

## Phytoplankton-zooplankton inter-relationships in tropical waters—Grazing and gut pigment dynamics

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An examination of the feeding mechanisms in two taxonomically dissimilar classes of tropical planktonic herbivores *Evadne tergestina* (Cladocera) and *Acrocalanus* spp. (Copepoda) revealed a distinct rhythmicity of food intake. Brief bouts of phytoplankton intake were interspersed with breaks during which grazing activity ceased probably due to the onset of digestive enzyme activity. Over 90% of the chl *a* ingested was rapidly degraded during its passage through the digestive tract of the animals suggesting a high assimilatory and metabolic capacity within tropical planktonic herbivores as compared to temperate and polar forms. When subject to prolonged periods of starvation, both animals exhibited a clear tendency to reingest their own fecal pellets. In tropical oligotrophic waters where an invariably limiting size of phytoplankton food stock imposes constraints on zooplankton growth, the ability of tropical planktonic herbivores to resort to coprophagic feeding assumes particular importance as existing models make no allowances for reingestion of fecal pellets when quantifying and computing energy transfer in the food chain.

An unusually high biomass of mesozooplankton, even during the less productive periods is known to occur in the mixed layer of the Arabian Sea<sup>1-3</sup>. A sustained sampling effort, which formed part of the Indian Arabian Sea JGOFS programme, enabled Madhupratap *et al.*<sup>3</sup> to provide a possible explanation to this paradox. Based on preliminary results<sup>3</sup>, it was suggested that the continued presence of the mesozooplankton community was possible, because the herbivorous forms which were predominant, presumably possessed the capability to switchover from phytoplankton-based feeding during the productive seasons to the microbial-loop during oligotrophic periods. In invoking the microbial loop concept to explain this survival strategy of mesozooplankton, the authors relied mainly on the premise that the presence of an unusually high biomass of bacteria and microzooplankton during the oligotrophic period sustained the high mesozooplankton community. Although evidence is available to support this dual feeding strategy in planktonic herbivores<sup>4-6</sup>, it is our belief that a better insight into this problem could be gained by understanding the feeding behavior of the local planktonic herbivores, particularly the grazing community. In this study, for example, we provide

experimental evidence on two herbivores to demonstrate that tropical mesozooplankton are capable of resorting to 'coprophagic' feeding when starved for food, a feeding strategy which seems to have been overlooked<sup>3</sup> in explaining the Arabian Sea paradox. Of the two forms experimented with, one belonged to the order Copepoda and the other to the order Cladocera. Among the copepods, *Acrocalanus* spp. was chosen for these studies because of their known predominance in the northern Indian Ocean<sup>2</sup>. For a similar reason and for their voracious feeding habits, their occurrence as swarms and their strong relationship to mackerel fisheries, *Evadne tergestina* (Cladocera) was also selected<sup>7</sup>.

### Materials and Methods

Mesozooplankton samples for this study were collected from the Mandovi estuary, Goa, India, using a Heron-Tranter plankton net (mesh size 300 µm). In the laboratory, zooplankton were concentrated on a nybolt net (250 µm mesh size), washed in filtered seawater and kept aerated continuously at approximately 27°C. Samples of *E. tergestina* and *Acrocalanus* spp., each of approximately the same size were carefully sorted out from the samples, transferred to filtered seawater and starved overnight.

All grazing and gut evacuation experiments were conducted at 27°C on the subsequent day, using starved animals. Unialgal cultures of phytoplankton used as feed in the experiments were isolated from the same locality and maintained in *f/2* medium<sup>8</sup>.

#### Grazing experiments

Three sets of grazing experiments were conducted in which the increase in total gut pigments (chl *a* + phaeopigments) within zooplankton over a time course (gut fluorescence technique) was used as a measure of ingestion rates. All grazing experiments were carried out in the dark. Two of the experiments were performed with *E. tergestina*; one in which they were fed on the unialgal suspension of the diatom *Thalassiosira* sp. and, in the second they were fed on the Chlorophycean *Isochrysis* sp. In the third experiment performed on *Acrocalanus* spp., *Isochrysis* sp. was used as the feed. At the start of each experiment, pre-starved animals were transferred to flasks containing appropriately diluted suspensions of the phytoplankton culture and continuously aerated. During the experiments, the flasks were gently swirled. Together with the process of aeration, the swirling helped ensure that both the phytoplankton feed and the test zooplankton did not settle to the bottom of the flasks. Every 15 min, a known volume of the mixture was sampled and then filtered through a 100 µm nybolt mesh into measuring cylinders.

Zooplankton retained on the net were counted, washed with filtered seawater to minimize contamination by ungrazed algal material or fecal debris, and then back-filtered on Whatman<sup>®</sup> GF/C filters at a very low vacuum. The filtrate in the measuring cylinder, which represented pigments in the feed medium, was also filtered on GF/C. The material retained on the filters was transferred to vials containing cold 90% acetone and then subjected to bursts of sonication under cold conditions to ensure cell disruption and release of pigments. The vials were kept overnight under cold and dark conditions with 90% acetone, and chl *a* was estimated the following day on a Turner Designs fluorometer<sup>9</sup>, model 10<sup>®</sup> which was calibrated using standard chl *a* from Sigma Chemicals, USA<sup>®</sup>. Grazing rates were calculated using the expression<sup>10,11</sup>

$$C_t = C_0 e^{-rt} \quad \dots (1)$$

where  $C_0$  is the initial value of chl *a* in the suspension,  $C_t$  is the concentration of chl *a* at time *t* and *r* is the grazing rate constant.

#### Evacuation experiments

One set each of evacuation experiments were performed with *E. tergestina* and *Acrocalanus* spp. which were pre-fed for one hour with unialgal cultures of *Thalassiosira* sp. and *Isochrysis* sp. respectively. At the end of feeding, the animals were washed with filtered seawater and then transferred to Nucleopore<sup>®</sup>, 0.2 µm - filtered seawater, in separating flasks which helped easy dispensation of the aliquots and minimize possible contamination of the filtrates during each subsampling. Subsamples were taken at every 15 min, starting at time 'zero' immediately after the animals were transferred to the filtered seawater, and filtered onto a 100 µm nybolt net. The flasks were continuously swirled and aerated during the experiments to prevent the animals and feed from settling in the flask as well as to achieve a homogeneous aliquot of sample during sampling. Animals retained on the net were washed with filtered seawater and sonicated under cold conditions in 90% acetone for gut pigment analysis as in the grazing experiments.

Time course changes in the levels of gut pigments *E. tergestina* and *Acrocalanus* spp. pre-fed and starved in filtered seawater (0.2 µm) were utilized to estimate gut evacuation rate constants using the following relationship<sup>12</sup>:

$$S_t = S_0 e^{-kt} \quad \dots (2)$$

where  $S_0$  is the gut pigment content at the start of the experiments,  $S_t$ , the gut pigment content at time *t* and *k* is the evacuation rate constant ( $h^{-1}$ ).

The gut passage time  $G(t)$  defined as the time interval between the ingestion of food material to its egestion in the form of fecal pellets was calculated from the reciprocal of the gut evacuation rate constants.

Ingestion rates (*I*), µg chl *a* individual  $h^{-1}$  were calculated from the variation in total gut pigments using the following expression<sup>10</sup>.

$$I = \frac{dC}{dt} + kC \quad \dots (3)$$

where *C* is the gut pigment content at time *t* (*h*) in ng individual<sup>-1</sup>  $h^{-1}$ ,  $C'$  is the mean gut pigment content between consecutive sampling points and *k* is the gut

evacuation constant from Eq (2) averaged over the first hour of gut pigment decline<sup>12</sup>.

Filtration rates (F) were calculated from the ingestion rates (I) using the relationship<sup>10</sup>.

$$F = \frac{I}{C_i} \quad \dots (4)$$

where  $C_i$  is the initial chl *a* concentration in the food suspension.

## Results

### Feeding behavior and dynamics of gut pigments

Despite being starved overnight prior to the grazing experiments, the animals did not empty their guts completely. In *E.tergestina*, gut pigment concentrations ranged between 3.05 and 3.75 ng individual<sup>-1</sup> at the start of the experiment, and about 0.5 ng individual<sup>-1</sup> in *Acrocalanus* spp. Almost 99% of the gut pigments at this stage was, however, degraded chl *a*. We attempted to examine the feeding behavior and gut pigment dynamics of the animals by plotting changes in total gut pigments against time (Fig. 1). In *E. tergestina*, although gut pigment levels increased during the grazing experiments (depicted by the solid regression lines in Fig. 1A and B), the animals appeared to follow a peculiar rhythmic feeding behavior, where periods of increase in gut pigment levels were interspersed with periods of decline. There were differences however, in the times at which the pigment peaks appeared in *E. tergestina*, depending on the food type (Fig. 1A and B). *Acrocalanus* spp. also exhibited this rhythmic feeding behavior (Fig. 1C), but the first peak occurred quite early, i.e. 20 min. after the grazing experiments were begun and the second after 60 min (Fig. 1C).

Chlorophyll *a* degradation during its transit through the guts of the animals was examined by calculating the percentage decrease in chl *a*, relative to total pigments ingested by the animals. No particular trend of change was noticeable. However, throughout the experiment, phaeopigments accounted for over 90% of the total gut pigments indicating rapid metabolic activity after the intake of food by these animals

In all three grazing experiments, an overall decline in the levels of chl *a* was observed in the food suspension, but the decline was discontinuous and was interrupted by periods when chl *a* concentrations

increased (Fig. 2). It is difficult to explain with certainty what would have caused the increase in chl *a* at after each decline in the flasks during each experiment, in particular, the significant increase observed around 90 min. The flasks were continuously aerated during each experiment and furthermore were agitated especially prior to sampling. This rules out the possibility that the increases in chl *a* were an artifact caused by settling of phytoplankton cells in the flask. Additionally, since the experiments were conducted in the absence of light, an increase in chl *a* caused by phytoplankton

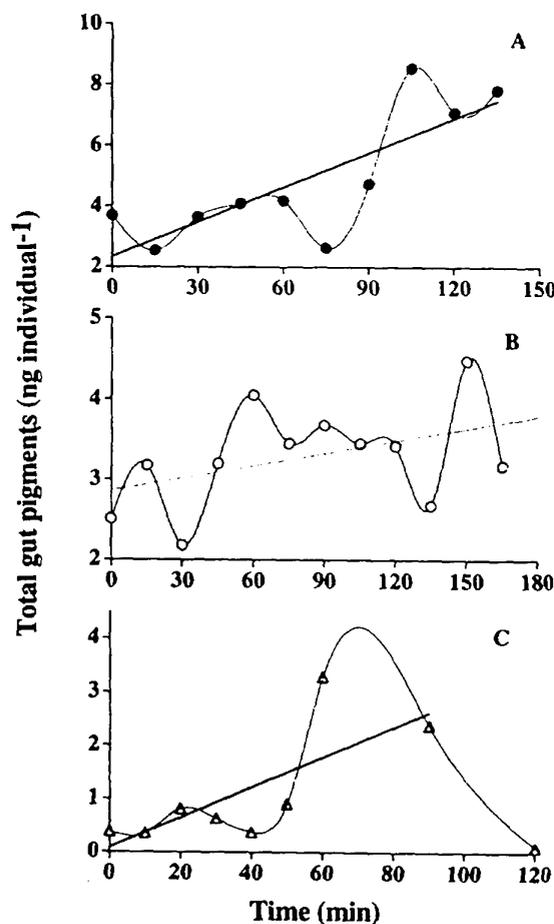


Fig. 1—Time course variations in total gut pigments in—A) *E. tergestina* fed on *Isochrysis* sp., B) *E. tergestina* fed on *Thalassiosira* sp. and C) *Acrocalanus* spp. fed on *Isochrysis* sp. Least square linear fits to the data have been plotted to indicate overall increase in gut pigments. Whilst applying the least square linear fit to Fig. 1C, the gut pigment value at 120 min was not considered.

growth would have been minimal. We noted however, that at no point in the experiment did the overall chl *a* concentrations in the flask exceed the starting concentrations.

Grazing rate constants calculated for *E. tergestina* fed on *Isochrysis* sp. and on *Thalassiosira* sp., and *Acrocalanus* spp. fed on *Isochrysis* sp. (Fig. 3), showed a general trend of decline with time. However, there was considerable scatter in the distribution of points about the regression line probably due to the peculiar trend of decrease and increase observed in the levels of chl *a* within the food suspension.

#### Dynamics of gut evacuation

A general decline in gut phaeopigments and total

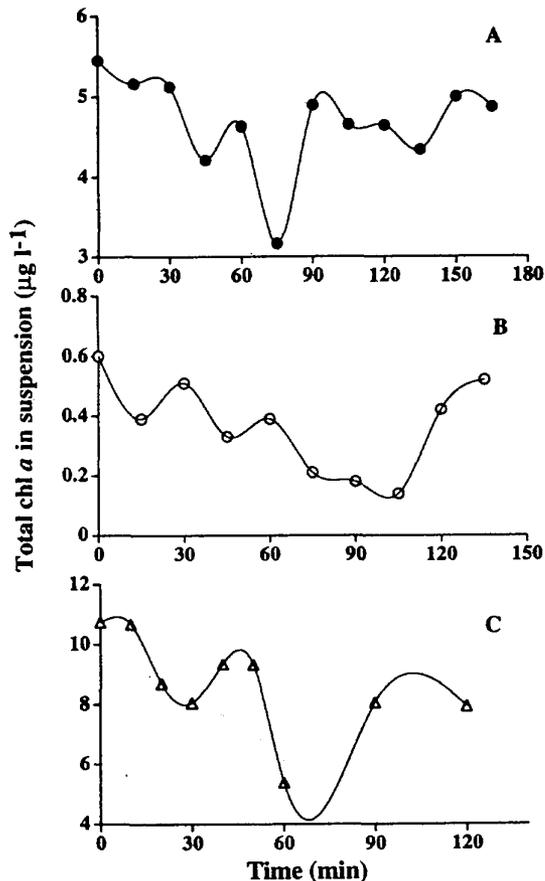


Fig. 2—Time course variations of chl *a* in the food suspension—A) *E. tergestina* fed on *Isochrysis* sp., B) *E. tergestina* fed on *Thalassiosira* sp. and C) *Acrocalanus* spp. fed on *Isochrysis* sp.

gut pigments was observed when pre-fed samples of *E. tergestina* and *Acrocalanus* spp. were transferred to filtered (0.2 µm) seawater (Fig. 4). In both sets of experiments, the rate of decline in gut pigments was intense at the commencement of the starvation period but, declined more or less exponentially with time, to attain stable gut pigment values of around 3.5 ng individual<sup>-1</sup> in *Evadne* spp and 2.5 ng individual<sup>-1</sup> in *Acrocalanus* spp. A very significant fraction (>95%) of the total gut pigments during evacuation was comprised of phaeopigments. An unusual but conspicuous feature that was noticed in all three evacuation experiments, was the increase in gut pigments after about 150 min. of starvation. During this time, phaeopigments accounted for more than 99% of the total gut pigments, indicating strongly that the animals were reingesting particulate matter that had already been evacuated.

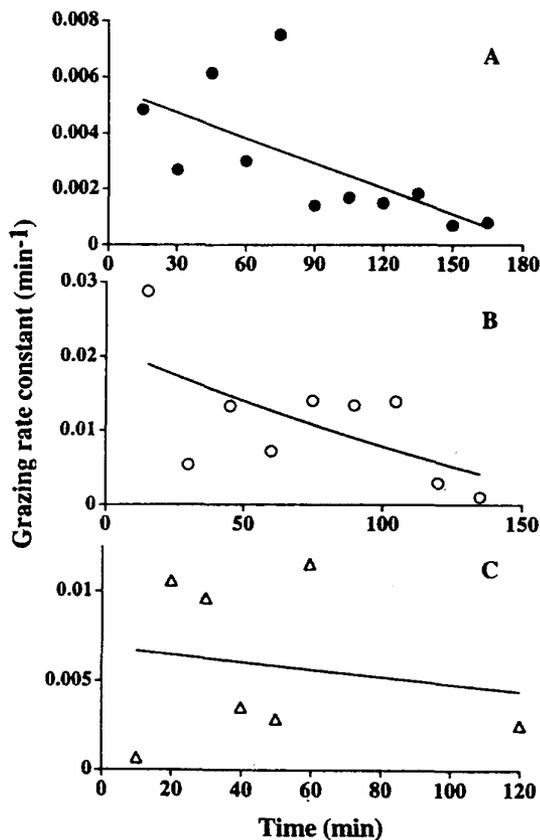


Fig. 3—Variations in grazing rate constants with time in—A) *E. tergestina* fed on *Isochrysis* sp., B) *E. tergestina* fed on *Thalassiosira* sp. and C) *Acrocalanus* spp. fed on *Isochrysis* sp.

Evacuation rate constants for *E.tergestina* as well as *Acrocalanus* spp. plotted in Fig. 5 respectively showed a steady decline with the period of starvation. Evacuation rates averaged-over the first hour were

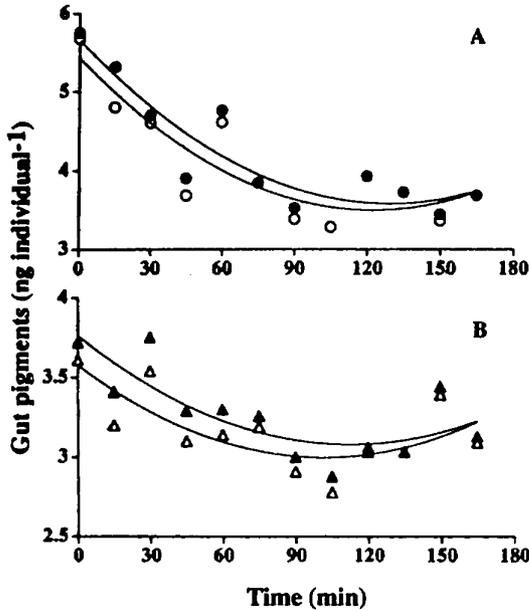


Fig. 4—Time course variations in gut pigments during starvation in—A) *E. tergestina*, B) *Acrocalanus* spp. Open circles and open triangles (phaeopigments) and closed circles and triangles (total gut pigments)

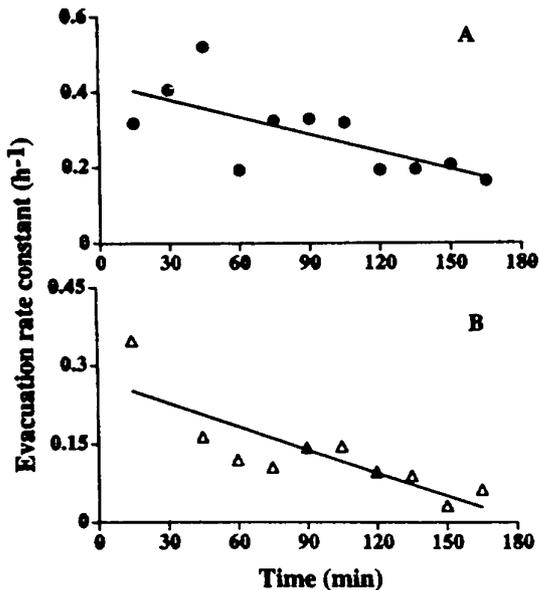


Fig. 5—Time course variations in gut evacuation rate constants in—A) *E. tergestina*, B) *Acrocalanus* spp.

0.35 h<sup>-1</sup> for *E. tergestina* and 0.18 h<sup>-1</sup> for *Acrocalanus* spp. The average evacuation rates calculated for the entire period of starvation in case of *E.tergestina* was 0.156 h<sup>-1</sup>, while in *Acrocalanus* spp. it was 0.055 h<sup>-1</sup>. Based on these values obtained for the entire period of starvation, the average gut passage time for *E. tergestina* was estimated at around 6 hours, 25 min., whereas for *Acrocalanus* spp. it was estimated as 18 hours. In both *E. tergestina* and *Acrocalanus* spp., the gut passage time increased with the length of starvation of the animals.

Both in terms of absolute values and trends of change during the experimental period, ingestion rates varied widely in all the experiments (Fig. 6A). In *E. tergestina* feeding on *Isochrysis* sp., hourly averaged ingestion rates increased from 1.29 ng individual<sup>-1</sup> h<sup>-1</sup> during the first hour to

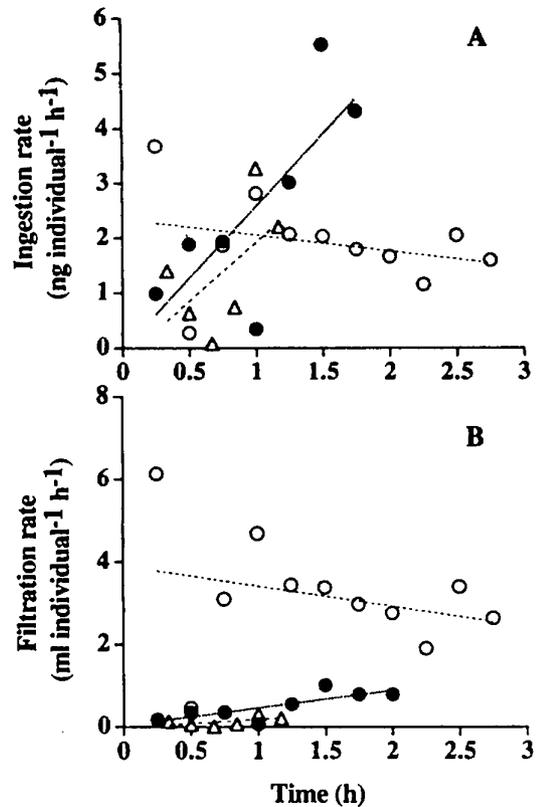


Fig. 6—Time course variations in—A) ingestion rates and B) filtration rates in *E. tergestina* fed on *Isochrysis* sp. (closed circles), *E. tergestina* fed on *Thalassiosira* sp. (open circles) and *Acrocalanus* spp. fed on *Isochrysis* sp. (open triangles). Regression lines plotted to indicate trends of change in these rates for each animal.

Table 1—Hourly averaged values for ingestion, filtration and grazing rates in *Evadne tergestina* and in *Acrocalanus* spp. fed on different phytoplankton suspensions.

Test zooplankton	Phytoplankton feed	Ingestion rate (ng individual <sup>-1</sup> h <sup>-1</sup> )			Filtration rate (ml individual <sup>-1</sup> h <sup>-1</sup> )			Grazing rate (h <sup>-1</sup> )		
		1h	2h	3h	1h	2h	3h	1h	2h	3h
<i>Evadne tergestina</i>	<i>Isochrysis</i> spp.	1.29	4.28	*	0.23	0.76	*	0.29	0.1	0.23
<i>Evadne tergestina</i>	<i>Thalassiosira</i> spp.	2.12	1.23	1.58	3.5	2.15	3.02	0.81	0.67	*
<i>Acrocalanus</i> spp.	<i>Isochrysis</i> spp.	1.21	*	*	0.11	*	*	0.53	0.35	*

\*Indicates no data available

4.28 ng individual<sup>-1</sup> h<sup>-1</sup> thereafter (Table 1). Ingestion rates for the same species fed on *Thalassiosira* sp. decreased from 2.12 ng individual<sup>-1</sup> h<sup>-1</sup> during the first hour to a low value of 1.23 ng individual<sup>-1</sup> h<sup>-1</sup> during the second hour. The ingestion rate for *Acrocalanus* spp. which was 1.21 ng individual<sup>-1</sup> h<sup>-1</sup> during the first hour, was practically negligible during the second hour.

Filtration rates were also not consistent and varied during the experimental period in all three experiments (Fig. 6B). For *E. tergestina*, fed on *Isochrysis* sp., hourly averaged filtration rates varied from 0.23 to 0.76 ml individual<sup>-1</sup> h<sup>-1</sup>. When fed on *Thalassiosira* sp., filtration rates for *E. tergestina*, ranged from 2.74 to 3.02 ml individual<sup>-1</sup> h<sup>-1</sup>. For *Acrocalanus* spp., fed on a high concentration of chl *a* within the food suspension, the rates were even lower, i.e. 0.11 ml individual<sup>-1</sup> h<sup>-1</sup>.

## Discussion

### Feeding behavior and dynamics of gut pigments

Although there was an overall increase in gut pigments during the grazing experiments with *E. tergestina* and *Acrocalanus* spp. (see least square linear fits to gut pigment data over the entire experimental period in Fig. 1), a feature that was particularly noteworthy was that the increase was discontinuous, alternating between increases and marginal decreases in gut pigment levels, indicating a rhythmic pattern of feeding in these animals. In order to illustrate the existence of this rhythmicity, least square linear regressions were fitted to the data from Fig. 1, but over short time intervals. The variability in the slopes of these fits have been plotted in Fig. 7. In all three experiments, the variability in the slopes was statistically significant indicating that this periodicity in feeding was not an experimental artifact. The change in sign of the slopes in particular, during each

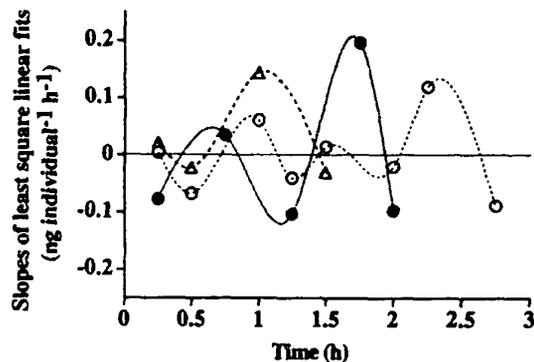


Fig. 7—Time course variations in the slopes of the least square linear fits to the data from Fig. 1A-C over short intervals. Other details as in Fig. 6.

experiment, indicates that in all the animals, periods of ingestion of food material were interspersed with periods of egestion. Microcinematographic techniques<sup>12,13</sup> clearly demonstrated that this rhythmicity in zooplankton was not an experimental artifact. It was shown that zooplankton in general, had a tendency to alternate brief bouts of feeding or swimming with breaks during which time feeding and swimming activities ceased<sup>13,14</sup>. In field studies also, it was established that zooplankton abruptly stopped their feeding activity and modified their swimming and migratory activities, but this occurred only when the animals became satiated<sup>15</sup>. In the present study, both *E. tergestina* and *Acrocalanus* spp. did show a tendency to sink during the course of the grazing experiments, but we were able to observe from the gut pigment increase that followed each break, that this occurred well before the animals were satiated. Although, there are other reports which contradict the existence of rhythmicity in feeding activities<sup>16,17</sup>, a study on the ultrastructure of the midgut of *Centropages typicus* showed that cellular structures responsible for most of the digestive processes, also

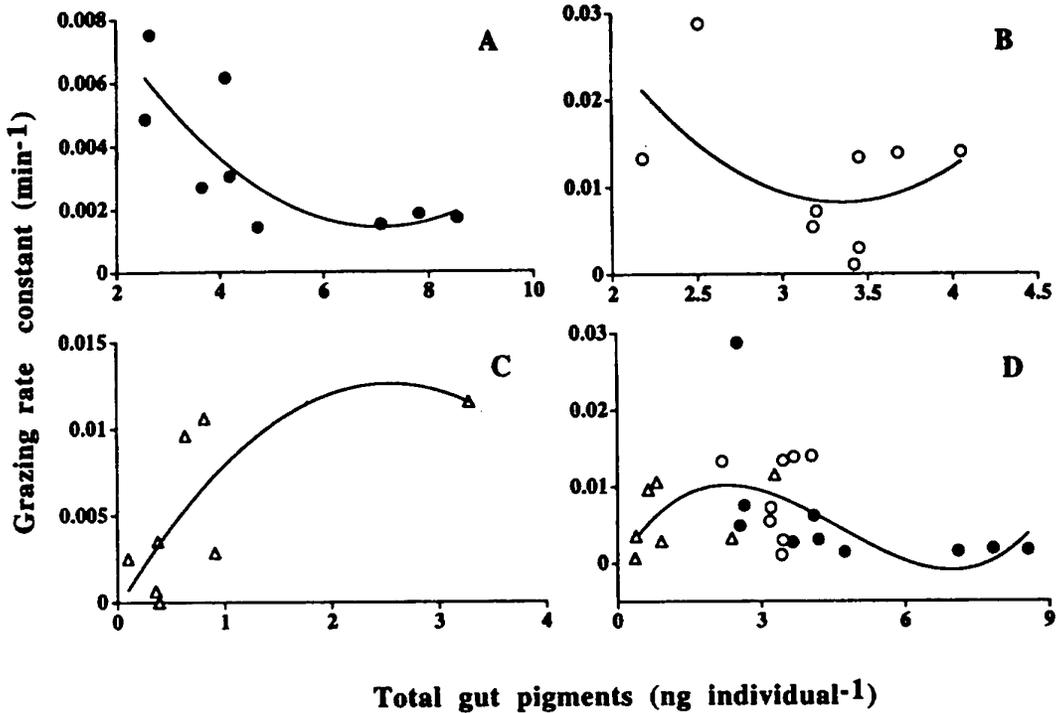


Fig. 8—Relationship between grazing constants and total gut pigments in—A), *E. tergestina* fed on *Isochrysis* sp., B) *E. tergestina* fed on *Thalassiosira* sp., C) *Acrocalanus* spp. fed on *Isochrysis* sp. and D) Composite plot of Fig. 8A-C. Other details same as in Fig. 6.

displayed a cycle in which degenerating cells were replaced by newly synthesized ones over periods less than an hour; the consequence of this periodicity resulting in a clear rhythmicity in feeding and ingestion rates of the animal<sup>18</sup>.

Grazing rate constants showed a marked dependency on gut pigment levels. In *E. tergestina*, a more or less exponential decline was observed along with an increase in gut pigments (Fig. 8). Thereafter these values remained stable at values of around 0.001 to 0.01  $\text{min}^{-1}$  when gut pigment levels were between 3.5 and 5.5  $\text{ng individual}^{-1}$ . Grazing constants obtained for *Acrocalanus* spp. also showed a marked dependency on total gut pigments, but, the relationship interestingly was just the opposite of what was obtained for *E. tergestina*. For *Acrocalanus* spp., the grazing rate constants increased until gut pigment levels were around 2  $\text{ng individual}^{-1}$ . A composite plot of grazing rate constants and gut pigment levels pooled from all three experiments (Fig. 8D), revealed a rapid decline in grazing rate constants at pigment levels beyond 2  $\text{ng individual}^{-1}$ . These results lead us to conclude that planktonic

herbivores probably have an efficient feeding mechanism by which they modulate the intake of food till their gut pigment levels reach optimum.

Ingestion rates varied over time, differing in all three experiments (Fig. 6A). In *E. tergestina* and *Acrocalanus* spp., fed on *Isochrysis* sp., ingestion rates increased over the period of the experiment but in *E. tergestina* fed on *Thalassiosira* sp., these rates declined over time. Ingestion rates showed an increase as gut pigment levels increased (Fig. 9A). Filtration rates calculated for the animals, also varied during the experiments showing a marked dependency on chl *a* in the food suspension (Fig. 9B). At food concentrations less than 0.5  $\mu\text{g l}^{-1}$  of chl *a* within the food suspension, filtration rates were extremely high but, declined rapidly beyond 1  $\mu\text{g l}^{-1}$  of chl *a*, to attain more or less stable values.

On an average, 96% of chl *a* ingested was degraded during its transit through the guts of the animals. These percentages of chl *a* degraded are much higher than those reported for planktonic herbivores from temperate and cold water environments<sup>19,20</sup>, suggesting that tropical

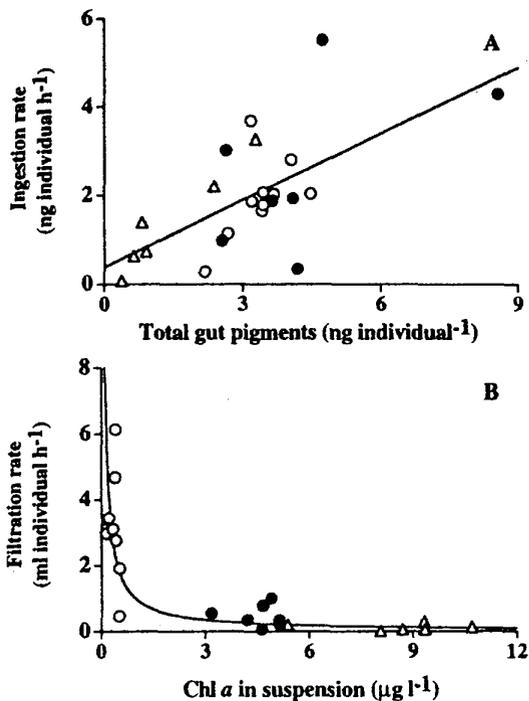


Fig. 9—Relationship between—A) ingestion rates and total gut pigments and B) filtration rate and chl *a* concentrations in the food suspension for *E. tergestina* fed on *Isochrysis* sp., *E. tergestina* fed on *Thalassiosira* sp. and *Acrocalanus* spp. fed on *Isochrysis* sp. Other details same as in Fig. 6.

zooplankton possess a more efficient enzymatic degradation process that results in high assimilation of food and ultimately faster growth rates.

It may be noted that in the calculation of ingestion and other related rate parameters by the gut fluorescence technique, we have made an implicit assumption that chl *a* ingested by zooplankton is stoichiometrically converted into phaeopigments. Until recently this was believed to be true, but a number of recent reports (see Head<sup>11</sup> and references cited therein), suggest that some fraction of ingested chl *a* could be broken down to non-fluorescing end products and hence not measurable by the gut fluorescence technique. The extent to which pigments can be destructed to non-fluorescing compounds reportedly<sup>11</sup>, varies depending on the zooplankton species being examined, their growth stage, feeding history, the type of feed etc. In this study, no attempt has been made to measure the extent of pigment destruction during feeding for want of which, the estimates of ingestion rates and other rate parameters presented here may be biased to a certain extent.

#### Dynamics of gut evacuation

The present observations showed that when the animals were transferred to seawater devoid of food, there was an exponential decline in the gut pigment content of *E. tergestina* and *Acrocalanus* spp. (Fig. 4). Gut evacuation rates calculated from gut pigment data also showed a decrease with time of starvation in agreement with the previous observations with temperate planktonic herbivores<sup>20,21</sup>. In these studies, it was reported that the decline in evacuation rates was linked to the turnover rates and levels of the digestive enzymes of the planktonic herbivores, which they found dropped dramatically when zooplankton were starved. In calculating the evacuation rates, it was suggested that the decline in gut pigments at the beginning of the evacuation experiments provided the best measure of both gut evacuation and gut passage time<sup>12,22</sup>. In the present set of experiments, no significant signs of gut evacuation were observed at the commencement of the evacuation experiments. These results lead us to believe that possible physiological shock induced by transferring animals from conditions of plentiful food to an environment devoid of food does not necessarily stimulate evacuation. These results also suggest that a better estimate of evacuation rates in zooplankton would be one averaged over the first hour of decline in gut pigments as suggested earlier<sup>12,22</sup>.

A feature of considerable interest that observed in the evacuation experiments, was the increase in the gut pigment levels towards the end of two hours starvation period (Fig. 4A,B). This tendency of zooplankton to retain a certain fraction of pigments in their guts when subject to long bouts of starvation was also noted when the animals were pre-starved overnight in filtered seawater prior to the feeding experiments. As mentioned earlier, one reason for the increase in gut pigments even in the absence of food may be related to the ability of planktonic herbivores to switch over from herbivory to coprophagy<sup>23</sup>. Separate studies on the tropical planktonic copepod, *Acartia* spp., also revealed a clear tendency of this animal for coprophagic feeding when starved<sup>24</sup>. These findings lead us to conclude that coprophagic feeding may not be unusual for tropical planktonic herbivores. Since sinking fecal pellets are known to rapidly acquire bacterial flora<sup>4,6,25</sup>, which can help account for the calorific and protein requirements of the feeders, it seems tempting to suggest that when

phytoplankton availability is scarce, the ability of tropical planktonic herbivores to resort to coprophagic feeding may be particularly important for ensuring their survival under oligotrophic conditions. In offering the microbial loop as a possible explanation for the Arabian Sea paradox of high biomass mesozooplankton during periods of low phytoplankton production<sup>3</sup>, it is possible that coprophagic feeding as a strategy for survival and growth may have been overlooked.

Besides its implications for the food structure in tropical marine environments, this feeding behavior has particular relevance to the transfer of energy and the flux of carbon in tropical marine environments. At present, existing models for tropical waters do not make allowances for reingestion of fecal pellets which could lead to discrepancies whilst computing and quantifying the transfer of energy in the marine food chain. Fecal pellets produced by crustacean zooplankton are recognized as the most important vehicle by which flux of carbon out of the ecosystem is achieved<sup>26</sup>. One of the most important attributes of fecal pellets in material transport into the water column, is their sinking rates. It has shown that when zooplankton resort to coprophagy, they usually resort to raptorial feeding wherein fecal pellets are broken into tiny particles leading to a considerable reduction in the sinking rates and amount of particle flux<sup>5,6, 26-28</sup>.

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