Evaluation of synchrony of feeding behaviour in individual *Acartia hudsonica* (Copepoda, Calanoida)

Valeriano Rodriguez[1], Edward G. Durbin[2]

[1] University of Málaga, Departament of Ecology, Campus Univesitario de Teatinos, E-29071 Málaga, Spain
[2] University of Rhode Island, Graduate School of Oceanography, South Ferry Road, Narragansett, Rhode Island 02882, USA

ABSTRACT: Variability in individual feeding behaviour of *Acartia hudsonica* was studied in 34 samples, each of 100 individuals. The samples were collected during 3 day-night cycles from a large experimental seawater system in Norfolk, Virginia, USA. Fluorometric measurements were made to determine gut pigment contents and evacuation rates, from which ingestion rates and daily rations were calculated. Results show that gut contents were almost always < 1.2 ng pigment copepod^{-1}. Coefficients of variation (CV) calculated for each sample, which were used as indices of synchrony, were always $< 70\%$. The highest frequency of synchronized behaviour was observed, independent of time, in individuals from bottom samples. At night, the probability of obtaining any particular CV in individuals from bottom or surface was the same. About 45% of individuals displayed moderately high contents (0.2 to 0.5 ng) both day and night, but the percentage of copepods with > 0.5 ng pigment increased from 16% in the day-time to 42% at night. This non-uniform pattern of gut contents suggests the copepods were feeding in short-term episodes which were perhaps more frequent at night. Since food was in excess at all times at all depths, and experimental temperatures did not vary, light was probably the principal factor controlling the observed feeding periodicity.

INTRODUCTION

Studies of feeding behaviour of any animal species above a certain body size are usually conducted on individual animals. However, for relatively small animals such as copepods, it is usual to work with groups of individuals. This is because it is difficult and time-consuming to make precise measurements on very small individuals. Measurements made on groups of animals are never entirely satisfactory, however, because they tend to mask a number of important features of feeding behaviour such as the deviation of individual values from the mean.

The recent proliferation of *in situ* studies of plankton feeding behaviour with different spatial and temporal scales, but especially those within a 24 h cycle (Baars & Oosterhuis 1984, Pagano & Saint-Jean 1985, Bautista et al. 1988, Durbin et al. 1990, Morales et al. 1990, Peterson et al. 1990, Rodriguez et al. 1991), was stimulated by the application of a fluorescence method (Mackas & Bohrer 1976) for measuring gut contents. There are methodological assumptions that have to be made and there are several potential sources of error such as pigment assimilation in the digestion process and evacuation in starving copepods, that have been widely discussed (Madin & Cetta 1984, Conover et al. 1986, Lorenzen & Downs 1986, Wang & Conover 1986, Dagg & Walser 1987), but the rapidity of this method allows a large number of replicates of gut contents of individual copepods in each sample to be made and compared. Several studies have used this approach and have demonstrated the existence of individual variability (Mackas & Burns 1986, Moebly 1987, Kleppel et al. 1988, Durbin et al. 1990). The objective of our present study was to analyse the *in situ* feeding behaviour of individuals of *Acartia hudsonica* and to explore the degree of possible synchrony or variance of these activities on a day/night scale at times of food excess, to determine how much individual variability contributes to the observed population pattern.

MATERIAL AND METHODS

All samples were collected from a single 120 m long phytoplankton-zooplankton patch over a 3 d period (April 4, 5 & 6, 1987). This 2000 m^3 patch was contained in a 120 m long center section of the 675 m long, 7.8 m wide, 3.4 m deep Langley tow tank at NASA Langley Research Center, Hampton, Virginia, USA (Donaghay 1988). The patch had been initiated 2 wk prior to sampling by filling the bag with a mixture of natural plankton and 3 μm filtered seawater. Light was provided with 1000 W metal halide lamps operated on a 16:8 h (L:D) photoperiod. These lights provided 100 μ Einstein at the surface with an average light intensity of 33 μ Einstein. The patch was enriched by adding N, P, Si to maintain concentrations above 2 μM N and Si and 0.2 mM P. The patch was mixed by an automated stirrer. There were 3 sampling stations along the innermost stretch of the channel at which bottom and surface samples were taken twice a day with a submerged pump. Sampling of water during the day and night experimental periods took place between 08:30 and 10:00 h, and between 16:00 and 18:00 h local time. Each sample consisted of between 70 and 100 l of seawater. This was filtered by a 100 μm sieve to capture the adult copepods; these were then immediately frozen in liquid nitrogen before being transferred to the laboratory of the Graduate School of Oceanography (Rhode Island). Pigment concentration [Chlorophyll a (chl a) + phaeopigments] measurements in seawater were made on 4 replicates of 10 ml surface and bottom samples taken at each sampling time at Stn 3 only.

To calculate evacuation rate constants, copepods were obtained from short horizontal trawls along the length of the patch during the night period. The material retained in the cod-end was washed gently several times with filtered seawater and immediately transferred to an incubation vessel containing filtered seawater. A series of samples were then removed from the vessel at intervals of 3, 6, 9, 12, 15, 18, 30, 45 and 95 min from the start of the experiment and each sample was immediately frozen and stored in liquid nitrogen for transfer to the laboratory.

In the laboratory, 100 adult females of Acartia hudsonica were picked out from each sample under cold and low light conditions, rinsed briefly with filtered water, and placed individually in tubes containing 4 ml of acetone. These were then left overnight in dark, cold conditions to extract. The gut contents of specimens for the evacuation-rate experiments were measured collectively in groups of 25 rather than individually, but they were processed in the same way as the other materials. Measurements were made of 4 replicates of the samples from each incubation interval,

except those taken at 45 min (3 replicates) and 95 min (2 replicates). The fluorescence of the extracts was measured with a Turner Designs Model 10 Fluorometer, before and after acidification. The experimental values were corrected by subtracting the mean value of 35 acetone blanks. Pigment content is expressed as chl a + phaeopigment; the calculations were based on the equations of Lorenzen (1966), as modified for use at the Marine Ecosystem Research Laboratory (Lambert & Oviatt 1986).

The size structure of the Acartia hudsonica adult females was determined from measurements of 300 randomly selected specimens from a mix of female specimens from all the samples. We measured cephalothorax width and total body length (from the top of the head to the base of the caudal rami) of each specimen in the group using an AMS (VIDS IV) semi-automatic image analyser that receives the image from an inverted microscope fitted with a television camera.

RESULTS AND DISCUSSION

Size structure

The total body length of the population of Acartia hudsonica adult females showed a normal size distribution with a mean value of 1052 μm, and coefficient of variation (CV) = 7.52 %. Values ranged from 850 to 1308 μm.

Environmental conditions

Throughout the experimental period, the thermal and trophic conditions of the seawater were very homogeneous along the length of the patch. Water temperature was 10 ± 0.2 °C and the phytoplankton biomass, expressed in term of fluorescent pigment concentration was always very high (range 32.10 to 42.73 μg l^{-1}, mean: 39.41 ± 3.20 μg l^{-1}, n = 48). The predominant pigment was active chl a and the phaeopigments represented between 11.56 and 33.25 % of the total: the mean value was 20.37 ± 6.38 % (n = 48). Diatoms dominated the phytoplankton community (Donaghay 1988).

Variability in individual gut contents

The mean value of individual gut pigment content of 3406 of the specimens processed was 0.39 ng (CV = 58.46 %); the maximum value was 1.56 ng Most of the frequency distributions of individual gut contents appeared to be log-normal (Fig. 1).
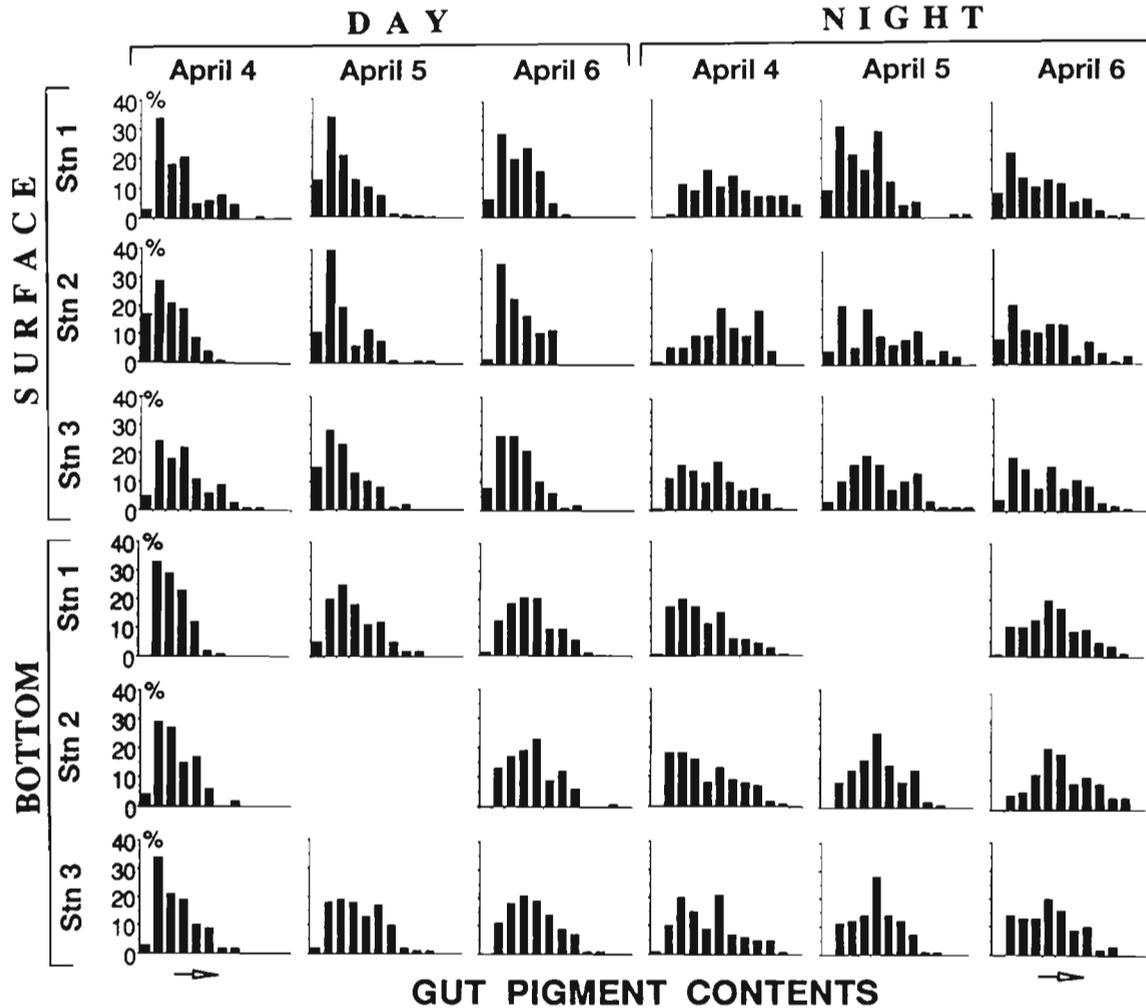
Fig. 1. *Acartia hudsonica*. Frequency distribution of individual gut pigment contents for each of the 34 samples analysed (100 females per sample) arranged to present 2 contrasts: light-dark (day-time, night-time) in columns and depth of capture (surface, bottom) in rows. The 3 successive days of sampling are shown in the subcolumns, and the 3 sample stations in the subrows. Class interval = 0.1 ng pigment. The first and last classes shown are 0.00–0.10 and 1.10–1.20 ng pigment

Previous studies (Mackas & Burns 1986, Kleppel et al. 1988) report the order of individual variability of gut pigments as 10-fold and warn that with this level of variability any estimates of individual levels based on the mean, made on large numbers of animals, should be interpreted with extreme caution. In the present case, the range of values within each sample always was 0.6 ng, and in 53 % of the samples the range was 1 ng.

In each sample individual synchrony or population variability in feeding behaviour was estimated as the coefficient of variation, i.e. the degree of dispersion of the individual gut pigment contents around the mean. Because it is expressed as the percentage of the mean, it is independent of the absolute value of the mean. Fig. 2 displays the frequency distribution of the CV in 5 % class intervals for the total sample set (Fig. 2A), for the sample subgroups that represent the day and night samples (Fig. 2B), and for the bottom and surface

samples (Fig. 2C). The complete set of coefficients show a bimodal distribution in which the first peak (29 % of the samples) represents the CV values between 45 and 50 % and the second peak (19.36 % of the samples) the values between 60 and 65 %. With the exception of bottom samples, a similar bimodal pattern was seen in each of the sample subgroups mentioned above, with the following differences. In the day samples, the basic bimodal pattern was intensified because the frequencies of the modal classes increased while those of the extreme classes decreased. On the other hand, in the nocturnal samples there was an increase in the relative importance of samples that displayed a more uniform individual behaviour (decrease of the CV values) and also of other samples which displayed more variance. There are interesting contrasts between samples of bottom and surface waters because in the bottom samples of both day and night
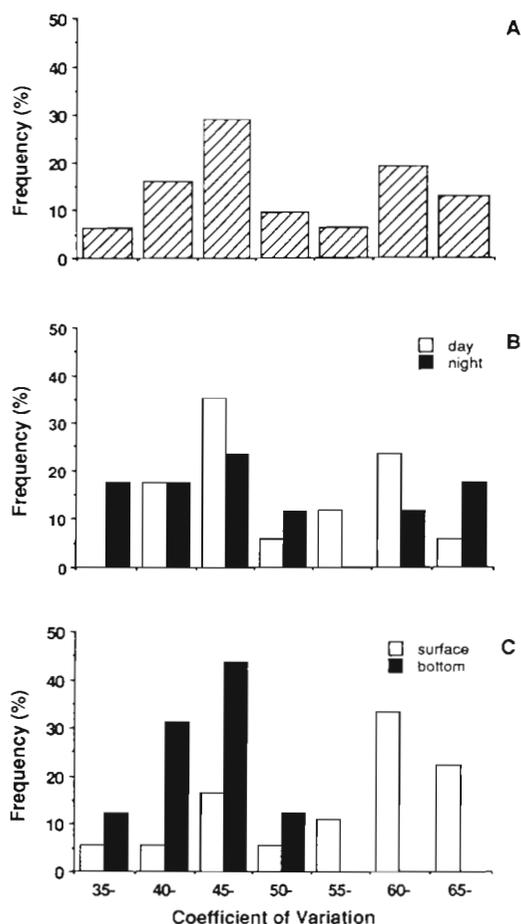
Fig. 2. *Acartia hudsonica*. Frequency distribution of the coefficients of variation: (A) all samples (n = 34); (B) day-time and night-time samples (n = 17); (C) surface (n = 18) and bottom samples (n = 16)

the second peak (larger values of variability) has disappeared, while at the surface it is intensified, perhaps in relationship with the observation (Head 1992) that light may have actually had a direct effect on the degree of pigment destruction occurring in copepod guts. In every case, the CV values were less than 70 %. This figure is less than that reported by Kleppel et al. (1988) for *Acartia tonsa*, where values > 100 % were normally found, but declining to ≤ 70 % during evening and morning twilight (1 h before sunset and 1 h after sunrise).

Daily feeding cycles

Individual variance found in the copepods in this work appears compatible with changes in the feeding behaviour of the population. Many studies of short-term variation of copepod feeding behaviour have shown diel periodicities, even when the distribution of

food in the water column is homogeneous (Mayzaud et al. 1984, Daro 1985, Durbin et al. 1990). Patterns can vary however; some have just one nocturnal peak, while others display peaks at both dusk and dawn (Dagg & Grill 1980, Simard et al. 1983, Pagano & Saint-Jean 1985, Stearns 1986, Head & Harris 1987, Bautista et al. 1988, Morales et al. 1990). The observed variation in the amount of gut contents throughout the day has been variously attributed by different authors to either continuous feeding of copepods which are vertically migrating in a water mass with irregular concentrations of food (Hart 1977, Boyd et al. 1980, Dagg & Grill 1980, Simard et al. 1983); or to diel variations in feeding activity (Mackas & Bohrer 1976, Pagano & Saint-Jean 1985, Bautista et al. 1988, Durbin et al. 1990). Furhermore, the day and night feeding behaviour of a given species of copepod may vary with season (Baars & Oosterhuis 1984). This observed 'plasticity' of feeding behaviour led to suggestions that physical and biological factors such as light and temperature, and food and predation could influence the diel grazing of copepods (Roman et al. 1988).

All the above *in situ* studies use the mean gut contents of several groups of copepods as the parameter to express feeding behaviour patterns. The supposition is that all the copepods in the group behave similarly, but this is not necessarily the case. For example, if the means of gut contents do not vary during a 24 h cycle it suggests that the individuals of the group are feeding continuously. The same pattern would occur, however, if the population of copepods is feeding intermittently and at random throughout the day. Intermittent feeding and the observation of a discontinuous pattern implies that the feeding behaviour of the copepods is similar, i.e. that there is synchronicity in the episodic feeding (Head & Harris 1987, Kleppel et al. 1988).

We used 2-way variance analysis to carry out a statistical analysis of the differences in the feeding behaviours of *Acartia hudsonica* on an individual basis according to either time of day (1st Factor: day-time–night-time) or the depth level occupied (2nd Factor: surface–bottom). The number of replicates was equal to the total number of individual measurements made for each of the 4 possible combinations of the 2 factors, independent of the station at which the samples were taken or the date of sampling.

Regrouping the data in this way (Fig. 3) showed that although *Acartia hudsonica* is probably a nocturnal feeder, like all the genus *Acartia* (Stearns 1986, Bautista et al. 1988, Kleppel et al. 1988), in this study it was feeding during the day as well as at night.

Our use of the gut-pigment-content categories employed by Kleppel et al. (1988) (low: < 0.2 ng, moderate: 0.2 to 0.5 ng, high: > 0.5 ng), showed that in day-time, 52 % of the individuals had moderate levels
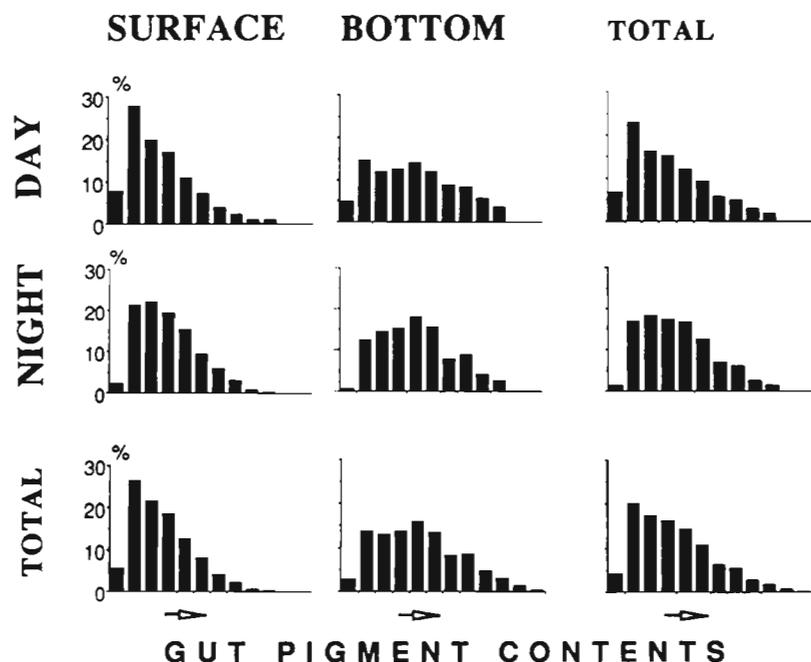
SURFACE BOTTOM TOTAL

Fig. 3. *Acartia hudsonica*. Frequency distribution of the amounts of individual gut-pigment contents in day-time and night-time samples from surface and bottom water

of pigments, 32 % had low levels, and only 16 % had high levels. The respective night-time values were 42, 16 and 42 %. Consequently, it appears that a relatively high percentage (42 % in this case) of copepods with high levels of gut pigment contents may be characteristic of nocturnal samples because it contrasts clearly with the lower percentage (16 % in this work) of copepods with high levels of gut pigment contents from day-time samples. This approximately 3-fold increase appears to have been produced by a decrease of some 50 % in those individuals with low levels of gut pigment contents at night in comparison with the daytime samples. On the other hand, for *Arcatia tonsa* (Kleppel et al. 1988), the differences between day and night are reported to affect mainly the relative importance of those copepods with moderate gut pigment contents, namely 17 % of day-time and 55 % of nighttime specimens, while the percentage of copepods with high levels of gut pigment contents remained constant, between 8 to 10 %, both day and night.

The results of the variance analysis (Table 1) show a very significant difference ($p \lll 0.001$) between the day-time and night-time gut contents, and also between individuals taken from the surface and bottom. The interaction is also significant. The observed differences between day and night coincide with other observations of daily feeding cycles of the *Acartia* genus (Pagano & Saint-Jean 1985, Bautista et al. 1988). The fact that the observations were of copepods that had

spent their total life-cycle in a medium with a superabundance of food distributed homogeneously means that we can discount the influence of any prior conditioning of feeding habits on the diel pattern observed in this present work. The main divergence between conditions was light intensity and this may have been the controlling factor of the observed difference in *A. hudsonica* feeding activity (Head et al. 1985, Stearns 1986).

Feeding rates

The ingestion rate was calculated as the product of gut contents (ng of pigment copepod^{-1}) and the evacuation rate constant (h^{-1}) assuming the gut contents represent the amount of phytoplankton ingested during a period of time equal to a constant gut-passage time. The key factor in these determinations is the evacuation rate constant (Kiørboe et al. 1985, Kiørboe & Tiselius 1987) because its value appears to depend on temperature (Dagg & Grill 1980, Kiørboe et al. 1982, Dagg & Wyman 1983, Dam & Peterson 1988), or on the initial gut content (Baars & Oosterhuis 1984, Baars & Helling 1985, Dagg & Walser 1987).

The decrease in gut pigment contents that occurred after placing the copepods in filtered seawater is shown in Fig. 4A and is best fitted by a negative exponential model in which the slope of the curve represents the evacuation- or gut clearance-rate constant. However, some authors (Penry & Jumars 1986, Penry & Frost 1990) mention that an exponential-decay

Table 1 ANOVA of the data in Fig. 3 to determine the influence of time of day and depth on individual gut-pigment contents of *Acartia hudsonica*

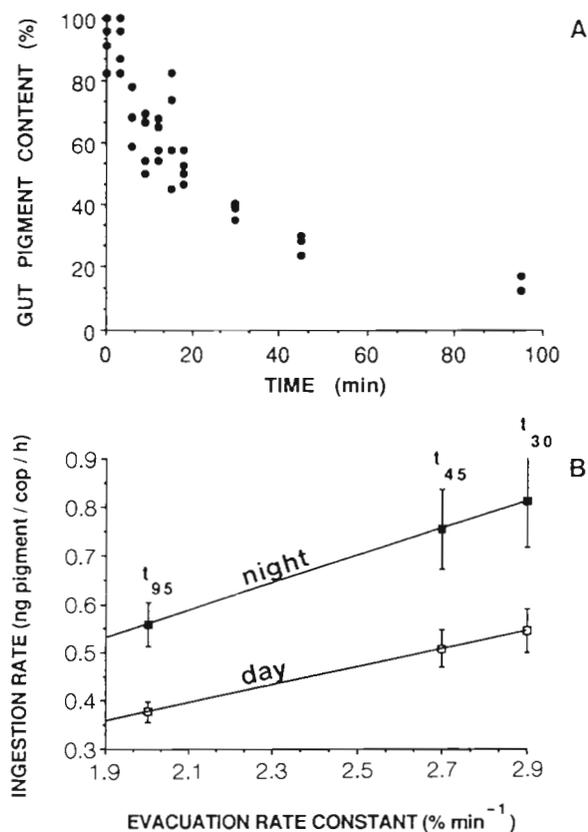| Source of variation	Sum of squares	df	Mean square	F
Main effects	20.829	2	10.414	227.576
Time of day	20.010	1	20.010	437.250
Depth	0.822	1	0.822	17.923
2-way interactions	1.238	1	1.238	27.042
Time of day × Depth	1.238	1	1.238	27.042
Explained	22.066	3	7.355	160.731
Residual	155.272	3393	0.046	
Total	177.339	3396	0.052	

Fig. 4. *Acartia hudsonica*. (A) Time-dependent changes in gut-pigment contents (percentage of initial ng pigment) measured in the gut clearance experiment. (B) Changes in ingestion rate calculated from the evacuation rate constants of a series of 3 progressively longer starvation times (t = 30, 45, 95 min)

process may not be the best model of egestion. In the present study, the value of the slope of the chosen exponential process decreased as starvation time increased. Values calculated after 30, 45, and 95 min were 2.9, 2.7, and 2.0 % min^{-1} respectively. The percentages of the initial gut contents that persisted at the end of these 3 incubation times fell within the ranges 30 to 40 %, 20 to 30 %, and 10 to 20 %, respectively. The average gut passage time, calculated as the reciprocals of the evacuation rate constants, were 40 min. This assumed equilibrium may well hold true for long-term feeding periods, but not for short ones, especially if the copepods are feeding intermittently or intensely for only a few hours by day.

The ingestion rates for all the determinations of individuals from the day-time and night-time samples were calculated separately using the evacuation rate constants discussed above. The mean values are shown in Fig. 4B. The day-night differences in gut contents revealed that the nocturnal ingestion rate was on average (n = 1700) 133 % of the daytime rate: this is

much less than the 260 to 300 % difference reported by Durbin et al. (1990). The values calculated for day-time and night-time were, respectively, 0.51 and 0.76 ng copepod^{-1} h^{-1} using the evacuation rate of 2.7 % min^{-1} obtained with 45 min of incubation. We extrapolated day and night grazing rates during the light and dark periods to calculate the total daily consumption of phytoplankton. The amount of food ingested throughout the whole day, calculated for a 16:8 h (L:D) rhythm was 14.24 ng pigment copepod^{-1} d^{-1}. If we use a C/pigment ratio of 60, the daily consumption will be 0.85 µg C d^{-1}, or, using a carbon constant of 4 µg C copepod^{-1}, 21 % body C d^{-1}.

To recapitulate, the individual variance of gut contents of *Acartia hudsonica* in this work is less than that of other species of the same genus reported by other authors. This could be due to the persistence and homogeneity of the environmental conditions. The greatest synchrony was found in the bottom samples. Feeding activity was higher during the night, although a high proportion of night-time samples showed maxima and minima of individual variance. This nocturnal feeding was probably characterized by intense feeding burst of short duration. The random and discrete, step-by-step defecation process as compared with the semicontinuous pigment ingestion may contribute to the observed individual variance within nocturnal feeding pattern of the population.

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