, 1963; Mullin, 1966). While this may have affected the results of some of the above experiments (Landry, 1981), Lonsdale et al. (1979) found no significant decrease in predation by the omnivorous copepod *Acartia tonsa* in the presence of an alternative food source.

A problem with laboratory feeding studies utilizing cultured foods is their inherent artificiality. However, several recent measurements of copepod ingestion rates on natural assemblages of food have employed phytoplankton quantification by either electronic particle counters (Poulet, 1973, 1974, 1978; Richman et al., 1977; Cowles, 1979; Dagg et al., 1980, 1982; Harris, 1982), copepod gut fluorescence (Boyd et al., 1980; Dagg and Grill, 1980; Dagg and Wyman, 1983), or microscopic examination (Huntley, 1981; Turner and Anderson, 1983). The latter approach was adopted in the present study, and ingestion rates of *Centropages hamatus* and *Labidocera aestiva* were determined by microscopic enumeration utilizing natural phytoplankton assemblages and co-occurring copepod nauplii as food. In addition, quantitative samples of the field populations of *C. hamatus*, *L. aestiva*, and food organisms (phytoplankton and nauplii), were collected in order to estimate the potential impact of feeding by the target copepods on a natural estuarine plankton assemblage.

## MATERIALS AND METHODS

Experiments were performed on an approximately weekly to biweekly schedule from 11 April to 30 September, 1980. All collections were made in the Westport River estuary, Massachusetts (41° 34' N 71° 05' W). Experimental animals were collected at the surface and transported to the laboratory within 1 to 2 h at ambient field temperature. Estuarine water, containing natural phytoplankton, was collected at the same time and location as the experimental animals. In order to remove extraneous zooplankton, this water was screened through a 73 µm mesh. All experiments were performed in 400 ml subsamples in 473 ml containers at field temperatures (8 to 23 °C).

Adult *Centropages hamatus* or *Labidocera aestiva* were sorted from the zooplankton collections within 1 to 5 h of capture. Although it was impossible to similarly identify and stage live nauplii as they were being

sorted, on each experimental date the same size and genus of nauplii were used in all containers. Subsequent to the experiments, wet mounts were made of the remaining nauplii and examined under a compound microscope. The nauplii were measured to the nearest µm and identified according to the criteria presented by Faber (1966).

On each experimental date, the experimental regime included: 2 control containers containing phytoplankton only, 4 grazing containers in which 5 to 10 adult male or female *Centropages hamatus* or *Labidocera aestiva* were allowed to graze in estuarine water containing phytoplankton, and 6 predation containers containing a single adult male or female *C. hamatus* or *L. aestiva* and either 25, 37.5, or 50 nauplii l<sup>-1</sup> in 0.45 µm filtered seawater.

Feeding experiments were performed in the dark, in a temperature controlled room set at field temperature, for 12 to 24 h. Feeding containers were placed on a rotating plankton wheel (1 to 2 rpm) to retard algal sedimentation. Visual examination at the end of each experiment ensured that the copepods were still active. Experiments were terminated by preservation with formalin for the predation containers, or Utermöhl's solution (Guillard, 1973) for the grazed containers.

Phytoplankton concentrations were determined by microscopic enumeration in a Sedgwick-Rafter counting chamber following concentration by a factor of ten by sedimentation. Aliquots of at least 500 cells were counted to obtain statistical reliability (Guillard, 1973). Phytoplankton cells were measured with an ocular micrometer, cell volumes were determined, and phytoplankton carbon was estimated by the volume to carbon conversions of Mullin et al. (1966). Carbon ingestion of phytoplankton by *Centropages hamatus* and *Labidocera aestiva* was determined by the formula:

$$I = 24 \cdot (C_{\bar{x}} - C_g) / n \cdot t \quad (1)$$

where I = ingestion rate (µgC copepod<sup>-1</sup> d<sup>-1</sup>);  $C_{\bar{x}}$  = mean carbon concentration (µgC l<sup>-1</sup>) of the controls;  $C_g$  = carbon concentration (µgC l<sup>-1</sup>) of the grazed containers; t = duration of the experiment in h; n = number of grazers. This equation is essentially the same as that utilized by Paffenhöfer (1971) expressed as carbon rather than particle volume. If the carbon concentration in the grazed container was not lower than that in the controls by an amount greater than that of the counting error, then it was assumed that no grazing had occurred. Percent error, on each sampling date, was calculated as:

$$\%E = [(C_2 - C_1) / C_{\bar{x}}] \cdot 100 \quad (2)$$

where  $C_1$  = carbon concentration (µgC l<sup>-1</sup>) in the first control;  $C_2$  = carbon concentration (µgC l<sup>-1</sup>) in the

second control;  $C_{\bar{x}}$  = mean carbon concentration ( $\mu\text{gC l}^{-1}$ ) in the control containers.

Predation upon nauplii by adult copepods was determined on each experimental date by subtracting the number of nauplii remaining at the end of each experiment from the number initially introduced. Nauplii were recovered on a 20  $\mu\text{m}$  mesh screen, since repeated trials revealed that such recovery was complete. With few exceptions, the nauplii employed in the experiments were those of *Acartia tonsa* or *A. hudsonica*; hence naupliar carbon was estimated using Landry's (1978) carbon values for the appropriate sizes of *Acartia* spp. nauplii. However, on 24 and 28 June, 1980, *Acartia* spp. nauplii were essentially absent. Thus, nauplii of *Pseudocalanus minutus* s.l. were utilized on these dates. Carbon values for these nauplii were estimated from length: carbon relationships (Landry, 1978) for the morphologically similar (Faber, 1966) *Paracalanus* sp. nauplii.

In order to present ingestion of both phytoplankton and nauplii on a ration basis (% of copepod body carbon ingested per individual per unit time) carbon values for male and female *Centropages hamatus* and *Labidocera aestiva* were determined with a Hewlett-Packard 185B CHN analyzer.

In order to quantify field populations of *Centropages hamatus*, *Labidocera aestiva*, and nauplii, surface tows were made with 73  $\mu\text{m}$  mesh nets (for nauplii) and 363  $\mu\text{m}$  mesh nets (for adult copepods) equipped with flowmeters. Due to the relatively shallow depth (ca 4 m), and rapid current velocity (maximum 2.5 kts; US Department of Commerce, 1972), it is not likely that horizontal stratification occurred at the sampling station. Samples were collected on all experimental dates, preserved in 5 to 10 % formalin: seawater solutions, and split with a Folsom plankton splitter. Aliquots of 500 to 1000 individuals were counted and identified for each tow. Phytoplankton field populations (for the < 73  $\mu\text{m}$  fraction) were determined from control samples.

## RESULTS

The phytoplankton was dominated, throughout the study, by small (nominally 5 to 10  $\mu\text{m}$ ) nanoflagellates and chlorophytes. These cells comprised most of the carbon content of the phytoplankton. Carbon values fluctuated between 52.95 and 206.57  $\mu\text{gC l}^{-1}$  (Fig. 1a). In September, a bloom of *Peridinium trochoideum* (maximum = 68 cells  $\text{ml}^{-1}$ ) equaled or exceeded the carbon contribution of the nanoplankton. In August, *Skeletonema costatum* (maximum = 1,603 cells  $\text{ml}^{-1}$ ) was present in the same order of magnitude as, but never exceeding, the carbon contribution of the nanoplankton. *Gymnodinium nelsoni* (maximum = 31 cells

$\text{ml}^{-1}$ ) and *Leptocylindricus danicus* (maximum = 54 cells  $\text{ml}^{-1}$ ) also contributed significantly in late August.

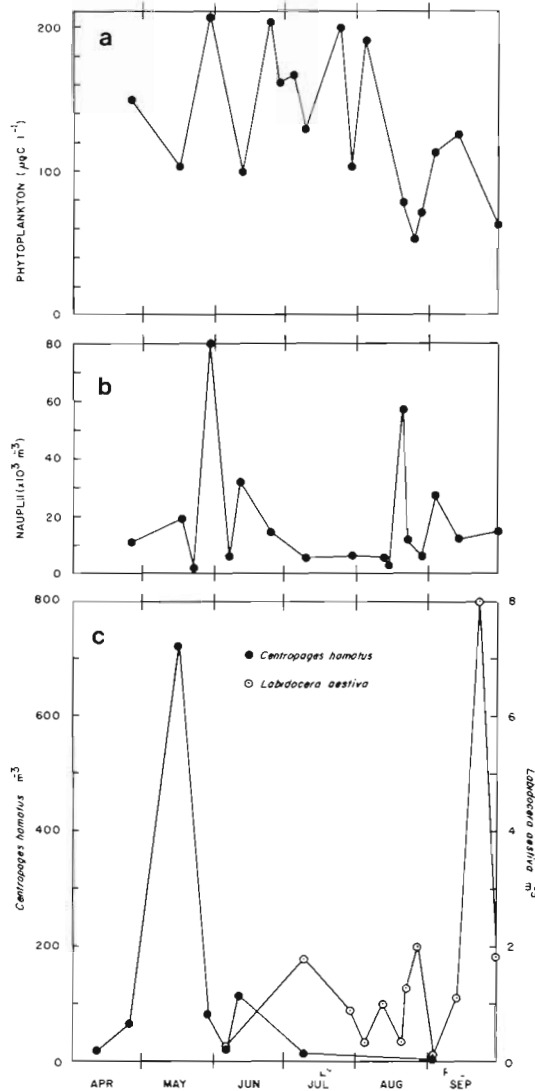


Fig. 1. *Centropages hamatus* and *Labidocera aestiva*. Field concentrations of phytoplankton (a), copepod nauplii (b), and adults (c) (males and females combined). Scales differ by 2 orders of magnitude for adult abundance

The zooplankton was dominated, in terms of numbers, by copepod nauplii. These comprised 87.0 to 99.0 % of the total number of animals collected on each sampling date (Conley, 1983). The maximum number of nauplii (80,304  $\text{m}^{-3}$ ) was collected on 29 May, 1980 (Fig. 1b). The nauplii, throughout the study, consisted mostly of *Acartia* spp. nauplii. *Centropages hamatus* was present at the initiation of the study and reached its period of maximum abundance (722  $\text{m}^{-3}$ ) in mid-May (Fig. 1c). This species was represented by small numbers throughout the summer months and was

absent from the study area by mid-September. *Labidocera aestiva* was first observed in early June and was never abundant in the net collections. Maximum abundance ( $8 \text{ m}^{-3}$ ) occurred in late September (Fig. 1c).

Grazing rates for *Centropages hamatus* (Fig. 2) ranged from undetectable to  $7.29 \mu\text{gC copepod}^{-1} \text{ d}^{-1}$ , with an overall average of  $2.05 \mu\text{gC copepod}^{-1} \text{ d}^{-1}$  (Table 1). Utilizing the carbon values for adult *C. hamatus* (Table 2), grazing represented means of 14.49

Since grazing rates for *Centropages hamatus* were determined over a wide range of temperatures (10 to  $22^\circ\text{C}$ ) and a relatively narrow range of phytoplankton concentrations ( $98.80$  to  $206.57 \mu\text{gC l}^{-1}$ ), the ingestion rates were not significantly related to food concentration when considered separately. However, when the effects of the 2 independent variables are combined (stepwise multiple regression), the ingestion rate increases significantly (Table 3) with increasing temperature and concentration. *Labidocera aestiva* did not

Table 1. *Centropages hamatus* and *Labidocera aestiva*. Ingestion of natural food items. All ingestion rates expressed as  $\mu\text{gC copepod}^{-1} \text{ d}^{-1}$

Species	Food type offered	Average ingestion	Minimum ingestion	Maximum ingestion	Standard error
<i>C. hamatus</i>	Phytoplankton	2.05	0	7.29	0.41
<i>C. hamatus</i>	Nauplii	0.98	0	4.22	0.15
<i>L. aestiva</i>	Phytoplankton	0.66	0	2.62	0.23
<i>L. aestiva</i>	Nauplii	3.35	0	8.38	0.28

Table 2. *Centropages hamatus* and *Labidocera aestiva*. Carbon content of adults

Species	$\mu\text{gC copepod}^{-1}$ (female)	n	$\mu\text{gC copepod}^{-1}$ (male)	n
<i>C. hamatus</i>	14.22	80	12.71	70
<i>L. aestiva</i>	24.19	100	23.12	50

and 16.05 % of body carbon ingested per day by the females and males, respectively. Grazing rates for *Labidocera aestiva* were lower than those of *C. hamatus*. Grazing rates for *L. aestiva* (Fig. 2) ranged from undetectable to  $2.62 \mu\text{gC copepod}^{-1} \text{ d}^{-1}$ , with an overall average of  $0.66 \mu\text{gC copepod}^{-1} \text{ d}^{-1}$  (Table 1). Utilizing the carbon values for adult *L. aestiva* (Table 2), grazing represented means of 2.73 and 2.85 % of body carbon ingested per day by the females and males, respectively.

exhibit a significant increase in grazing rate with increased phytoplankton concentration. However, a combination of low field concentrations of both phytoplankton (Fig. 1a) and *L. aestiva* (Fig. 1c) and a relatively narrow temperature range (21 to  $25^\circ\text{C}$ ) limited the scope of the investigation of the effects of temperature and food concentrations on its grazing.

Predation rates, over the natural range of naupliar concentrations offered, increased with increasing prey concentrations for both target species. *Centropages hamatus* (Fig. 3) ingested averages of 2.86, 4.03 and  $5.29 \text{ nauplii d}^{-1}$  at concentrations of 25.0, 37.5 and  $50.0 \text{ nauplii l}^{-1}$ , respectively. *Labidocera aestiva* (Fig. 3) ingested considerably more with averages of 9.15, 13.89 and  $22.35 \text{ nauplii d}^{-1}$  at the same naupliar concentrations. In order to compare rates of ingestion of phytoplankton and nauplii on an equivalent basis, numbers of nauplii ingested vs. numbers offered were converted to carbon (Fig. 4). Ingestion rates ranged

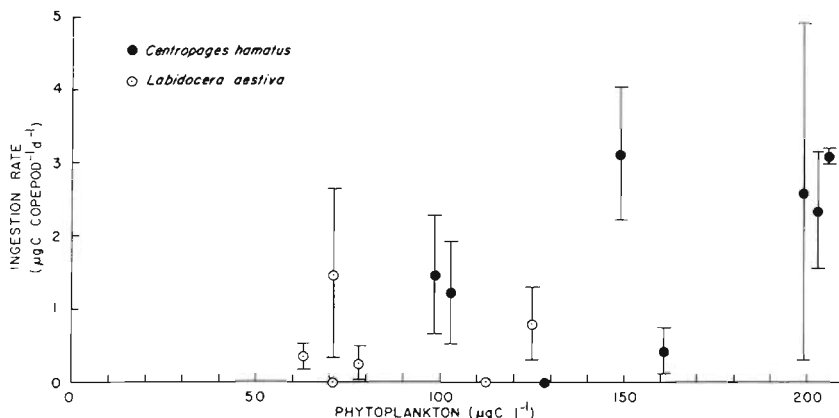


Fig. 2. *Centropages hamatus* and *Labidocera aestiva*. Grazing (ingestion) rates of adults (males and females combined;  $\mu\text{gC copepod}^{-1} \text{ d}^{-1}$ ) feeding on natural concentrations of phytoplankton. Means of 3 to 4 replicates; error bars:  $\pm$  standard error

Table 3. *Centropages hamatus* and *Labidocera aestiva*. Effect of the independent variables, food concentration and temperature, on the dependent variable, ingestion rate ( $\mu\text{gC copepod}^{-1} \text{d}^{-1}$ )

Species	Food type	Independent variable (s)	Significance level
<i>C. hamatus</i>	Phytoplankton	Concentration	$P < 0.1021$
<i>C. hamatus</i>	Phytoplankton	Concentration & temperature	$P < 0.0253$
<i>C. hamatus</i>	Nauplii	Concentration	$P < 0.0033$
<i>C. hamatus</i>	Nauplii	Concentration & temperature	$P < 0.0070$
<i>L. aestiva</i>	Phytoplankton	Concentration	$P < 0.3013$
<i>L. aestiva</i>	Phytoplankton	Concentration & temperature	$P < 0.5656$
<i>L. aestiva</i>	Nauplii	Concentration	$P < 0.0001$
<i>L. aestiva</i>	Nauplii	Concentration & temperature	$P < 0.0001$

from 0.00 to 4.82  $\mu\text{gC copepod}^{-1} \text{d}^{-1}$  for *C. hamatus* and from 0.00 to 8.38  $\mu\text{gC copepod}^{-1} \text{d}^{-1}$  for *L. aestiva*. Regression analyses revealed that the slopes are significantly different from zero ( $P < 0.05$ ) for both species. Further, *L. aestiva* ingested more animal prey than did *C. hamatus* at the same concentration of prey offered. In addition, the lower coefficient of regression for *C. hamatus* ( $r = 0.51$ ) compared to *L. aestiva* ( $r = 0.77$ ) may be indicative of the less predaceous nature of *C. hamatus*.

Predation and grazing rates, at food concentrations closest to those in the field, were converted to percent body carbon ingested and compared to field concentra-

tions ( $\mu\text{gC l}^{-1}$ ) of phytoplankton (Fig. 5 upper) and nauplii (Fig. 5 lower). Grazing rates for *Centropages hamatus* and *Labidocera aestiva* appear to track the peaks of phytoplankton abundance. When the combined effects of concentration and temperature are considered (stepwise multiple regression), the relationship is significant (Table 4). The mean grazing rates (Fig. 5 upper) follow the same patterns as those of the phytoplankton. Ingestion of nauplii by *C. hamatus* and *L. aestiva* were also significantly related to field concentrations of nauplii and temperature (Table 4).

The potential grazing and predation impact on natural phytoplankton assemblages in the Westport River estuary was extrapolated for each target copepod species during its period of maximum abundance (Table 5). The population of *Centropages hamatus* (maximum = 722  $\text{m}^{-3}$  on 16 May, 1980) was capable of

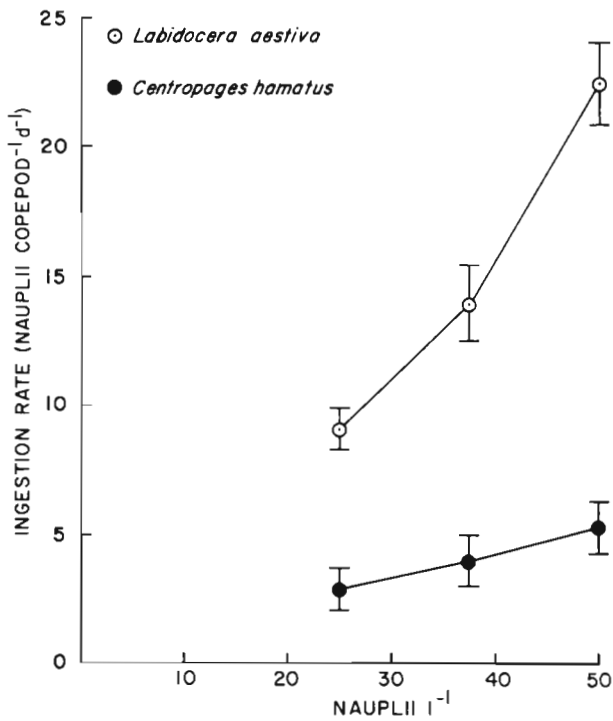


Fig. 3. *Centropages hamatus* and *Labidocera aestiva*. Predation (ingestion) rates of adults (males and females combined) feeding upon copepod nauplii (number of nauplii ingested copepod $^{-1} \text{d}^{-1}$ ) over a range of natural concentrations. Means of 14 to 19 replicates; error bars:  $\pm$  standard error

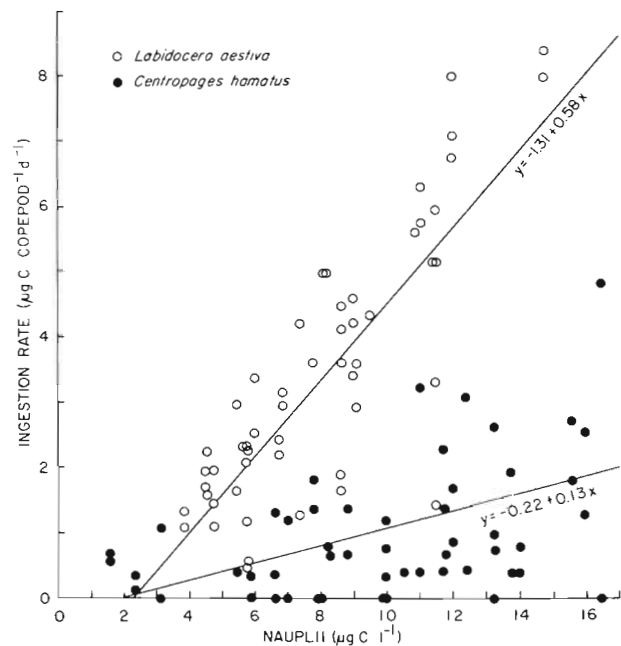


Fig. 4. *Centropages hamatus* and *Labidocera aestiva*. Predation (ingestion) rates of adults (males and females combined);  $\mu\text{gC copepod}^{-1} \text{d}^{-1}$ ) feeding on copepod nauplii over a range of natural concentrations. Single determinations

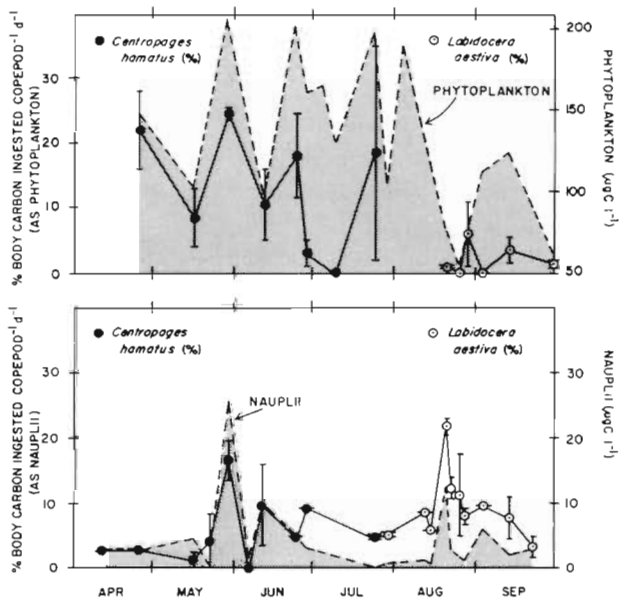


Fig. 5. *Centropages hamatus* and *Labidocera aestiva*. Percentage of body carbon ingested as phytoplankton vs. phytoplankton abundance (upper) and percentage of body carbon ingested as nauplii vs. field abundance of nauplii (lower) by adults (males and females combined). Means of 2 to 4 replicates; error bars:  $\pm$  standard error

Table 4. *Centropages hamatus* and *Lapidocera aestiva*. Effect of field concentrations of food items and temperature on ingestion rate (% body carbon ingested copepod<sup>-1</sup> d<sup>-1</sup>) for both species

Food type	Independent variable (s)	Significance level
Phytoplankton	Concentration	P < 0.0005
Phytoplankton	Concentration & temperature	P < 0.0005
Nauplii	Concentration	P < 0.0004
Nauplii	Concentration & temperature	P < 0.0001

Table 5. *Centropages hamatus* and *Labidocera aestiva*. Potential grazing and predation impact upon phytoplankton and nauplii in Westport River estuary

Species	Maximum # m <sup>-3</sup>	% Phytoplankton carbon removed	% Nauplii removed
<i>C. hamatus</i>	700	0.85	8.23
<i>L. aestiva</i>	8	0.01	0.29

daily grazing an average of 0.85 % of the available phytoplankton carbon present on the same date. At the naupliar concentrations of 16 May, 1980 (19.4 l<sup>-1</sup>), *C. hamatus* was capable of ingesting an average of

8.23 % of the naupliar population. Maximum numbers of *Labidocera aestiva* in the field (8 m<sup>-3</sup>) were recorded on 22 September, 1980. Since no grazing data are available for that date, grazing rates from 13 September, 1980 were utilized. The population of *L. aestiva* was capable of daily ingesting an average of only 0.01 % of the phytoplankton carbon available. The same field population of *L. aestiva* could daily ingest 0.29 % of the available nauplii.

Therefore, even though individual *Labidocera aestiva* exhibit higher predation rates than those of individual *Centropages hamatus*, due to low numbers of *L. aestiva*, the predation impact of their population is lower than that of the more abundant *C. hamatus*. The highest feeding impact on the planktonic communities in the Westport River estuary is likely by the adults and juveniles of *Acartia hudsonica* and/or *A. tonsa*, which were the numerically dominant zooplankters in the estuary (Conley, 1983).

### DISCUSSION

Both *Centropages hamatus* and *Labidocera aestiva* are omnivorous, but ingestion of one food type over another appears to be a matter of degree. Although *L. aestiva* was considered to be a carnivore by Anraku and Omori (1963), this species does ingest phytoplankton. Individual *L. aestiva* were often collected with green guts, indicating that herbivory may be more intense in the field than in our experiments. There is little doubt, however, that animal prey is preferred by this species. At natural food concentrations, rates of carbon ingestion of animal prey ( $\bar{x}$  = 3.35  $\mu\text{gC copepod}^{-1} \text{d}^{-1}$ ) were approximately 507 % higher than those on phytoplankton ( $\bar{x}$  = 0.66  $\mu\text{gC copepod}^{-1} \text{d}^{-1}$ ). Conversely, *C. hamatus* ingested more plant than animal material. *C. hamatus* consumed an average of 209 % more carbon when feeding upon natural concentrations of phytoplankton ( $\bar{x}$  = 2.05  $\mu\text{gC copepod}^{-1} \text{d}^{-1}$ ) than when feeding carnivorously ( $\bar{x}$  = 0.98  $\mu\text{gC copepod}^{-1} \text{d}^{-1}$ ). This indicates that *C. hamatus* is less predaceous, when feeding on natural prey items, than when feeding on artificial prey items such as *Artemia* nauplii (Anraku and Omori, 1963). *Artemia* nauplii are considerably larger, more sluggish, and therefore easier to capture, than *Acartia* spp. nauplii. Animal prey also appears unnecessary for growth and reproduction of *C. hamatus*, since this species has been successfully reared in the laboratory on phytoplankton cultures (Klein Breteler, 1980).

In a similar study of copepod omnivory by Paffenhöfer and Knowles (1980), *Centropages velificatus* ingested more animal prey than *Temora stylifera*, although both were omnivorous. Paffenhöfer and

Knowles' results were discussed in relation to the swimming behavior of the predators and their prey. *T. stylifera* was described as a 'cruising' copepod, swimming almost constantly while creating a strong feeding current. This type of behavior could lead to maximum particle encounter. However, the strong feeding current could also be more readily detected by the naupliar prey, thereby allowing a greater chance of escape. *C. velificatus* was described as a 'hop and sink' swimmer, creating a relatively weak feeding current. This type of behavior would allow for 'ambush' predation since the copepod could more readily achieve proximity to the prey nauplii and 'once a nauplius is close to such a predator (within a few mm) and at a certain angle towards its feeding appendages, there is little chance of escape' (Paffenhöfer and Knowles, 1980).

Since *Labidocera* exhibits a 'cruising' type behavior and *Centropages hamatus* is a 'hop and sink' swimmer, the results of the present study might seem contradictory to those of Paffenhöfer and Knowles (1980). However, *L. aestiva* creates a feeding current noticeably weaker than does *C. hamatus*. The weaker current, in combination with a 'cruising' type swimming behavior, could allow for a greater area of search while concurrently preventing detection by prey items. In addition, our results combined with those of Paffenhöfer and Knowles form an omnivory continuum, in that *Temora* appears more herbivorous and less carnivorous than *Centropages*, whereas *Centropages* appears more herbivorous and less carnivorous than *Labidocera*.

The advantage of omnivory in estuarine systems characterized by pulses of phytoplankton (Martin, 1965, 1970; Bruno et al., 1983; Turner et al., 1983) and microzooplankton (Turner, 1982; Conley, 1983) is obvious. The ability of some estuarine copepods to adjust their ingestion rates according to the relative abundance of food items has been demonstrated here (Fig. 5) and for various estuarine copepods by Poulet (1973, 1974, 1978). Further, *Acartia tonsa*, the most abundant summer copepod in temperate west Atlantic estuaries (Hulsizer, 1976; Turner, 1982), is also capable of supplementing its diet with animal prey in the form of copepod nauplii (Lonsdale et al., 1979).

It appears that adjustive omnivory is not restricted to estuarine copepods. The oceanic copepod *Calanus pacificus* ingested more animal prey as phytoplankton concentrations dropped and more plant material when phytoplankton was abundant (Landry, 1981). Turner (1984a) also noted an increase in the occurrence of crustacean appendages in the fecal pellets of the shelf copepod *Eucalanus pileatus* at stations where phytoplankton numbers were low.

Although it has long been known that most plank-

tonic copepods are omnivores (Lebour, 1922; Marshall, 1924), previous quantitative comparisons of herbivorous and carnivorous feeding of copepods upon natural food items have been rare (Paffenhöfer and Knowles, 1980; Landry, 1981). In the absence of additional studies for numerous abundant copepod taxa, it will be impossible to assign these consumers to their proper niches in marine food webs. This will preclude realistic understanding or quantification of marine trophodynamics.

**Acknowledgements.** We thank Leah Curran for technical support, Teresa Hastings for aid in field collections and manuscript preparation, and the Biology Department, South-eastern Massachusetts University, for partial funding of this research.

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This paper was presented by Professor G.-A. Paffenhöfer; it was accepted for printing on August 15, 1984