A model of diel vertical migration of zooplankton and its potential for the redistribution of organic material through the water column

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Abstract Many species of small herbivorous zooplankton have been observed to perform diel vertical migrations through the water column. Such animals are often located in a phytoplankton rich surface layer during the night but spend much of the day in deeper water where their phytoplankton food source is less abundant. It has been suggested that these species may provide a mechanism where significant amounts of organic material are redistributed down the water column. A net downward flux of material will result if on average animals egest material deeper than where prey is consumed. The downward flux of organic material can be an important food source for deep dwelling communities. In this paper models of zooplankton movement and feeding are coupled so that the potential for animals to vertically redistribute organic material can be investigated. The model is individual-based where each animal moves in a stochastic manner and its gut dynamics are described by an ordinary differential equation. The model is general and parameter values are considered which typify the swimming and feeding abilities of a wide number of copepod species. The results of simulations suggest that such species are not an effective mechanism by which organic material is vertically redistributed. Much of the matter ingested is assimilated into the body and the remaining material is quickly egested before animals have had time to move significantly down the water column.

1. INTRODUCTION

Although diel patterns of vertical migration have been observed for a number of small species of zooplankton it is still unclear how such movements are coupled with patterns of feeding activity [Starkweather, 1983; Angeli *et al.*, 1995]. One consequence of this coupling is that material may be egested at places which are far from where it is ingested. It is common for phytoplankton to be concentrated within the first few tens of metres below the surface. Some species of zooplankton which primarily feed on such phytoplankton have been observed to be located within the food rich waters at night but are later located well below the food layer during the day. The result is a pattern of periodic grazing pressure on the phytoplankton community. It has been suggested that in these situations zooplankton may be redistributing significant amounts of organic material down the water column. Redistribution will occur if animals fill their guts with prey when they are in the surface layer during the night, and then retain such material in their gut for a sufficient time so that it is egested later when animals are at the deeper depths. It would appear then that the amount of material that is redistributed will be strongly dependent on; (1) the speed at which the animal swims during their migration phase; (2) the time that material remains in the gut before it is egested; and (3) the fraction of the ingested material which is egested and not assimilated into the animals body. The fate of zooplankton faecal material is of interest as it can be an important food source for deeper dwelling communities [Paffenhofer and Knowles, 1979; Angel, 1984].

Due to their small size and the environment in which they live it is often difficult to take accurate measurements of herbivorous zooplankton movements and feeding dynamics. It is clear that a number of factors are important at governing where organic material is redistributed in the vertical. Despite the difficulties involved, field and laboratory experiments have been performed which provide insights about some of these factors. Measurements of vertical swimming speeds of zooplankton have been made as have rates at which food is either assimilated or passed through the gut, and how feeding rates are related to prey densities. A mathematical model is presented in the next section which combines these factors and predicts levels of vertical redistribution. Estimates of most of the model parameters can be found in the literature. Sensitivity analyses of the models results to changes in these parameter values can provide insights into which factors are important in determining redistribution.

2. THE MODEL

In this section an individual based model of zooplankton vertical migration and feeding is presented. It is assumed that the zooplankton population is composed of 2000 individuals and we investigate population dynamics for a period of a few days so births and deaths can be ignored. The model monitors the level of gut fullness within each individual in the population by explicitly noting the depths where animals ingest and egest material. This information is then used to calculate the vertical flux of organic material as a direct result of the zooplankton migrations. The assumptions and equations used to describe zooplankton swimming and feeding are now described.

2.1 Zooplankton Swimming

The timing and regulating of vertical swimming is likely to be the result of animals responding to a number of exogenous and endogenous factors. Light is generally regarded as being the main factor which zooplankton use as a cue to initiate their ascent and descent and to also regulate their speed of movement [Forward, 1988]. In this paper it is assumed that animals swim in response to one cue only, namely the relative rate of change in light intensity (RRC). Other characteristics of the light field which may be used as a cue for vertical migrations have been modelled by Richards *et al.* [1996].

If we denote the light intensity at depth z and time t by $I(z,t)$ and assume that light intensity decreases exponentially with depth, as is often observed, then the relative rate of change in light intensity, S, is described by

$$S(t) = \frac{1}{I(z,t)} \times \frac{d}{dt}\left(I(z,t)\right) \qquad (1)$$

Note that (1) states that the relative rate of change in light intensity experienced by an animal is independent of its depth below the surface. Here we assume that sunrise and sunset occur at 6 am and 6 pm respectively and the RRC can be well represented by two log-normal functions, namely

$$S(t) = \begin{cases} f(60(t-3.5)) & \text{if } 3.5 \le t \le 8.5 \\ -f(60(20.5-t)) & \text{if } 15.5 \le t \le 20.5 \\ 0 & \text{otherwise} \end{cases} \qquad (2)$$

where t is the time in hours from midnight and

$$f(\tau) = 0.151\exp\left(-4.16\left(\ln(\tau) - 4.604\right)^2\right) \qquad (3)$$

The RRC given by (2) and (3) has units of (min^{-1}) and agrees quantitatively with measurements recorded by Ringelberg [1993] in a lake environment. The RRC is generally low during much of the day and night but has a positive peak around sunrise and a negative peak around sunset. Animals are assumed to maintain their current depth if the absolute magnitude of the RRC experienced is below a threshold value called the Rheobase, R. If the RRC is greater than R then animals migrate deeper and if RRC is less than R then animals swim towards the surface. The average speed that zooplankton swim vertically at time t is described by

$$\overline{w}(t) = \begin{cases} \min\left(w_d, [S(t) - R]\mu\right) & \text{if } S(t) \ge R \\ 0 & \text{if } -R \le S(t) \le R \\ \max\left(-w_u, [S(t) + R]\mu\right) & \text{if } S(t) \le -R \end{cases} \qquad (4)$$

where w_d and w_u are the maximum maintainable swimming speeds in the down and up direction and μ is a parameter which describes how sensitive animals are to the RRC. Note that a positive value indicates a downward movement of animals and negative upward.

In reality, individuals within the population will be moving at different speeds at any given time. This is due to differences in swimming abilities among individuals and also due to the influence of eddy turbulence within the water column. The model accounts for this by including a stochastic element to animal movement. The vertical speed of the i-th animal in the population, w_i, is calculated using,

$$w_i(t) = \overline{w}(t) + w'\,\mathrm{N}(0,1) \qquad (5)$$

where N(0,1) is a normal variate with mean 0 and variance 1 and w' is a parameter which describes the amount of variability in movement within the population. For simplicity it is assumed that the level of variability is independent of the time of day and depth. The depth of each animal is updated after time steps of duration Δt using,

$$z_i(t + \Delta t) = z_i(t) + \Delta t\, w_i(t) \qquad (6)$$

Typical vertical profiles of the zooplankton population at midday and midnight are presented in Figure 1. The parameter values used to generate these distributions are given in Table 1. Parameter values have been chosen which results in animals which generally migrate to the surface at sunset and then migrate to below 50 m depth at sunrise. The ascent phase of migration starts at sunset and lasts 90 minutes after which most animals are located near the surface and vertical movements are then minimal. Descent begins approximately 90 minutes before sunrise and continues until sunrise. Vertical migrations of this magnitude and form have been observed in the field for a number of species of copepods [Dagg *et al.*, 1989; Atkinson *et al.*, 1996].

2.2 Zooplankton Feeding

The way in which the gut content of fish and small zooplankton varies over time is often modelled by the following ordinary differential equation [Elliot and Persson, 1978; Dam *et al.*, 1991],

$$\frac{dg}{dt} = I - K\,g \qquad (7)$$

where $g(t)$ is the amount of ingested material present in the animals gut at time t, I is the rate at which material is ingested, and K is a parameter often referred to as the gut evacuation rate. Laboratory experiments often show that for many species of zooplankton when they are suddenly starved of food their gut fullness, g, decreases in a negative exponential manner. This is consistent with (7) when $I = 0$, and the rate of decrease can be used to calculate an estimate for K. The inverse of the gut evacuation rate, K^{-1}, is referred to as the gut passage time and starvation experiments generally result in estimates of gut passage times for copepods ranging between 20 and 90 minutes [Dagg *et al.*, 1989].

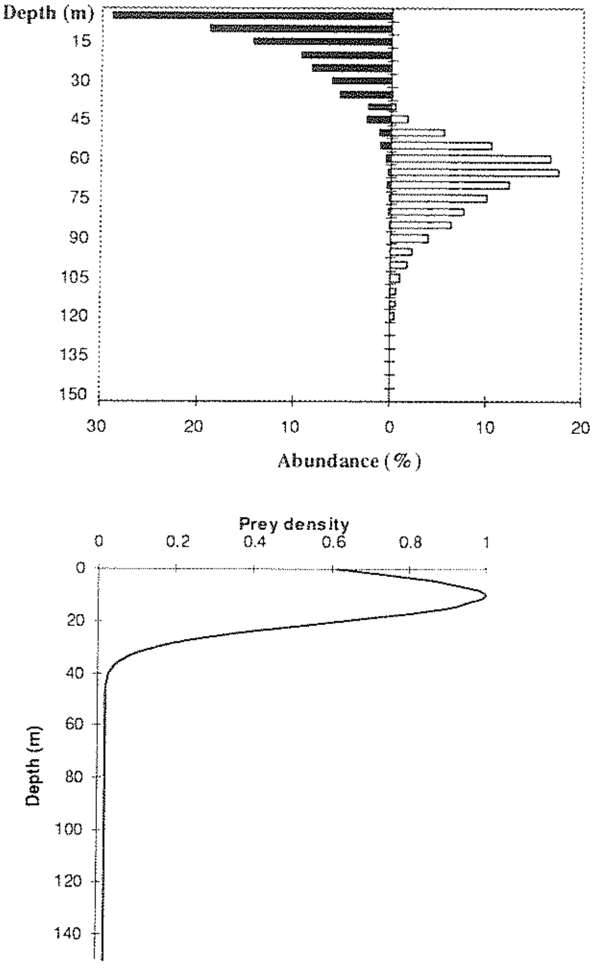


Figure 1: Vertical distribution of the zooplankton population at midday (open bars) and midnight (closed bars) and the vertical distribution of phytoplankton prey.

Organic material which is ingested is subsequently either assimilated into the animals body or egested in the form of pellets. Material that is assimilated may be used for processes which include: growth, moulting, reproduction, and respiration. The fraction of the material removed from the gut that is assimilated is referred to as the assimilation efficiency [Urabe and Watanabe, 1991] and denoted, a. The rate of assimilation and egestion are related to gut fullness by

$$A(t) = aK\,g(t) \qquad (8)$$

$$E(t) = (1 - a)K\,g(t) \qquad (9)$$

Assimilation efficiencies are likely to be dependent on properties of the prey items and vary between species. Reliable estimates are few [Urabe and Watanabe, 1991] but assimilation efficiencies of around 75% appear to be common for copepods.

Table 1. Parameter values used for the vertical migration model

Δt	2 minutes
w_d	1.5 cm s^{-1}
w_u	1.7 cm s^{-1}
w'	0.4 cm s^{-1}
R	0.07 min^{-1}
μ	12.75 m
ρ_{min}	0.02 (dimensionless)
σ_{ρ}	10 m
z'	10 m
a	0.75
K^{-1}	30 minutes
α	2.5

Here it is assumed that the modelled zooplankton species is primarily herbivorous and its vertical distribution of food can be well described by the vertical distribution of phytoplankton. This distribution is represented by a shifted Guassian profile [Platt *et al.*, 1994],

$$\rho(z) = \rho_{\min} + (1 - \rho_{\min})\exp\left(-\frac{1}{2\sigma_{\rho}^{2}}(z - z')^{2}\right) \qquad (10)$$

A maximum density of 1 unit of food per unit area is assumed to peak at a depth of z' which declines to a minimum density, ρ_{min}. The vertical spread of the peak is governed by the parameter, σ_{ρ}. It is assumed that the density of prey remains stable and hence the phytoplankton community regenerates at a rate similar to the rate at which it is grazed. The vertical distribution of prey which is assumed and described by the parameter values of Table 1 is presented in Figure 1. Prey densities peak 10 m below the surface and decline to low levels below 40 m. As the zooplankton population tends to migrate between the surface and below 50 m, animals will experience large variations in surrounding prey densities each day. Is it likely that in this scenario animals will fill their gut with prey in the food rich surface waters at night and then egest much of this material after they have completed their downward phase of migration? In order to complete the model and examine this possibility we need to relate the rate of ingestion, I, to the density of prey.

It is assumed that the rate of ingestion is related to prey densities by an equation of the Ivlev form, namely

$$I(\rho,g,t) = h(t)\, I_{\max}\left(1 - e^{-\alpha\rho}\right)\left(1 - g^{2}\right) \quad (11)$$

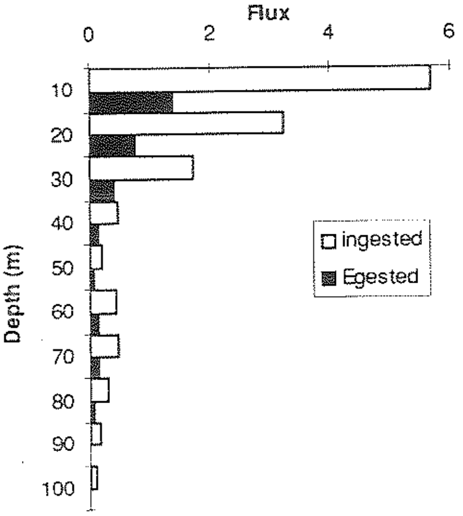
where $I_{\max}$ is the maximum possible rate of ingestion. The ingestion rate is modelled to slow in a quadratic manner as the gut fills [Caparroy and Carlotti, 1996]. We choose a value for the parameter α which represents a situation where animals come close to their maximum ingestion rates when they are within the phytoplankton peak. Note that the ingestion rate is measured as "gut fulls" per unit time. Some experiments suggest that zooplankton may alter their feeding rates throughout the day and night by changing the proportion of times spend feeding, swimming and resting [Durbin *et al.*, 1990]. Such temporal changes are represented by the function, $h(t)$. If the zooplankton species exhibits no feeding rhythm then h takes the value 1 for all time. A feeding rhythm where activity peaks at midnight and is minimal at midday could be represented by

$$h(t) = \frac{1}{2}\left(1 + \cos\left(\frac{2\pi}{T}t\right)\right) \quad (12)$$

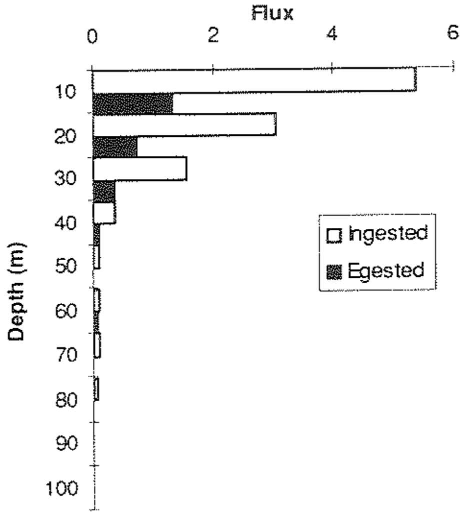
In the next section we examine what affect such a rhythm has on redistribution.

3. RESULTS

In order to evaluate how much material is vertically transported within the gut of an animal we divide the water column up into 10 m long discrete depth intervals. For each individual in the population at each time step the model identifies which segment the animal lies. The amount of material ingested and egested by the animal in the segment during the time step is then estimated by noting the amount of material in its gut. We repeat this process for 4 days of simulation and the results are summed and averaged in order to provide an estimate of the average amount of material egested and ingested per individual each day within each segment. The segments where the amount of egested material exceeds the amount of ingested material is where the population is increasing the abundance of organic material in the water column as a result of their vertical migrations. Animals are assumed to have a gut passage time of 30 minutes which is typical of a number of copepod species. Note that in the unrealistic case that every bit of material consumed is assimilated into the body the population will not redistribute organic matter regardless of the pattern of feeding and migration as no material is ever egested.



No feeding rhythm



Feeding rhythm

Figure 2 : The average number of "gutfulls" of prey ingested and egested by a zooplankton animal each day within 10 m depth intervals. Fluxes are presented when animals filter feed at a continuous rate and also when filtering activity decreases during the day.

Model results are presented in Figure 2. The gut dynamics of each animal, i.e. the solution to (7), was approximated using the Runge-Kutta method of order 4 [Conte and de Boor, 1988] with a constant time step, Δt = 2 min. Regardless of whether animals exhibit a feeding rhythm or not, the model predicts that over all depths the amount of material ingested is always greater than the amount of material egested. Hence, for the situation as described by the parameters presented in Table 1, zooplankton are not predicted to increase the abundance of organic material anywhere within the water column as a result of their vertical migrations. Although some material is transported vertically within the gut the amount which is then expelled back into the water column is less than that which is consumed. The ascent and descent phase of migration both last 90 minutes and much of the material ingested is either assimilated or egested before the active periods of migration cease.

It is not surprising that the model predicts that zooplankton species characterised by the parameters presented in Table 1, are unlikely to contribute significantly to the downward flux of organic material. If animals did not migrate at all then we would expect the ratio of ingested material to egested material *(I/E)* to be

$$\frac{I}{E}=\frac{1}{1-a} \qquad (13)$$

When 75% of the material ingested is assimilated this ratio is 4 which is well above a ratio of 1 which would indicate that the amount of organic material in the water column remains constant. Figure 3 shows how the ratio varies with depth when animals migrate and how it is affected by the presence of a feeding rhythm. A ratio less than 4 indicates that on average some material is transported down the water column in the gut. The model predicts that if redistribution was to occur it would be most pronounced at around 50 m which is where phytoplankton densities drop dramatically to low background levels. The model also suggests that redistribution is more likely to occur for species that decrease feeding activity during the day. We would expect animals to be most effective at downward redistribution if they completely cease to feed when they swim down.

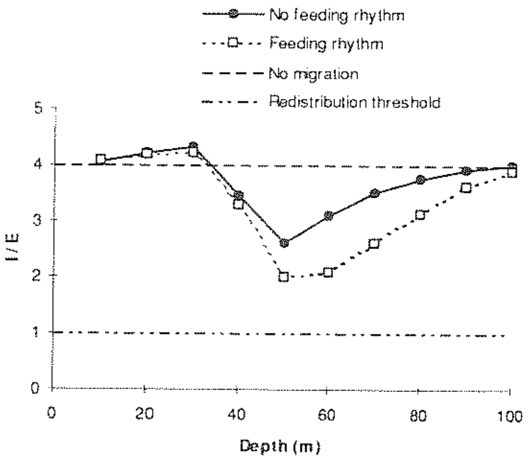


Figure 3 : The ratio of the ingestion rate to the egestion rate. The density of organic material would increase in sections of the water column if this ratio was less than 1.

Further simulations have shown that animals need to be characterised by low assimilation efficiencies, long gut passage times and fast speeds of descent if they are to significantly enhance the downward redistribution of organic material. Even if redistribution does occur the amount redistributed may be quite low when compared with the amount of material consumed in the surface waters and this is obviously going to be highly dependent on the animals assimilation efficiency.

4. CONCLUSION

The results of the model suggest that many species of zooplankton may not be effective at enhancing the amount of organic material in deep water as a result of their vertical migrations. It has been suggested by other authors that sinking of faecal pellets may be important and the fraction of material that is transported within the gut of an animal and then expelled is minimal [Dagg *et al.*, 1989; Tett *et al.*, 1993; Atkinson *et al.*, 1996]. Zooplankton faecal pellets may aggregate with other organic and inorganic detrius to form marine snow characterised by a range of sinking rates [Green and Dagg, 1997]. Physical and biological factors which influence the formation and destruction of such aggregations may play important roles in determining the amount of organic material, originating near the surface, which then becomes available at deeper depths.

The timing and regulating of both zooplankton swimming and feeding may be dependent on a number of exogenous and endogenous factors which have not been explicitly incorporated into the model. Increasing model complexity leads to difficulties when one attempts to infer the interaction between factors. However, given an understanding of the dynamics produced by the relatively simple model presented here, a number of refinements could be made and their effect on dynamics examined.

It has been assumed that swimming behaviour is independent of the state of the animals gut or the surrounding density of prey. Hypothesis on how swimming speeds may be affected by such factors could be incorporated into the model equations.

Gut passage times of copepods have been observed to increase with a decrease in temperature [Wlodarczyk *et al.*, 1992]. Introducing temperature effects into the model would allow one to investigate the possibility of redistribution being enhanced below a thermacline.

Zooplankton have been assumed to have little impact on the abundance of phytoplankton. If prey densities fluctuate as a result of predation pressure and zooplankton migrations are influenced by prey densities, then the general pattern of redistribution may differ to that predicted here. Possible interactions between the two plankton communities could be investigated by coupling the zooplankton model with a phytoplankton production model.

5. ACKNOWLEDGMENTS

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