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Seasonal contrasts in the diel vertical distribution, feeding behavior, and grazing impact of the copepod *Temora longicornis* in Long Island Sound

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ABSTRACT

We studied diel variability in vertical distribution, feeding behavior and grazing impact of female *Temora longicornis* in Long Island Sound on seven cruises from March to July. *T. longicornis* usually performed diel vertical migration characterized by deep residence during the day and ascent to near-surface waters at night for variable periods. The pattern of diel migration was independent of either the vertical distribution or relative abundance of chlorophyll in the water column. There was no clear evidence linking the amplitude of vertical migration to food concentration. Rather, the amplitude of migration decreased toward the end of the season probably due to animals avoiding warm waters ($> 17°C$) near the surface. Gut pigment content showed diel variation characterized by maximum values during the nighttime. However, the estimated mean ingestion rate from the nighttime period was significantly greater than that of the daytime period in only 2 of 11 comparisons indicating that this copepod usually fed throughout the day at about the same rate. The shape of the diel curve was usually similar for females at 5 and 20 m. Usually there was no difference in gut content of females with depth even when differences in chlorophyll with depth were pronounced. Therefore, the diel variability in gut content was unlikely to result from continuous feeding in a vertically stratified food environment. Short-term (hourly) changes in chlorophyll concentration could not entirely account for changes in gut content over a diel cycle. We estimate that female *T. longicornis* removed daily < 1–34% of the phytoplankton stock and < 1–49% of the primary production in Long Island Sound. Estimates of daily carbon rations indicate that a herbivorous diet can satisfy the metabolic requirements and support egg production of *T. longicornis* throughout most of its season.

1. Introduction

Understanding the *in situ* feeding behavior and grazing impact of copepods requires knowledge of diel changes in their feeding activities and distribution in the water column. Among many species of copepods the usual pattern of vertical distribution is one of residence at depth during the day and near the surface at night.

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An increase in copepod gut content at night may be due to the daytime disassociation and nighttime association of diel migrators and their food (e.g., Gauld, 1953). Several field studies support this hypothesis (Hart, 1977; Daro, 1980; Hayward, 1980; Simard *et al.,* 1985). On the other hand, copepods can exhibit increased feeding at night in the absence of vertical migration from regions of low to high food abundance (e.g., Mackas and Bohrer, 1976; Boyd *et al.,* 1980; Nicolajsen *et al.,* 1983; Head *et al.,* 1985), or in situations in which the amount of food (chlorophyll *a*) is vertically homogeneous (Baars and Oosterhuis, 1984; Mayzaud *et al.,* 1984; Daro, 1985). One explanation for these observations is that copepods can feed more actively at night regardless of food concentration (Dagg, 1985; Dam, 1986; Stearns, 1986; Durbin *et al.,* 1990). This behavior may be endogenously controlled (Duval and Geen, 1976) or under the influence of light intensity (Fernández, 1977; Head, 1986; Stearns, 1986; Head and Harris, 1987). Enhanced feeding activity at night could be an adaptive behavior if grazers utilized the maximal amount of photosynthetic algal cell products (McAllister, 1970; Enright, 1977). Alternatively, it has been suggested that enhanced nocturnal feeding has evolved under predation-driven selection (Durbin *et al.,* 1990).

Other researchers have suggested an apparent link between diel vertical migration and feeding behavior by reporting cases in which individuals performed full migration when food was abundant, but they either did not migrate or they reduced the amplitude of migration when food was scarce (Boyd *et al.,* 1980; Huntley and Brooks, 1982; Dagg, 1985). These observations may be explained by the hypothesis that when food is not limiting whatever bioenergetic costs are associated with migration can be offset by increased feeding at night, but when food is limiting this may not be so (Dagg, 1985). Hardy and Gunther (1936) linked food, feeding activity and migration when they hypothesized that the time spent at the surface by migratory herbivores might be inversely proportional to food availability; i.e., satiated animals would remain near the surface for a short time; conversely, unsatiated animals would stay longer near the surface or, in extreme cases, remain at the surface continuously. Although the relationship between diel feeding behavior and vertical migration may be obscured by other factors such as predation (Zaret and Suffern, 1976; Stich and Lampert, 1981; Ohman *et al.,* 1983), light and temperature (cf. review in Bougis, 1976) and endogenous rhythms (Harris, 1963; Enright and Hamner, 1967), there is evidence that hunger can sometimes override these factors (Huntley and Brooks, 1982, review in Lampert, 1989).

One may conclude from the above discussion that in order to understand the relationship between diel feeding behavior and vertical migration of zooplankton, one must be able to characterize these behaviors under a suite of different food conditions throughout the seasonal cycle of abundance of a given species.

In this paper, we examine the relationship between diel feeding behavior and vertical migration throughout the season of growth of females of the calanoid copepod *Temora longicornis.* This animal dominates the copepod biomass (peak

biomass is 500 μg dry weight l^{-1}, 2 to 5-fold greater than that of *Acartia hudsonica,* the numerical dominant) in Long Island Sound from January through July (Peterson, 1985). *T. longicornis* has been shown to have a greater gut fullness and/or ingestion rate at night than during the daytime (Baars and Oosterhuis, 1984; Head *et al.,* 1984; Daro, 1985; Dam, 1986; Tiselius, 1988). It also has been shown to perform diel vertical migration characterized by nocturnal ascent to surface waters (Harding *et al.,* 1986), although the depth of ascent can be modified by the vertical distribution of chlorophyll in the water column (Bohrer, 1980). From December to July the abundance, vertical distribution and size of the phytoplankton in Long Island Sound vary markedly. From December through late March or mid-April, the phytoplankton is dominated by cells >20 μm; chlorophyll is more or less vertically homogeneous and in excess of 2–3 μg l^{-1}. From late April onward, the phytoplankton is dominated by nanoplankton (<20 μm) and chlorophyll concentration near the surface may be two or three-fold greater than near the bottom. These patterns are consistent from year to year (Peterson, 1986; Dam and Peterson, 1991). Finally, seasonal studies of *T. longicornis* in Long Island Sound suggest that it experiences food limitation during some periods of its seasonal cycle as evidenced by significant correlations between ingestion and egg production rates and chlorophyll, respectively (Peterson and Bellantoni, 1987; Dam and Peterson, 1991).

The objectives of this research were to describe and compare the patterns of diel feeding behavior and vertical distribution of female *T. longicornis* under different ambient food conditions. The following questions were addressed:

(1) Are the diel patterns of feeding and vertical distribution similar when chlorophyll is vertically homogeneous and vertically stratified; are these patterns similar when chlorophyll is abundant and when it is scarce?

(2) Are there any differences in the patterns of diel feeding behavior between animals caught near the surface and those caught at depth; i.e., is the shape of the diel feeding curve similar for the two depths?

(3) Are ingestion rates at night greater than during the daytime?

(4) Do changes in gut content throughout the day reflect feeding rhythmicity or can they be explained by changes in chlorophyll concentration throughout the day?

Finally, the information derived from these studies was used to ask two questions that can yield insight into the dynamics of interactions of phytoplankton and zooplankton in Long Island Sound:

(5) What is the grazing impact of the female *Temora longicornis* in Long Island Sound?

(6) Can a herbivorous diet satisfy the metabolic needs of *Temora longicornis?*

2. Materials and methods

Cruises were conducted on seven occasions at a station located 5 km offshore from Port Jefferson Harbor (for station location see Peterson, 1985). Dates of cruises are

Table 1. Number of profiles of temperature, chlorophyll and vertical distribution of female *Temora longicornis* during the cruises. Numbers in parentheses indicate the times at which profiles were made.

Date	Temperature	Chlorophyll	Vertical Distribution of *T. longicornis*
15–16 May 84	4 (1115, 1405, 1555, 1154h)	2 (1430, 2400h)	8 (every 2–3h)
7–8 May 85	1 (1500h)	1 (1500h)	2 (1600, 2130h)
11–12 June 85	1 (1310h)	1 (1400h)	2* (1400, 2245h)
7–8 May 86	5 (0800, 1210, 1600, 2130, 0430h)	2 (1200, 2115h)	18 (every 1.5h)
5–6 March 87	6 (0830, 1055, 1445, 1610, 2100, 2400h)	12 (every 2h)	12 (every 2h)
1–2 July 87	2 (1200, 0530h)	2 (1200, 0535h)	8† (1200, 2015, 2310, 2135, 2155, 2310, 0535, 0610h)
9–10 July 87	5 (0840, 1140, 1510, 1945, 0530h)	3 (1000, 2400, 0600h)	10‡ (every 2–4h)

* = plus 8 profiles in which animals were sampled at 3, 10 and 30 m, every 20 to 45 min from 1900h to 2200h.

† = Profiles at 2015, 2135 and 2155h were not included in the analysis because the total abundance of females per profile was less than 10.

‡ = only two profiles (1030 and 2330h) were included in the analysis. The eight other profiles were excluded for the same reason as in †.

given in Table 1. In every instance the boat was allowed to drift within the area defined by the 40 m isobath. The tidal excursion at the sampling location varies from 6 to 10 km (Riley, 1956; Dam, 1985).

a. Vertical distribution of copepods, chlorophyll and physical properties. The vertical distribution of *T. longicornis* for the first three cruises was investigated by collecting water from 1, 3, 5, 10, 15, 20, 30 and occasionally 37 m with a pump fitted with a neopropene impeller and a 1.9 cm internal diameter hose (flow rate = 15 liters min^{-1}). A comparison of female abundance (No. m^{-3}) estimated from the pump

employed here (Y) and from a 0.75 m diameter, 202 μm mesh WP-2 net (X) yielded the regression equation $Y = -72.7 + 1.43*X$, $r^2 = 0.83$, $n = 15$, indicating that the pump does not underestimate the abundance of females. The order of depth sampling was always from deepest (37-30 m) to shallowest (1 m). The sampling depths were estimated from wire angle and length of hose out. A 4 kg cement weight was attached to the end of the hose to keep it taut in the water column.

Sample size varied from 7.6 l (15–16 May 1984) to 12.0 l (7–8 May and 11–12 June 1985). The sample from each depth was filtered through a 64 μm mesh, rinsed into a bottle and preserved with 5% buffered formalin solution. At each depth water was allowed to run through the pump for at least one minute before taking the sample to avoid contamination from the previous depth.

In May of 1986 and March of 1987 the protocol used to examine the vertical distribution of the animals was slightly modified. Integrated stratified samples were produced by pumping 4 l of water from each of the following depths and pooling them together: 30, 22 and 15 m (deep stratum); 15, 10 and 5 m (intermediate stratum); and 5, 3 and 1 m (shallow stratum). These strata represented the bottom mixed layer, the pycnocline region (when present) and the surface mixed layer, respectively. Each sample was processed and preserved as described above. Although this sampling scheme sacrificed some resolution on the vertical distribution of the animals, it allowed more frequent sampling and better temporal resolution, which was a question of more significance to this research. In July of 1987, a combination of discrete and stratified sampling was employed. Discrete sampling was the same as described for the first three cruises, and sample size was 12.0 l. Stratified sampling was the same as described for the May 1986 and March 1987 cruises.

In the laboratory, the entire contents of each sample were examined under a dissecting scope and the number of female *T. longicornis* enumerated.

Samples for chlorophyll *a* (from here on, chlorophyll will refer to chlorophyll *a*) were obtained by pumping water from 1, 3, 5, 10, 15, 20, 30 and 35 m. From each depth, a 50 ml sample was filtered through a 0.8 μm AA Millipore filter. The filters were placed in capped, 15 ml plastic centrifuge tubes, filled with 10 ml of 90% acetone solution, and placed in ice or on-board freezers overnight (−20°C). Samples for size-fractions (<20 and <10 μm) of chlorophyll (Runge and Ohman, 1982) were pumped from near the surface (either from an integrated sample from 1, 3 and 5 m or from 5 m only) and at depth (20 m). Chlorophyll measurements were done in the laboratory by conventional fluorometric techniques (Strickland and Parsons, 1968). Starting with the cruise in 7–8 May, 1986, chlorophyll samples for different size-fractions of phytoplankton (total, <20 and <10 μm) at 5 and 20 m were also taken simultaneously with samples for gut pigment content of animals. This was done to

examine the possibility that changes in gut pigment content were related to *short-term* changes in chlorophyll concentration.

Measurements of temperature, conductivity and salinity were made at the same depths used to sample chlorophyll by means of a BECKMAN RS-5 induction salinometer. A summary of the number of profiles of temperature, chlorophyll and vertical distribution of *T. longicornis* and for all the cruises is presented in Table 1.

b. Gut content of copepods. Copepods were collected from depths of 5 and 20 m at variable intervals (usually 1–2 h). The plankton net (0.57 m diameter, 202 μm-mesh size) was bridleless, with a line of rope attached to one side of the net ring and a 5 kg-weight to the opposite end. When lowered and retrieved the net mouth remained vertical and thus did not sample. While at the desired sampled depth, the net sampled for 2–5 minutes while the ship drifted. A portion of the zooplankton catch from the tow was passed through a 500 μm screen and gently rinsed with filtered (GF/C) seawater to remove debris and any cells that may have adhered to the animals. The animals retained on the screen were placed under a dissecting scope and about 10 female *T. longicornis* were individually picked with jeweller's forceps, placed in a 15 ml plastic centrifuge tube to which a few milliliters of 90% acetone solution were added. The tube was capped and stored either in a cooler with crushed ice or in an on-board freezer (−20°C) until transferred to the laboratory. This operation took ca 5 min. With the exception of the first cruise, replicate samples were usually taken.

In the laboratory, the number of females in each centrifuge tube was verified, then the contents of each tube were homogenized in a glass pyrex tube, transferred back to the centrifuge tube, diluted to 10 ml with 90% acetone solution and centrifuged for 10 minutes. The fluorescence of the supernatant from each tube was measured before and after acidification with 10% HCl using a Turner Designs model 10 fluorometer equipped with a 5–60 excitation filter and a 2–64 emission filter. The above procedures were done under very dim light. The fluorometer was calibrated once or twice per year during the study period. The variation in acid ratios and door factors from calibration to calibration was less than 10%.

The concentrations of chlorophyll *a* and pheophorbide *a* per animal were calculated using the equations in Dam and Peterson (1988) and the gut content per animal was expressed as the amount of chlorophyll originally ingested. Pheophorbide loss was assumed to be constant and equal to 33% (review in Dam and Peterson, 1988; Lopez *et al.,* 1988; Downs, 1989), but see Penry and Frost (1991), Mayzaud and Razouls (1992). No correction for background pigment was employed (see Baars and Oosterhuis, 1984). In any case, "background" pigment content of female *T. longicornis* starved for 24 h in the laboratory was very low (mean = 0.056 ng pigment female^{-1}; std. dev. = 0.014, n = 60).

c. Estimation of in situ ingestion rates, daily rations and grazing impact. Total food consumption per individual female (C_t) for each time interval (t) was calculated from the model of Elliot and Persson (1978) using the formula:

$$C_t = (G_t - G_o e^{-Kt})*Kt/(1 - e^{-Kt}) \quad (1)$$

where G_o and G_t = gut content at the beginning and end of the time interval, respectively and K is the instantaneous gut evacuation rate constant. This relation assumes that gut evacuation is exponential and that ingestion rate remains constant during the time interval. The instantaneous gut evacuation rate constant (min^{-1}) was estimated from the equation $K = 0.0119 + 0.001904*T$ (Dam and Peterson, 1988) where T is the temperature (°C) at the depth from which animals were collected. Hourly ingestion rates were estimated by dividing C_t by the length of the time interval (t). The daily ration per female, C_{total}, was calculated from addition of the different values of C_t throughout the day.

The grazing impact of female *T. longicornis* was estimated in two ways. The percentage of the chlorophyll standing stock removed per day was estimated by multiplying the females' daily ration, C_{total}, (mg chl. $female^{-1}$ day^{-1}) by their abundance (number m^{-2}) and dividing by the standing stock of chlorophyll (mg chl. m^{-2}). This calculation assumes that the phytoplankton standing stock is in steady state (cf. Welschmeyer *et al.,* 1984). To estimate the percentage of the primary production grazed on a daily basis, a carbon to chlorophyll ratio of 52, typical of Long Island Sound (Tantichodok, 1990), was assumed to convert chlorophyll rations to carbon rations; the product of daily carbon rations and female abundance was then divided by the primary production. Abundance of female *T. longicornis* and chlorophyll standing stock were estimated from integration of each profile using the trapezoidal rule and averaged over 24 hours. Primary production rates were estimated by the ^{14}C technique. Incubations were performed from 1200 to 1600 h in integrated samples from the upper 5 m and at 10 m (Peterson, unpublished). Hourly rates were multiplied by the number of daylight hours to obtain daily rates. In May 1984 eight primary productivity (^{14}C) values were integrated over a 24 h period (McManus and Fuhrman, 1986). In July 1987 primary productivity was not measured. We estimated primary productivity from $Y = 3.29 + 4.88*X$ ($r^2 = 0.67$, $n = 61$) (Dam, 1989), where $Y = \mu gC\ l^{-1}\ h^{-1}$ and X = chlorophyll concentration ($\mu g\ l^{-1}$). In this case, we used the average chlorophyll concentration at 5 m (see Fig. 12).

d. Gut content of copepods at the shore station. These observations were conducted during the spring of 1987 and were designed to complement those from the diel cruises to the central basin of Long Island Sound and to test the hypothesis that ingestion rate of *T. longicornis* females increases near sunset. All observations were done at the Mount Sinai Dock in water depth ranging from 2 to 4 m depending on the height of the tide. Sampling was conducted during days in which tidal flood occurred

during the morning and from late afternoon to evening so that gut content of *T. longicornis* females during the daytime and periods near sunset could be compared. Sampling during periods of flood was necessary to ensure that animals were collected from waters in the Sound. Collection of animals and processing of samples were done as described in the previous section; however, sampling frequency was increased to 30 min during the daytime and 10–30 min during late afternoon and evening. The chlorophyll concentration of the water from which the females were sampled was also measured, although not always as often as the gut pigment content of females.

3. Results

Although the study spanned three different years, the cruises covered most of the season of *Temora longicornis* in Long Island sound and were done at times that represented different physical and food conditions. Therefore, the results will be presented by months rather than chronologically. The seasonal progression in the vertical distribution of temperature and chlorophyll in Long Island Sound is sufficiently constant from year to year (Peterson, 1986) to justify this approach.

a. Vertical distribution of temperature and chlorophyll. Figure 1 shows the vertical distribution of temperature and chlorophyll. Temperature rose from a minimum of 1.1°C near the surface in March to between 9 and 11°C in May. In June and July, near surface temperature ranged from 15 to 21°C. The temperature below 20 m was not greater than 15.9°C in any of the cruises. The water column was nearly isothermal in March and became progressively stratified as the season progressed—the temperature gradient over the entire water column increased from a minimum of 0.012°C m^{-1} in March to a maximum of 0.17°C m^{-1} in mid-July (Table 2). The thermocline was usually found between 5 and 10 m, with the largest temperature gradient, in this depth interval, occurring in June.

Chlorophyll was evenly distributed with depth in March and ranged from 2 to 5 $\mu g\ l^{-1}$ throughout the day. As the season progressed chlorophyll became vertically stratified. Stratification was slight on 15–16 May 1984, but pronounced in the rest of the cruises in May, June and July. In these instances, chlorophyll concentration was high in the upper 10 to 15 m of the water column (3–10 $\mu g\ l^{-1}$) and relatively low (1–4 $\mu g\ l^{-1}$) below 20 m. The contribution of nanoplankton (<20 μm cells) to the total chlorophyll concentration varied from a minimum of 56% in 7–8 May 1986 to a maximum of 98% in 7–8 May 1985 (Table 3).

b. Vertical distribution of copepods. The vertical distribution of female *Temora longicornis* varied as the season progressed (Figs. 2–8). In March, when the temperature was low and the water column was well mixed, up to 50% of the females were found below 15 m during daytime (Fig. 2). However, the mode in abundance was at times between 15 and 5 m during the daytime. Females were always present in the upper 5 m during the daytime and, at times, in large proportions. Females became

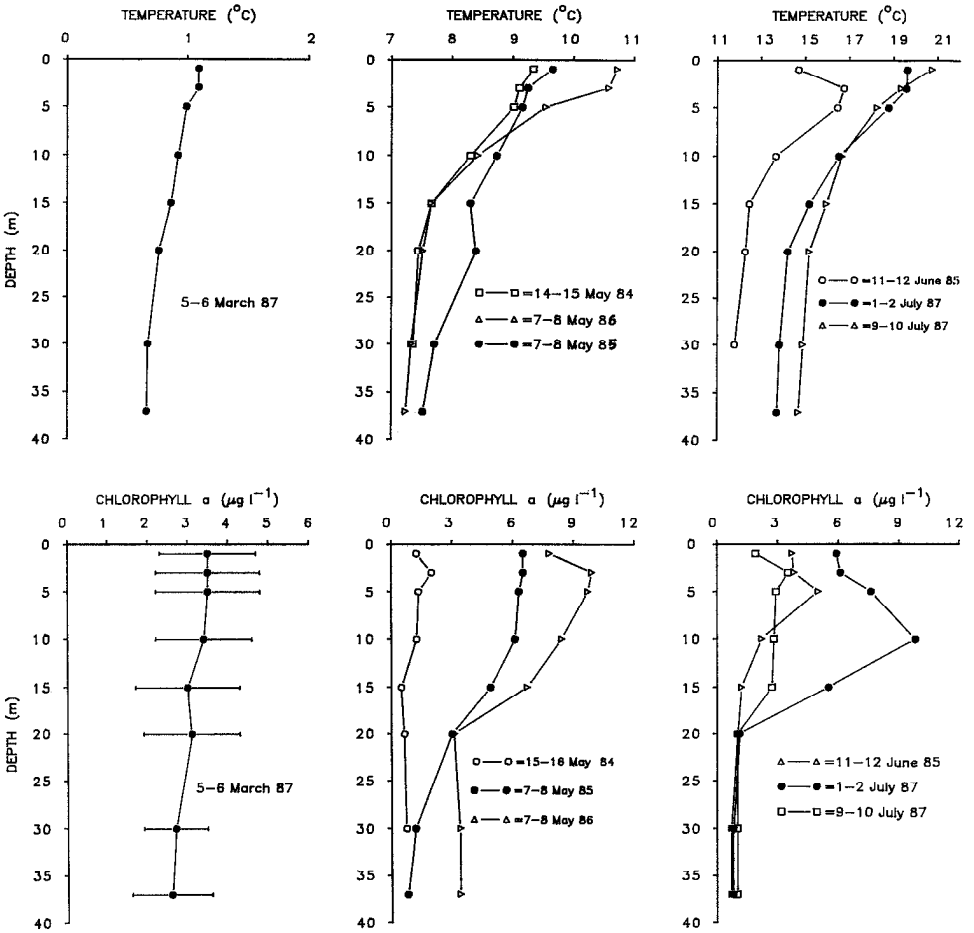

Figure 1. Vertical distribution of temperature and total chlorophyll *a* during the diel cruises. Profiles are means for the entire day. The number and time of day for each profile are presented in Table 1.

evenly dispersed throughout the water column from 2015 to 2200 h. By midnight, less than 20% of the females remained in the upper 5 m and by dawn 80% of them were below 15 m.

In May there were no females in the upper 1 m of the water column and very few at or above 5 m during daytime (Figs. 3–5). In 1984 and 1985, when discrete depths were sampled, the mode during the daytime was at 15 or 20 m. In 1986, when samples were pooled, the mode was in the deep stratum (15-22-30 m). In all cases, more than 70% of the females were at or below 15 m during daytime. In all cases, by dusk or early evening, females had reached the upper 5 m, and by early morning they had resumed deep residence.

Table 2. Temperature gradients during the diel cruises. Unless otherwise indicated the thermocline was located between 5 and 10 m. When the thermocline was not located between 5 and 10 m, the depth interval is indicated by *Z*.

Date	0–37m (°C m^{-1})	5–10 m (°C m^{-1})	Thermocline (°C m^{-1})	*Z* (m)
15–16 May 84	0.07	0.14		
7–8 May 85	0.06	0.08		
11–12 June 85	0.10	0.56		
7–8 May 86	0.10	0.22	0.52	3–5
5–6 March 87	0.01	0.01	0.05	3–5
1–2 July 87	0.16	0.45		
9–10 July 87	0.17	0.32		

In June the daytime peak in abundance of female *Temora longicornis* was deeper in the water column when compared with March and May (Fig. 6), and females were virtually absent from the upper 15 m of the water column. At night, females concentrated (75% of the total) in the upper 5 m of the water column.

In July, near the end of the season of *T. longicornis* in Long Island Sound, females were usually found below 20 m during the daytime (Figs. 7 and 8). On 1–2 July, females had ascended to the surface by dusk, although the mode was at intermediate depths (5–15 m). By dawn, females had left the upper 5 m of the water column and by early morning all females were below 20 m. On 9–10 July ten profiles were done—two sampling at discrete depths and 8 sampling integrated, pooled depths. The latter had so few females altogether (< 10 females total for the entire profile) that they were not used in the analysis of vertical distribution. The other two profiles indicate that, as in early July, females were also deep during the daytime. However, females did not ascend to the upper 5 m of the water column during the nighttime.

c. Diel feeding behavior of copepods. In March, gut pigment content varied relatively little over the 24 hours except for two peaks, one in the late afternoon (1630 h) and

Table 3. Summary of the percentage of chlorophyll concentration in the < 20 and < 10 μm size fractions during the diel cruises. ND = No data available.

	Near surface (5 m)		Deep (20 m)	
	< 20 μm	< 10 μm	< 20 μm	< 10 μm
15–16 May 84	69	69	ND	ND
8–7 May 85	98	84	ND	ND
11–12 June 85	ND	81	ND	ND
8–7 May 86	56	16	ND	ND
5–6 March 87	75	59	76	57
1–2 July 87	69	47	92	56
9–10 July 87	80	65	84	69

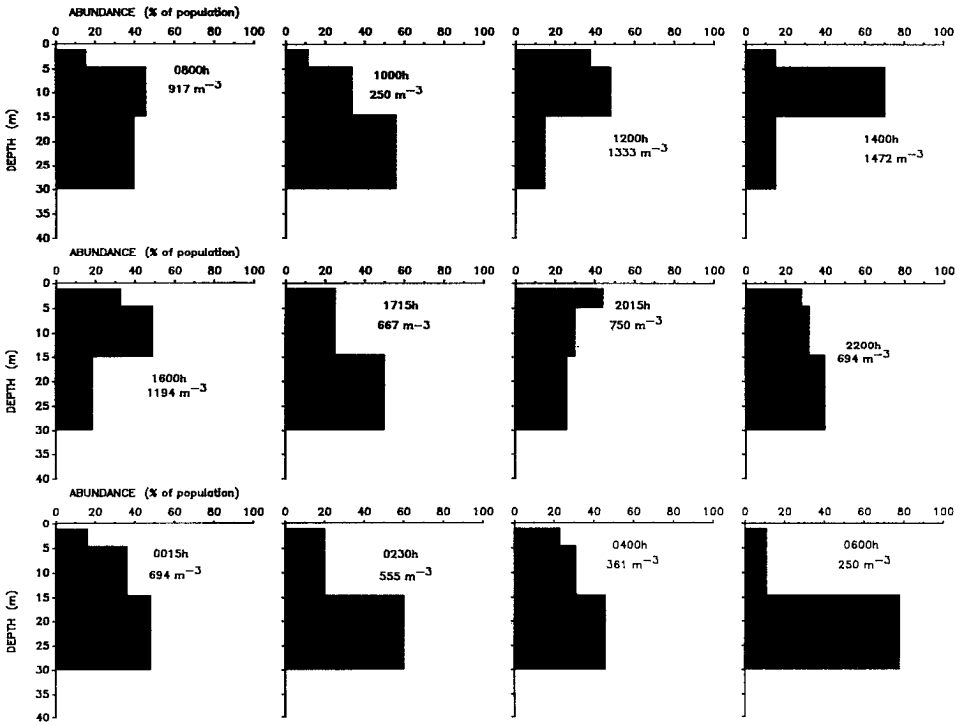

Figure 2. Vertical distribution of female *Temora longicornis* during 5–6 March 1987. Abundance is expressed as per cent of the total number of females for the entire profile at three depth strata: 1–5 m, 5–15 m and 15–30 m (see text for details of sampling). The time represents the midpoint of each profile. The estimated mean abundance of female *T. longicornis* for the portion of the water column sampled (in this case 1–30 m) for each profile is also given. Sunset = 1750 h; Sunrise = 0620 h.

another one late at night (0300–0500 h) (Fig. 9). Gut content of females at 5 m was the same as females at 20 m. The shape of the diel feeding curve did not differ with depth. There was no apparent correlation between changes in chlorophyll concentration and gut pigment concentration.

In May, the diel feeding curve was characterized by relatively constant values of gut pigment content during the daytime, an increase at sunset, with the maximum in gut content occurring before midnight, and a decline from then on until early morning when gut content values were similar to those from the previous morning (Fig. 10). Differences in gut pigment content (GPC) between day and night were two to eight fold. In one case, GPC was similar for females at 5 m and 20 m (1985); in another case, GPC of females at 20 m was greater than those at 5 m (1986). The difference in GPC between depths was not related to differences in chlorophyll concentration between depths (Fig. 10).

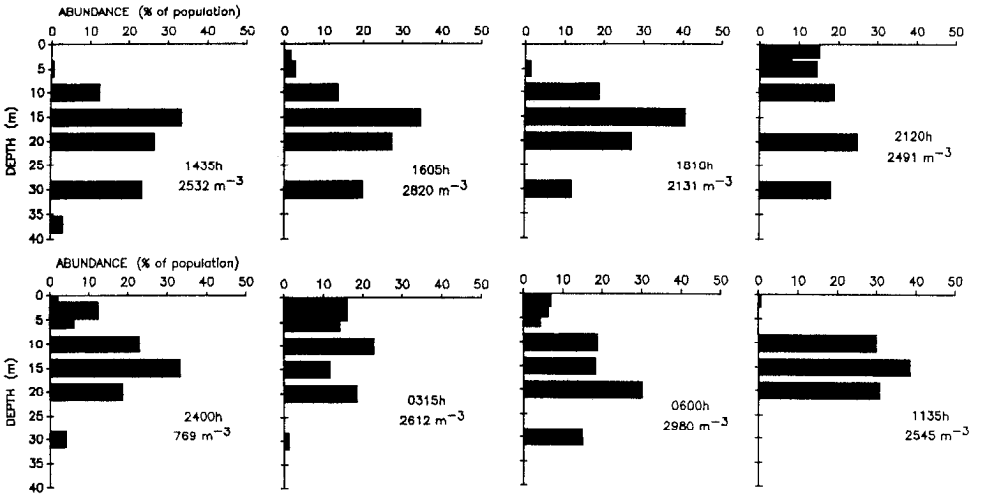

Figure 3. Vertical distribution of female *Temora longicornis* during 15–16 May 1984. Abundance is expressed as per cent of the total number of females for the entire profile at a given depth. Depth sampled were: 1, 3, 5, 10, 15, 20, 30 and occasionally 37 m. Time and mean water column abundance estimates for each profile as in Figure 2. Sample from 30 m at 1135 h profile was lost. Sunset = 2008 h; Sunrise = 0546 h.

In June of 1985, the shape of the diel feeding curve was different for females at 5 and 20 m. Females at 5 m had high gut content during mid-day followed by a decline and levelling off lasting until midnight, a maximum at 0500 h and a rapid decline afterwards (Fig. 11). Gut content of females at 20 m was very low during the daytime, increased sharply to a maximum one hour before sunset (1930 h), declined rapidly thereafter, and showed a second maximum at 0445 h, followed again by a rapid

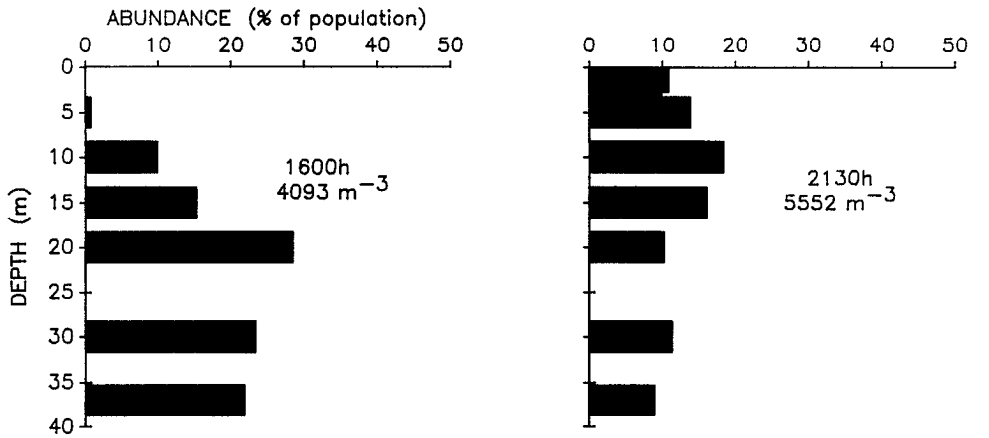

Figure 4. Vertical distribution of female *Temora longicornis* during 7–8 May 1985 (details of legend as in Fig. 2). Sunset = 2001 h; Sunrise = 0553 h.

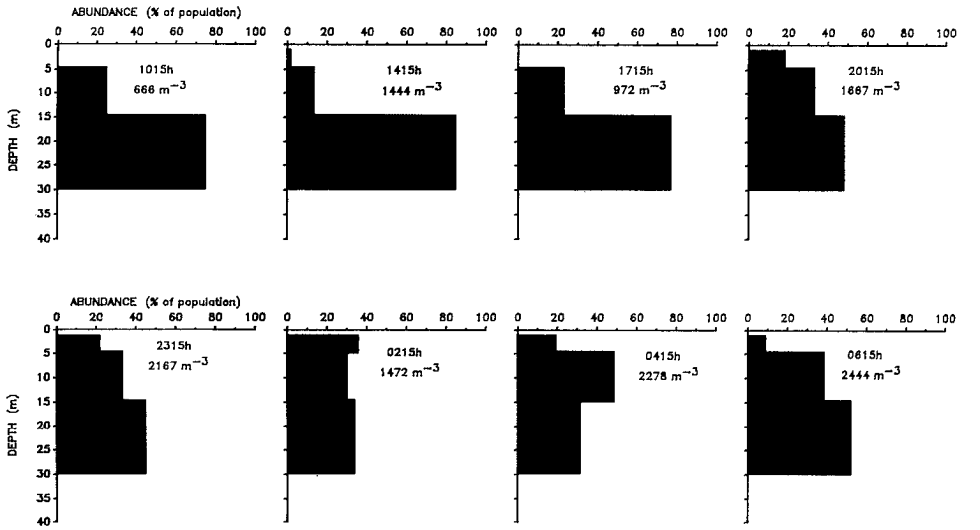

Figure 5. Vertical distribution of female *Temora longicornis* during 7–8 May 1986 (details of legend as in Fig. 2). Eight representative profiles of a total of 18 are shown. Sunset = 2001 h; Sunrise = 0553 h.

decline to values similar to those from the previous afternoon. Gut content of females at 5 m was greater than at 20 m in all but one instance.

On 1–2 July, females were absent from the upper 5 m most of the time. Gut content of females at 20 m during the night was greater than the day by four-fold (Fig. 12). Females at 20 m usually had a greater gut pigment content than those at 5 m, but the data are limited. On 9–10 July there were again no females at 5 m; at

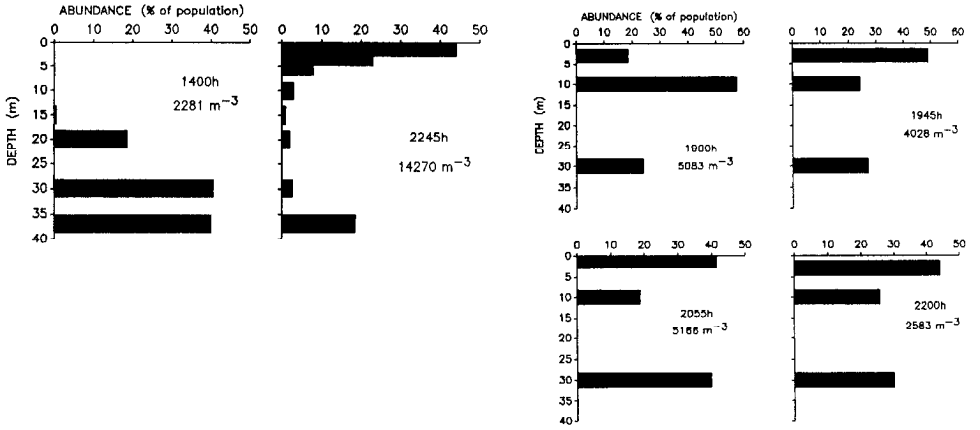

Figure 6. Vertical distribution of female *Temora longicornis* during 11–12 June 1985. Left (details of legend as in Fig. 3). Right (see Table 1 for explanation; four representative profiles are shown). Sunset = 2026 h; Sunrise = 0527 h.

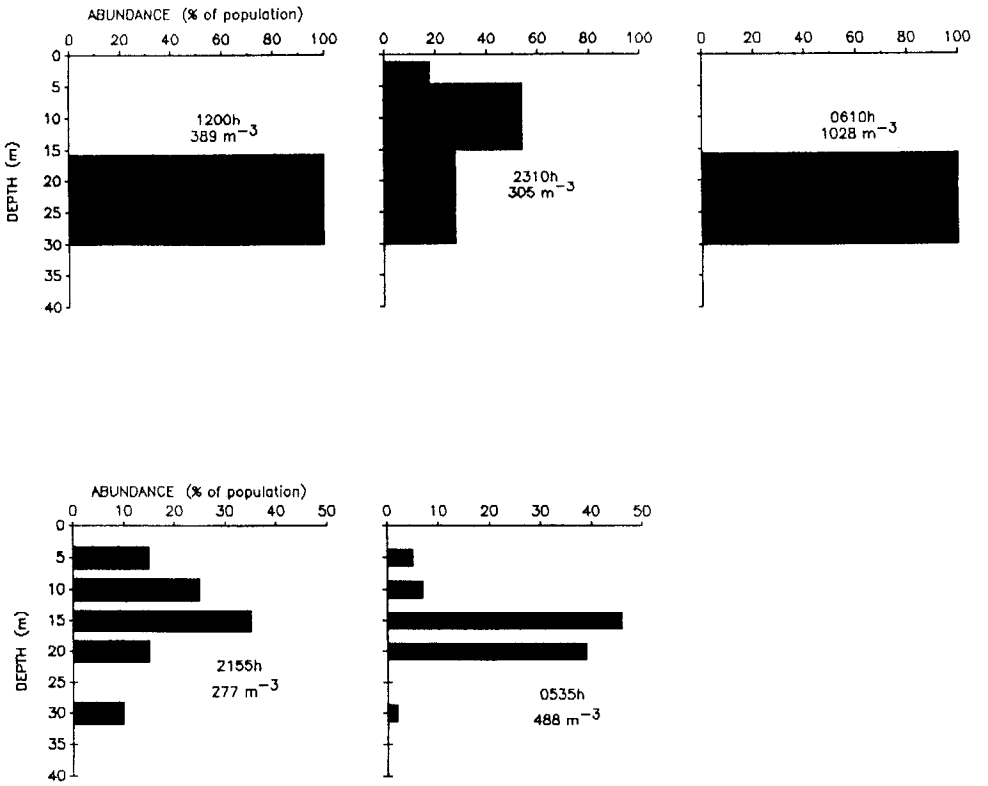

Figure 7. Vertical distribution of female *Temora longicornis* during 1–2 July 1987. Upper panels (details of legend as in Fig. 2). Lower panels (details of legend as in Figure 3). Three profiles were not included because less than 10 females were counted for the entire profile (see text). Sunset = 2027 h; Sunrise = 0525 h.

20 m there was also an increase in gut pigment content from daytime to night. Overall, the increase in gut content from daytime to night was not as pronounced as in the previous cruise. There was a small increase in gut content around sunset and a sharp increase at 0500 h.

The observations in nearshore waters (Fig. 13) were consistent with those from the deeper waters in central Long Island Sound. On the first two occasions (25 April and 11 May 1987) gut content changed little during the daytime and increased steadily from late afternoon until sampling stopped in mid-evening. Gut content increased five-fold from daytime to nighttime on the first occasion and three-fold on the latter. On June 1 *T. longicornis* was absent from the surface waters until just before sunset. Gut pigment content increased two-fold from just before sunset until 2200 h.

We tested the hypothesis that changes in gut content of *Temora longicornis* throughout the diel cycle reflected changes in chlorophyll concentration on three cruises when gut pigment content and chlorophyll concentration were measured

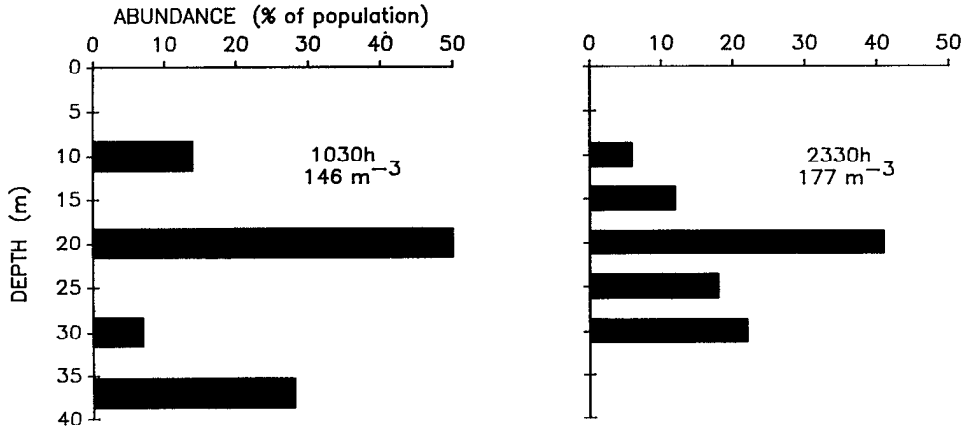

Figure 8. Vertical distribution of female *Temora longicornis* during 9–10 July 1987 (details of legend as in Fig. 3). Ten profiles were not included because less than 10 females were counted for the entire profile (see text). Sunset = 2026 h; Sunrise = 0530 h.

simultaneously (7–8 May 1986, 5–6 March 1987 and 9–10 July 1987). We found that gut pigment content and chlorophyll concentration at 5 m were not correlated in any of the cruises (Table 4); however, in two of the three occasions, gut content was positively correlated with chlorophyll concentration at 20 m (total and net fraction on 5–6 March and total and nanoplankton fraction on 9–10 July). On these two dates, the slopes of the regression lines were different from zero (Table 4), but the amount of explained variance was only 26 and 35%, respectively.

Gut pigment content of *Temora longicornis* was usually highest during the nighttime in all the cruises. However, were differences between night and day significant? To test this hypothesis, we compared ingestion rates of *T. longicornis* for different times of the day (Eq. 1) from the diel cycle of gut pigment content. The null hypothesis was that ingestion rate at night was not different from ingestion rate during the day for females at 5 and 20 m, for all seven cruises (Table 5). In all but two cases (females at 5 m on 15–16 May 1984 and 7–8 May 1985), we were unable to reject the null hypothesis. Therefore, we conclude that although the mean ingestion rate for the night period tended to be greater than for the day period, the variability was such that these differences were statistically insignificant.

d. Herbivorous ration and grazing impact of copepods. Estimates of daily rations and grazing impact of *T. longicornis* are presented in Table 6. Rations of female *T. longicornis* at 20 m throughout the season varied by a factor of three (27 to 85 ng chl. fem^{-1} d^{-1}) and at 5 m by a factor of four (47 to 195 ng chl. fem^{-1} d^{-1}). Female *T. longicornis* removed from <1 to 49% of the total primary production per day and <1 to 34% of the phytoplankton standing stock per day. The 20-fold difference in

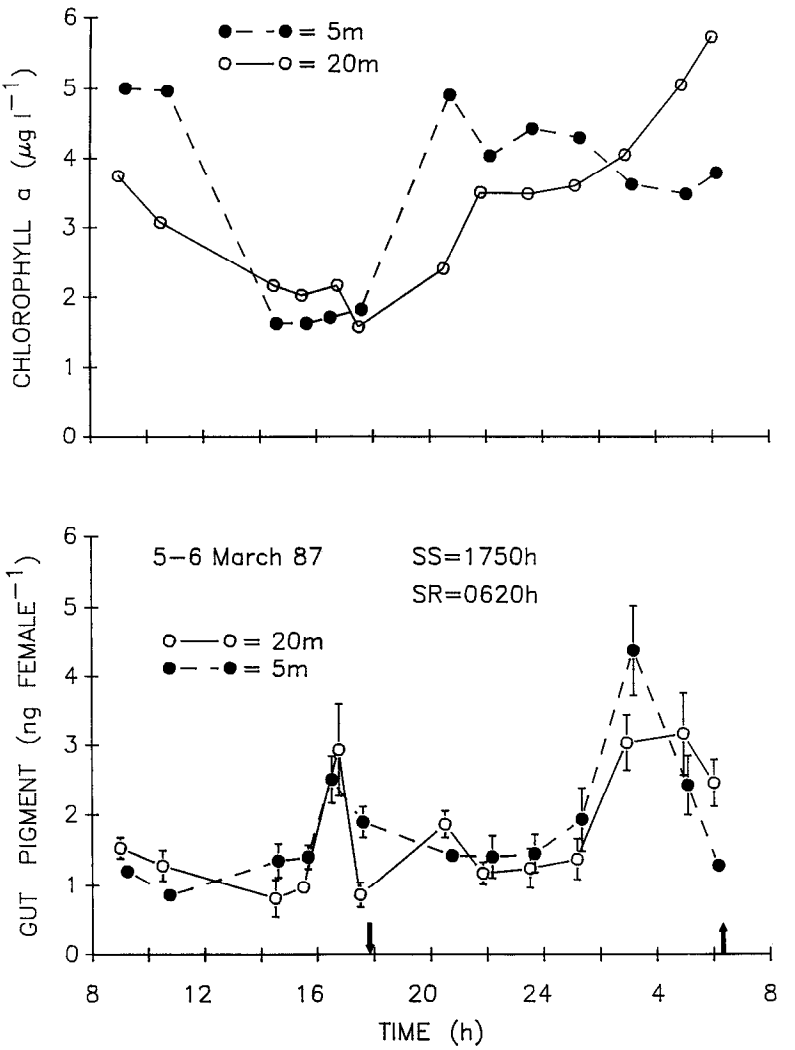

Figure 9. Gut pigment content of female *Temora longicornis* (lower panel) and total chlorophyll *a* concentration (upper panel) during 5–6 March 1987. The local times of sunset (SS) and sunrise (SR) are shown in the lower panel and also indicated by the downward and upward pointing arrows, respectively. Points in the lower panel are means and range (vertical bars) of duplicate samples for any given time (some vertical bars are smaller than the points). Points in the upper panel are single observations.

grazing impact of female *T. longicornis* throughout the season reflected differences in the size of the population rather than differences in daily rations.

Based on the estimated mean herbivorous daily rations (Table 6), the size of the females and the average temperature of the water column, we constructed a carbon budget for *T. longicornis* for each of the cruises (Table 7). The dry weight of female

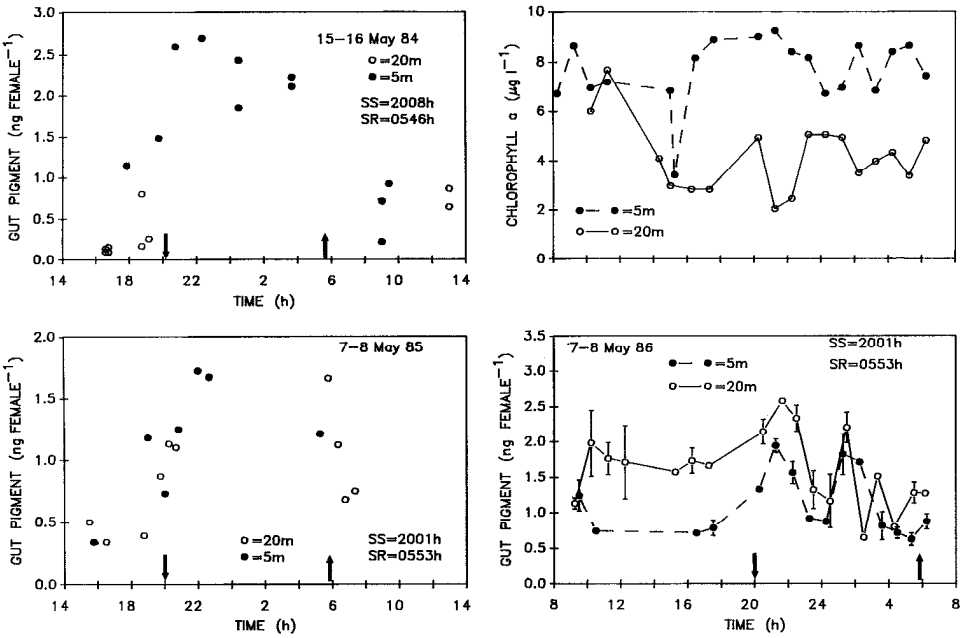

Figure 10. Gut pigment content of female *Temora longicornis* during 15–16 May 1984 (upper left; solid curve is for females at 5 m. Females at 20 m were not sampled at night) and 7–8 May 1985 (lower left; dashed curve is for females at 5 m. Solid curve is for females at 20 m). Points are single observations. Gut pigment content of female *T. longicornis* (lower right) and total chlorophyll *a* concentration (upper right) during 7–8 May 1986 (see Figure 9 for details of legend).

T. longicornis was estimated from a length-weight regression presented in Dam and Peterson (1991). Dry weights were converted to carbon assuming that 40% of the dry weight is due to carbon (Parsons *et al.*, 1979). Respiration rate, $R1$ (µl O_2 individual h^{-1}), was estimated from the dry weight, W (mg dry), of the females and temperature, T (°C), of the water column using the equation $\ln(R1) = -0.2512 + 0.7886*\ln(W) + 0.0490*T$ (Ikeda, 1985), and converted to carbon units (µgC individual h^{-1}) using a respiratory quotient, RQ, equal to 1.0.; i.e., $R2 = R1*RQ*12/22.4$. (Omori and Ikeda, 1984). Daily rates of respiration were estimated from hourly rates assuming no diel changes. The daily phytoplankton ration was converted to carbon units assuming a C/Chl. ratio of 52, typical of Long Island Sound (Tantichodok, 1990) and to assimilated carbon assuming a 70% assimilation efficiency (Conover, 1978). The amount of carbon available for egg production was estimated by subtracting respired carbon from assimilated carbon and compared to that estimated from 24 h egg production incubations performed during the cruises (Peterson, unpublished). Carbon content of eggs for *T. longicornis* was estimated using an average egg diameter of 80 µm to be 0.037 µg (Peterson, unpublished). This figure compares well with the 0.04 µg C reported for *T. longicornis* (Frost, 1980; his Table 4).

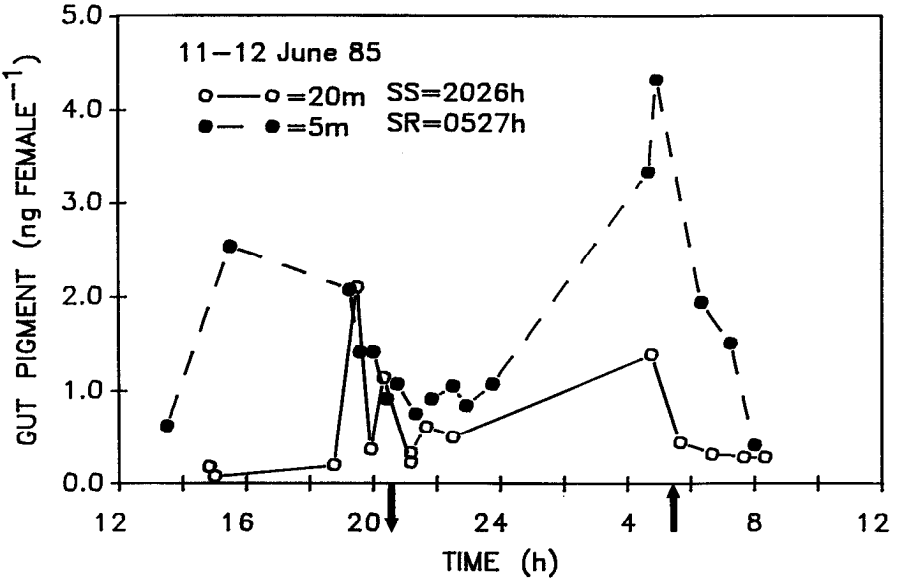

Figure 11. Gut pigment content of female *Temora longicornis* during 11–12 June 1985 (see Figure 10 for detail of legend). Points are single observations.

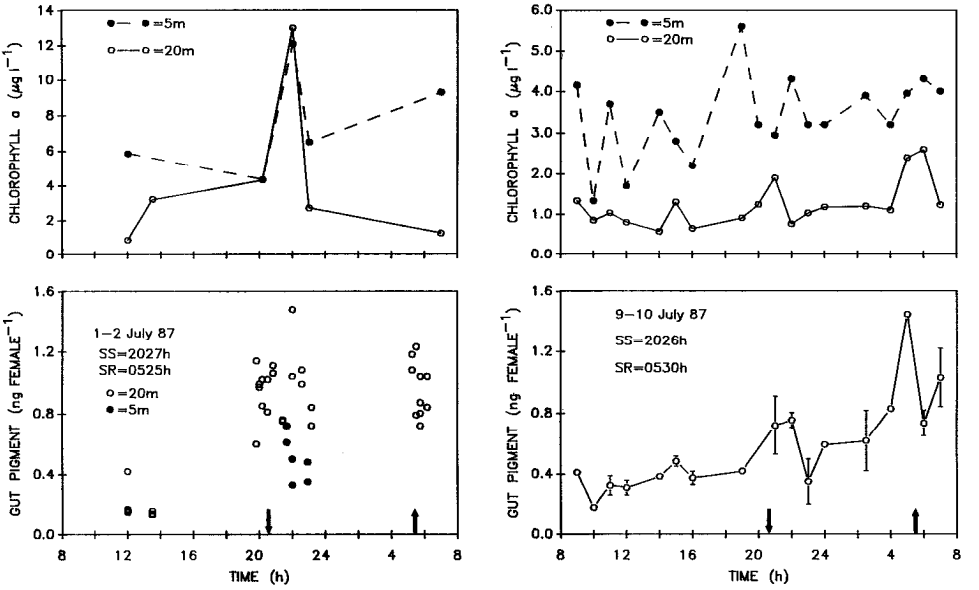

Figure 12. Gut pigment content of female *Temora longicornis* and total chlorophyll *a* concentration during 1–2 July 1987 (left) and 9–10 July 1987 (right). Points in the lower left panel are single observations. Females were present at 5 m only from 2100 to 2300 h. See Figure 9 for details of legend in right panels. Females were absent at 5 m throughout the day on 9–10 July 1987.

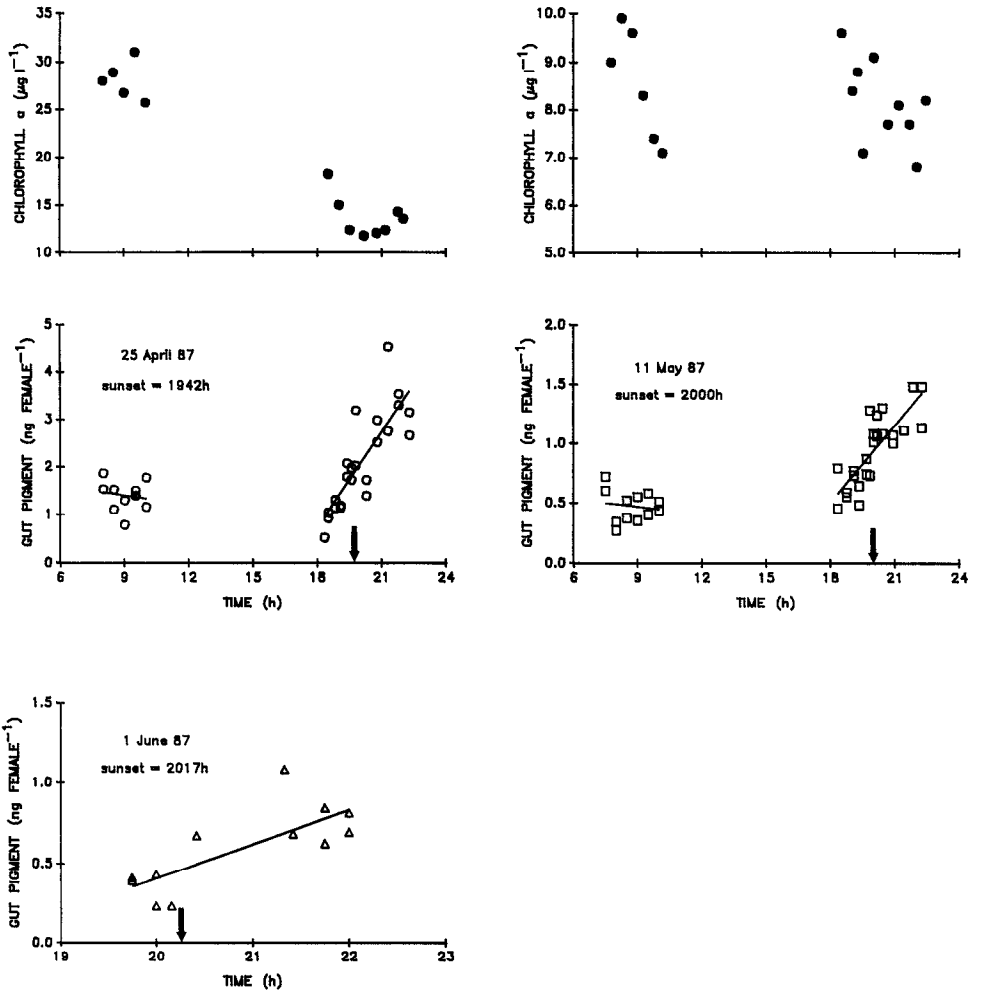

Figure 13. Experiments conducted at Mount Sinai Harbor dock. Gut pigment content of female *Temora longicornis* and total chlorophyll *a* concentration during 25 April 1987 (two upper left panels) and 11 May 1987 (two upper right panels). Lower left panel—gut pigment content of female *Temora longicornis* during 1 June 1987. Chlorophyll *a* concentration was not measured during this experiment. All points are single observations.

Daily carbon rations derived from herbivorous feeding by female *T. longicornis* ranged from 13 to 82% of their body carbon weight (Table 7). In all the cruises, herbivorous rations were sufficient to satisfy respiration requirements and to support some egg production. Carbon derived by *T. longicornis* from herbivorous feeding exceeded the costs of respiration and egg production except for the two cruises in July. On these dates the observed egg production rates exceeded the predicted rates by 15 and 12%, respectively.

Table 4. Summary of statistical analysis of gut pigment content (ng female^{-1}) vs chlorophyll concentrations in various size fractions. Regressions are of the form $Y = A + BX$, where Y equals gut pigment content and X equals chlorophyll size fraction. F_s is the statistic for deviation of the slope from zero. N is sample size and r is the correlation coefficient. * = $p <$ 0.05. Significance tests were done employing an initial $\alpha = 0.05$ and correcting for multiple correlations using $\alpha' = (1\text{-}\alpha)^{1/k}$, where k is the number of multiple correlations (Sokal and Rohlf, 1981).

Date	Regression on:	A	B	F_s	N	r
7–8 May 86	total chl at 5m	0.45	0.07	0.50	29	0.13
	> 20 μm chl at 5m	0.88	0.04	0.18	29	0.08
	total chl at 20m	1.93	0.06	0.82	34	0.16
5–6 March 97	total chl at 5m	2.28	−0.14	0.90	26	−0.19
	> 20 μm chl at 5m	2.00	−0.19	0.72	26	−0.13
	total chl at 20m	0.46	0.39	8.66*	26	0.51
	> 20 μm chl at 20m	0.87	0.88	9.40*	26	0.53
9–10 July 97	total chl at 20m	0.18	0.33	16.34*	33	0.59
	< 10 μm chl at 20m	0.24	0.40	24.45*	33	0.66
	> 10 μm chl at 20m	0.63	−0.09	0.17	33	−0.07

4. Discussion

a. Vertical distribution of copepods in relation to vertical distribution and concentration of chlorophyll. Pearre (1979) has shown that unless migration of animals is synchronized; i.e., most members of the population move at the same time and with the same velocity, conclusions regarding the strength and existence of vertical migration derived from counts of organisms as a function of time and depth can be erroneous. Furthermore, rates of motion of individual animals cannot be equated with mean rates of motion from the population. Despite this caveat, the patterns observed in this study are clear enough that there is no doubt about the occurrence of diel vertical migration in female *T. longicornis.*

Except for the cruise on 9–10 July 1987, female *T. longicornis* usually showed movement from deep water (> 20 m) during the daytime to intermediate (5–15 m) or shallow (1–5 m) water at night regardless of the vertical distribution of chlorophyll. There was no clear relationship between the vertical distribution of chlorophyll and the pattern of vertical migration of females. For example, in March 1987 and May 1984 the gradient of chlorophyll with respect to depth was the least pronounced of all cruises (Fig. 1); however, the pattern of vertical migration of females on these occasions differed. In March 1987 most females resumed deep residence after midnight, with little evidence of further ascent to surface waters from midnight to dawn (Fig. 2). In contrast, in May 1984 females were more or less evenly distributed throughout the water column.

It has been suggested that food availability determines the amplitude of migration; i.e., the distance animals will migrate (cf. Boyd *et al.,* 1980; Huntley and Brooks, 1982). According to this hypothesis, when food is scarce animals should remain near

Table 5. Comparison of mean ingestion rates (ng chl. fem^{-1} hr^{-1}) of female *Temora longicornis* for daytime and nighttime periods during the diel cruises. Comparisons are based on *t*-tests for differences between two means or Wilcoxon's two sample tests (Sokal and Rohlf, 1981) when the assumptions for the parametric test are not met. $\bar{X}$ = mean; S = std. deviation, n = number of observations (each observation is the mean of 1–4 replicates). T_s = *t*-test statistic; W_s = Wilcoxon's test statistic. * = $p < 0.05$ ** = $p < 0.01$.

Date	5 m	20 m
15–16 May 84	Daytime: $\bar{X} = 2.89$ $S = 0.99$ n 1 2 Nighttime: $\bar{X} = 6.16$ $S = 0.85$ $n = 4$ $T_s = 4.25$*	No samples taken at night
7–8 May 85	Daytime: $\bar{X} = 1.36$ $S = 0.64$ $n = 6$ Nighttime: $\bar{X} = 3.16$ $S = 0.64$ $n = 3$ $T_s = 4.39$**	$\bar{X} = 1.91$ $S = 1.48$ $n = 2$ $\bar{X} = 2.58$ $S = 0.68$ $n = 4$ $T_s = 1.10$
11–12 June 85	Daytime: $\bar{X} = 5.26$ $S = 3.05$ $n = 8$ Nighttime: $\bar{X} = 5.80$ $S = 6.92$ $n = 8$ $W_s = 27$	$\bar{X} = 2.35$ $S = 3.01$ $n = 7$ $\bar{X} = 1.40$ $S = 1.70$ $n = 5$ $T_s = 0.63$
7–8 May 86	Daytime: $\bar{X} = 1.51$ $S = 0.27$ $n = 4$ Nighttime: $\bar{X} = 2.49$ $S = 1.17$ $n = 10$ $W_s = 35$	$\bar{X} = 3.37$ $S = 0.61$ $n = 7$ $\bar{X} = 3.44$ $S = 1.44$ $n = 10$ $W_s = 36$
5–6 March 87	Daytime: $\bar{X} = 1.78$ $S = 1.23$ $n = 5$ Nighttime: $\bar{X} = 2.12$ $S = 1.56$ $n = 7$ $T_s = 0.99$	$\bar{X} = 1.44$ $S = 1.60$ $n = 5$ $\bar{X} = 2.14$ $S = 1.10$ $n = 7$ $T_s = 0.90$
1–2 July 87	Daytime: No animals Nighttime: $\bar{X} = 1.56$ $S = 0.23$ $n = 2$	$\bar{X} = 2.84$ $S = 1.09$ $n = 8$ $\bar{X} = 3.25$ $S = 1.63$ $n = 6$ $T_s = 1.40$
9–10 July 87	Daytime: No animals Nighttime: No animals	$\bar{X} = 1.69$ $S = 0.97$ $n = 9$ $\bar{X} = 2.31$ $S = 0.59$ $n = 7$ $T_s = 1.48$

the surface. On the other hand, when chlorophyll concentrations are high, animals can migrate farther away from the food-rich layer near the surface because the reduced ingestion rate at depth can be offset by a greater ingestion rate at night near the surface; consequently, the migration excursion is larger. A corollary from this hypothesis is that the amount of time spent near the surface is inversely proportional to the amount of food (Hardy and Gunther, 1936)—when food is abundant, migrating animals should satiate in a short period of time and leave the surface waters. When food is scarce, migrating animals should spend a longer time near the surface before satiating.

The results from this study are not entirely consistent with these hypotheses. For example, when May 1984 and May 1986 are compared, we found in May 1984 that chlorophyll concentration was low throughout most of the water column, but chlorophyll concentration and the proportion of cells > 10 μm were high in May 1986

Table 6. Daily grazing impact of female *Temora longicornis* during the diel cruises. Standing stock of chlorophyll and abundance of females were obtained by integrating each profile using the trapezoidal rule and averaging the values from all profiles over the entire cruise period.

Date	I* Ration ($\times 10^{-6}$)	II Females (No. m^{-2})	III Chlor. (mg m^{-2})	IV IxII/III (% d^{-1})	V† 1° prod.	VI‡ IxII/V (%)
15–16 May 84	114.0 (5m)	99,508	24.9	45.5	740£	49.2
	26.8 (20m)			10.7		
	$\bar{X}$ = 70.4			28.1		
7–8 May 85	66.5 (5m)	175,202	130.0	8.9	4,725	13.8
	76.6 (20m)			10.3		
	$\bar{X}$ = 71.6			9.6		
11–12 June 85	195.0 (5m)	147,458	54.8	52.5	4,488	21.5
	56.7 (20m)			15.2		
	$\bar{X}$ = 125.8			33.9		
7–8 May 86	50.7 (5m)	62,238	195.5	1.6	4,130	5.3
	85.2 (20m)			2.7		
	$\bar{X}$ = 67.9			2.2		
5–6 March 87	46.7 (5m)	23,103	110.0	1.0	767	7.0
	42.4 (20m)			0.9		
	$\bar{X}$ = 44.5			0.9		
1–2 July 87	77.9 (20m)	20,490	148.6	1.1	4,500	1.9
9–10 July 87	46.0 (20m)	6,246	66.6	0.4	3,165§	0.5

* = Units are mg chl fem^{-1} d^{-1}

† = Units are mg C m^{-2} d^{-1}

‡ = Daily carbon ration estimated assuming c/chl = 52 (Tantichodok, 1990). (See methods).

£ = Data from McManus and Fuhrman (1986). (See methods).

§ = Estimated from P/B ratio = 4.88 (Dam, 1989). (See methods).

(Fig. 1, Table 3). The amplitude of migration in 1984 was smaller (modes during the daytime were at 15 m) than in May 1986 (modes during the daytime were below 15 m). However, the amount of time spent at the surface by females on those dates did not seem to differ—10 to 15% of the females in May 1984 and about 20% of the females in May 1986 were in the upper 5 m from 2100 to 0600 h. Bohrer (1980) was also unable to establish any relationship between food availability and amount of time spent at the surface for *Temora longicornis*. Furthermore, on 1–2 July 1987 chlorophyll concentration was also high near the surface, but few females migrated to the surface at night (Fig. 7) resulting in a low amplitude of migration. Those

Table 7. Carbon budget for female *Temora longicornis*. T = average temperature of the water column (°C); W = carbon weight (mg); R = respiration rate (μg C ind^{-1} d^{-1}). C = carbon ration (μg C ind^{-1} d^{-1}); F_p = predicted carbon available daily for egg production = Cx0.7-R; F_o = estimated carbon used daily for egg production; I = Herbivorous daily carbon ration as percentage of body carbon; M = Daily carbon ration as percentage of body carbon estimated from respiration and egg production. $M = 1.43x(R + F_o)/W$.

Date	T	W† ($\times 10^{-3}$)	R‡	C£	F_p§	F_o¥	I	M
15–16 May 84	8.31	12.28	0.96	3.66	1.60	0.59	29.8	18.0
7–8 May 25	8.58	11.68	0.94	3.72	1.66	0.11	31.8	12.8
11–12 June 85	14.00	7.96	0.90	6.54	3.68	0.48	82.2	24.8
7–8 May 86	8.62	12.28	0.98	3.53	1.49	0.44	28.7	16.5
5–6 March 87	0.87	18.16	0.91	2.31	0.71	0.58	12.7	11.7
1–2 July 87	15.36*	9.20	1.08	4.05	1.75	2.07	44.0	49.0
9–10 July 87	15.46*	8.20	0.99	2.39	0.68	0.77	29.1	30.7

† = Dry weight of females was estimated from the length-weight regression presented in Dam and Peterson (1991) and converted to carbon by multiplying by a factor of 0.4 (Parsons *et al.,* 1979). (See results).

‡ = Respiration rate was calculated first as μl O_2 ind^{-1} d^{-1} from dry weight and temperature (Ikeda, 1985) and then converted to μg C ind^{-1} d^{-1} assuming RQ to be 1.0 (Omori and Ikeda, 1984). (See results).

£ = Carbon ration estimated assuming a C/chl ratio of 52 and using the mean chlorophyll rations from Table 6.

§ = Assumes assimilation efficiency of 70% (Conover, 1978).

¥ = Egg production measured in 24 h incubation experiments (Peterson, unpublished). Carbon content of egg estimated to be 0.037 μg (see results).

* = excludes temperatures in upper 4 m of water.

** = excludes temperature in upper 9 m of water.

females that migrated to 5 m at night stayed there for a short time (Fig. 12), although it is difficult to accept that the short visit to the surface was enough to produce satiation since females at 20 m had higher gut content (Fig. 12).

The evidence relating diel vertical migration to the vertical distribution of chlorophyll-*a* was equivocal. A possible reason for this is that the variation in migration may be related to changes in food concentration from day to day rather than to food concentration itself; i.e., migration may be conditioned by the previous feeding history of the animals (Bohrer, 1980). Since sampling during this study was not carried out for more than 24 h this possibility cannot be examined. In this study there was considerable variability in gut content of females during the premigration period (afternoon) among cruises, and one could hypothesize that hungrier females were more likely to migrate into the upper layers at night. This hypothesis was examined by comparing the level of gut fullness in females during the premigration period (afternoon) and the percentage of females found above 15 and 5 m at night during the cruises (Table 8). Females with low gut content in the afternoon (e.g., 15–16 May

Table 8. Relationship between degree of gut fullness (ng pigment female^{-1}) during the premigration period (afternoon) and the percentage of female *Temora longicornis* found at or above 15 and 5 m at night during the diel cruises. Values of gut content are means for the period from 1400 h to the last observation before sunset. Percentages of females are means for the period after sunset and before sunrise. Kendall's rank correlation coefficients (τ) between variables are shown. n = sample size. * = excludes high value at 1930 h (see Fig. 11). ** = excludes results from 9–10 July 1987.

Date	Gut content	% females in upper 15 m	% females in upper 5 m
5–6 March 1987	1.39	50.3	28.3
15–16 May 1984	0.21	56.5	34.9
7–8 May 1985	0.52	56.8	34.7
7–8 May 1986	1.66	56.8	24.1
11–12 June 1985	0.23*	79.0	75.9
1–2 July 1987	0.18	62.0	9.4
9–10 July 1987	0.42	6.0	0.0
		τ	n
Gut content vs % females in upper 15 m		0.09 ns −0.41 ns	7 6**
Gut content vs % females in upper 5m		−0.05 ns −0.7 ns	7 6**

1984) were not more likely to migrate into the upper layers than those with higher gut content (e.g., 5–6 March 1987 and 7–8 May 1986). Therefore, it appears that females in deeper waters were not hungry enough for a pronounced change in the diel migratory behavior of *T. longicornis* to occur.

Neither food availability nor its vertical distribution in the water column can account for these two observations: (1) as the season progressed the depth of residence of female *T. longicornis* increased; (2) after June the percentage of females migrating into the upper 5 m decreased considerably, with migration into the upper 5 m ceasing entirely by mid-July. A possible explanation for these observations is that *T. longicornis* was avoiding the warmer waters near the surface—once water temperature rose above about 17°C at a given depth, the percentage of females found above that depth decreased. The disappearance of *T. longicornis* from the upper 5 m of the water column once temperature rises above 17°C (usually occurring from late June to early July) has been consistently documented in Long Island Sound from 1982 until 1987 (Peterson, 1985 and unpublished observations). We suggest that temperature can modify the amplitude of migration in this species since females seem to be restricted to waters with temperatures below 17°C. Vidal (1980a,b), in a study of two boreal copepod species, has shown that the critical food concentration for growth increases with body size proportionately more at high than at low temperatures, and that adult copepods may grow best and transform food more efficiently at low temperatures. Because phytoplankton concentrations in the deeper waters of Long

Island Sound were always sufficiently high to support metabolism and some growth of *T. longicornis* (Table 7), Vidal's observations may provide an explanation for the disappearance of *T. longicornis* from the phytoplankton rich, but warm surface waters. In fact, Vidal (1980a) applied this concept to explain the vertical separation of copepod species, in relation to body size and food availability.

The presence of a pronounced thermocline has been shown to affect the vertical migration of copepods (cf. Williams, 1985). Although a thermocline developed towards the end of the season (Table 2) this was unlikely to have affected the vertical migration of female *T. longicornis* because migration into the upper 5 m occurred in June when the thermocline between 5 and 10 m was most pronounced.

Previous studies on the vertical distribution of *T. longicornis* indicate that it usually performs diel vertical migrations (references in Harding *et al.,* 1986). Bohrer (1980) using a 10 m-high tank documented that *T. longicornis* rose continuously from early morning to dusk and then descended slightly throughout the night with an occasional indication of a small dawn rise before descending to the deep waters of the tank in the early morning. This pattern was similar to what we observed in May 1984 and 1986. Harding *et al.* (1986) observed that *T. longicornis* ascended to the surface by dusk, remained there until midnight and slowly sank through the water column afterwards, with no indication of a predawn rise. In this study, dispersion of animals throughout the water column usually happened soon after animals ascended to the surface (before midnight). Daro (1985) has documented a unique situation for *T. Longicornis* in the northern North Sea—continuous residence throughout the day and night in the upper 20 m of the water column, above the thermocline. This behavior was never observed in any of the seven cruises of this study.

Obviously, there are no universal patterns of migration within this species. Diel vertical migration is a phenomenon which shows a great deal of plasticity. Ultimately, the causes of this plasticity can only be understood by describing migration under a suite of varying conditions—food availability, presence or absence of predators, light and temperature regimes, for example, which might become more or less important in different systems.

Diel vertical migration in zooplankton has been linked to predator avoidance (review in Lampert, 1989; Ohman, 1990; Bollens *et al.,* 1992). We did not test this hypothesis. However, one cannot assume a priori that predation drives diel vertical migration in *Temora longicornis.* The main predators of *T. longicornis* in Long Island Sound are the planktivorous fishes Sand Lance, *Ammodytes americanus,* and Atlantic Mackerel, *Scomber scombrus,* but they exert negligible impact on the population dynamics of this copepod (Peterson and Ausubel, 1984; Monteleone and Peterson, 1986). Although predator avoidance may be the evolutionary cause of diel vertical migration in *T. longicornis,* it is possible that the environment in Long Island Sound may have little to do with the evolution of this behavior. *T. longicornis* appears to have no endemic population in this system. Rather, seed populations are probably

advected from the shelf and Block Island Sound early in the winter. Thus, it may be that diel vertical migration in this species has evolved in populations of the continental shelf where *T. longicornis* is found year round (references in Harding *et al.,* 1986).

b. Diel changes in gut content of copepods in relation to vertical distribution and concentration of chlorophyll. If feeding activity of animals were only a function of food concentration and temperature, then one would expect to see no difference in gut content with depth when the water column is well mixed because both food concentration and temperature would be uniform with depth. In contrast, one would expect to see greater gut content near the surface than at depth when the water column is stratified because both food concentration and temperature are higher near the surface in Long Island Sound. The results from this study did not always support these expectations. For example, gut pigment content of females at 20 m was consistently greater than at 5 m, on cruises on 7–8 May 86 and 1–2 July 87. There was little difference in gut content of animals with depth (7–8 May 85) even though chlorophyll concentration at 5 m was greater than at 20 m. Therefore, we conclude that factors other than food concentration can regulate diel feeding behavior of *T. longicornis.*

For gut content not to differ with depth when the chlorophyll concentration near the surface is greater than in deeper waters requires either that there be a rapid exchange of animals between depths and that this rate of migration be considerably faster than the gut passage time, or that animals at depth have higher ingestion rates. Estimates of the mean swimming speed of *Temora longicornis* made over 30 to 60 minutes are about 7 m h^{-1} (Hardy and Bainbridge, 1954). Therefore, at this rate it would take about two hours for an individual to swim from 5 to 20 m in the water column. Gut passage times at 6.5 to 9.5°C (the temperatures near the surface in May 85 and 86 cruises) are 42 and 34 min, respectively (Model 1 in Table 2 of Dam and Peterson, 1988). Therefore, it seems unlikely that the similarity in gut content with depth in the cruises in which chlorophyll concentration was vertically stratified was due to sampling animals that had satiated at the surface and were later collected in deeper waters.

Changes in gut pigment content of *T. longicornis* throughout the day were related, albeit weakly, to changes in chlorophyll concentration (Fig. 14). The lack of, or the weak relationship between short-term changes in gut content and chlorophyll concentration may be due to: (1) chlorophyll concentration being too high to have an effect on gut content (Dam and Peterson, 1991)—this was usually the case for animals at 5 m for all cruises and at 20 m during 7–8 May 1986); (2) the confounding effect of individual feeding variability (Kleppel *et al.,* 1988) on average values of gut content; (3) animals moving in and out those depths from which chlorophyll was measured, or (4) the propensity of copepods to feed at high rates in microlayers unsampled by us. We therefore, conclude that short-term changes in chlorophyll

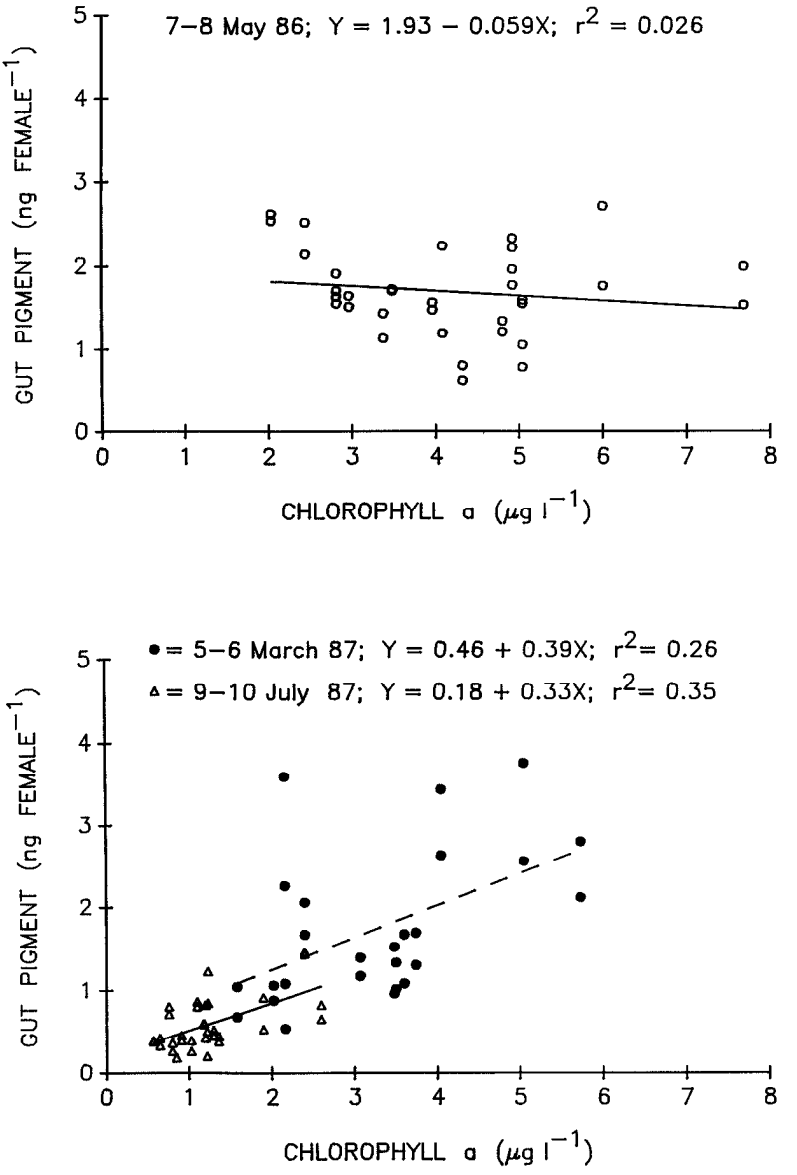

Figure 14. Gut pigment content of female *Temora longicornis* vs total chlorophyll *a* concentration at 20 m for 7–8 May 1986 (upper panel) and 5–6 March and 9–10 July 1987 (lower panel). The slope for the regression in the upper panel is not significantly different from zero; the other two slopes are significantly greater than zero (see Table 4).

concentration (as measured by conventional methods) cannot always account for diel changes in feeding behavior, particularly for the increase in gut content in female *T. longicornis* early in the evening. It will be difficult to examine this hypothesis further until we are able to observe animal behavior in situ in relation to time of day, and small-scale patchiness.

The observations that maximum gut pigment content always occurred at night and that the shape of the diel feeding curve was generally similar for animals near the surface and at depth further suggest that factors other than the concentration or the vertical distribution of food were responsible for the observed diel patterns in feeding behavior of female *T. longicornis.* Several studies suggest that light cues control the timing of nocturnal feeding in copepods (Fernandez, 1977; Head *et al.,* 1985; Stearns, 1986), with ingestion rate increasing as light intensity decreases. Our observations do in fact support the hypothesis that ingestion rate increases with decreased light intensity (e.g., Fig. 13). However, if feeding behavior had been entirely under light intensity control, one would have expected to see an increase in gut content in animals from 20 m earlier than in animals from 5 m. This was not the case. This suggests that there may also be an endogenous component to the diel feeding behavior of *T. longicornis.* Furthermore, there were occasions in which gut content remained high past sunrise suggesting that feeding behavior at this time is controlled by factors other than light intensity, perhaps by satiation of appetite.

c. Grazing impact and herbivorous ration of copepods. The grazing impact of the female *T. longicornis* varied widely because their abundance varied twenty-fold in comparison to a 3 to 4-fold variation in daily ration during the cruises. The largest estimates of daily removal of the phytoplankton stock and total primary production (about 30% and 21–49%, respectively) were obtained when the chlorophyll standing stock was relatively low (May 1984, June 1985), but daily removal of phytoplankton stock and production were also substantial (10% and 4%, respectively) during periods of high standing stock (May 1985). Despite uncertainties in the estimation of daily rations (see below) which would affect the calculation of grazing impact by the females in the population, the results of this study indicate that grazing impact of female *Temora longicornis* in Long Island Sound is comparable to that of the entire copepod assemblage in other temperate, coastal systems. Smith and Lane (1988) concluded that three species of calanoid copepods (*Calanus finmarchicus, Metridia lucens* and *Centropages typicus*) generally removed from 17 to 60% of the daily primary production during the spring bloom in shelf waters of the New York Bight. Tiselius (1988) reported that the mesozooplankton (several species) removed less than 4% of the phytoplankton standing stock and 9–48% of the primary production in the Skagerrak and Kattegat. Nicolajsen et al. (1983) reported that the mesozooplankton (dominated by *Centropages hamatus* and *Pseudocalanus* sp.) removed daily about 1% of the phytoplankton standing stock and 6% of the primary pro-

Table 9. Proportion of daily grazing by female *Temora longicornis* accounted for by nighttime grazing.

Date	Nighttime as % of 24 h	Nighttime grazing as % of 24 h grazing	
		5 m	20 m
5–6 March 1987	51.2	59.9	67.8
7–8 May 86	40.9	49.9	47.2
9–10 July 87	38.5	—	47.1

duction from January through May in the Øresund. Similarly, Baars and Fransz (1984) concluded that copepods (copepodid and adult stages of *P. elongatus, T. longicornis, C. hamatus, A. clausii* and *Calanus finmarchicus*) were able to remove daily from 2 to 8% of the phytoplankton stock and a maximum of 14% of the primary production from May to September in the central North Sea. Peterson et al. (1990) calculated that copepods in the Benguela upwelling region in October (spring) removed no more than 5% of the standing crop of phytoplankton per day. All of these studies combined daily pigment rations of copepods and estimates of their abundance to derive grazing rates and their results are, therefore, directly comparable with ours. The results of our study indicate that *T. longicornis* may exert a significant grazing pressure on the phytoplankton in Long Island Sound, particularly since the estimates of grazing impact consider only the females (biomass of males and copepodites combined may exceed that of the females by a factor of 2–5). However, it is unlikely that on the average, most of the primary production would be removed by *T. longicornis* because of its inability to feed efficiently on smaller phytoplankton (cf. Capriulo and Ninivaggi, 1982, O'Connors *et al.,* 1980; Dam and Peterson, 1991).

It has generally been assumed that a low grazing pressure during the daytime allows the accumulation of phytoplankton biomass which in turn allows copepods to feed at maximum rates in early evening (cf. Petipa and Makarova, 1969; McAllister, 1969). In addition, theories concerning the adaptive significance of vertical migration and diel feeding behavior incorporate the assumption that ingestion rates at night must be higher than during the daytime (McAllister, 1970; Enright, 1977). We found that maximum ingestion rates, calculated from the Elliot and Persson model (1978), usually occurred at night. However, ingestion rate over the night period was not necessarily higher than over the day period (Table 5) perhaps because animals may satiate in relatively short periods of time (few hours) and because there is a limit to how fast food may be processed in the gut (Nott *et al.,* 1985). We compared the integrated amount of grazing for the daytime and nighttime for the cruises in which sampling occurred for most of the 24 h (Table 9). The proportion of the total grazing accounted for by nighttime grazing was related to the number of nighttime hours. This result is in agreement with that of Welschmeyer *et al.* (1984). Therefore, the

assumption of increased ingestion rates and grazing pressure at night must be regarded with caution and should be verified before being incorporated in further models dealing with the dynamics of phytoplankton and zooplankton populations, or the adaptive significance of vertical migration.

The copepod carbon budgets derived in this study are crude estimates because of uncertainties in the calculations. First, the daily rations are based on the mean of the rations at 5 m and 20 m. A mean ration may not always be representative, particularly if the rations differ considerably with depth and the animals spend a disproportionate amount of time at any depth. However, since animals appear to migrate throughout the water column on a diel basis, this approach may be justified. Second, the value of 52 selected for the carbon to chlorophyll ratio is unlikely to be constant through time. The range of values reported by Tantichodok (1990) is 46–71. Third, assimilation efficiency may vary with food concentration (Conover, 1978). Assimilation efficiency of *Temora longicornis* has been reported to range from 50 to 98% (Berner, 1962; Harris and Paffenhöfer, 1976). Therefore, the assumed assimilation efficiency of 70% is a reasonable estimate. Despite these uncertainties, the results indicate that the herbivorous daily rations were sufficient to satisfy the metabolic requirements of *T. longicornis* in most cases. The conclusion would not be modified even if the lowest estimates of daily ration were used in the calculations. This is in contrast to previous studies that have concluded that, in the majority of cases, copepods could not meet their metabolic requirements on an herbivorous diet alone (Mullin and Brooks, 1976; Dagg *et al.,* 1980; Dagg and Grill, 1980; Dam *et al.,* 1993). A comparison of the daily carbon rations of *T. longicornis* with the cost associated with respiration and egg production also indicates that an herbivorous diet was sufficient to account for the observed egg production rates in 5 of the 7 cruises. In the two cruises in July predicted egg production fell short of observed egg production by 12–15% (Table 7). Because *T. longicornis* is considered an omnivore (Turner, 1984), in those instances in which herbivorous feeding could not account for the cost of respiration and egg production, animals may have supplemented their diets with non-pigmented food. However, at this time, the relative importance of carnivory and detritivory vs. herbivory in the autoecology of *T. longicornis* remains on open question.

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