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A pelagic ecosystem model simulating production and sedimentation of biogenic particles: role of salps and copepods

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ABSTRACT: Production and sedimentation of biogenic particles are investigated by a depth-dependent model of a Mediterranean coastal pelagic ecosystem during spring. The model considers living and dead phytoplankton (chiefly diatoms) and its sedimentation, 2 herbivores, salps and copepods, and sedimentation of their fecal pellets and carcasses; a sediment trap is assumed to be set up at 200 m depth. Results underline the major role played by fecal pellets and by both living and dead salps in vertical matter flux. Fecal pellets of salps and copepods constitute 65 % of the material in the trap after a 40 d simulation period. Although salp and copepod biomasses are similar, the magnitude and composition of the particle flux are much more influenced by salps than by copepods: salp fecal pellets and carcasses account for 72 % of the maximum overall flux. The fluxes calculated by this model are in good agreement with those generally recorded in the field: at 200 m depth, up to $72.3 \text{ mgC m}^{-2} \text{ d}^{-1}$ and a mean of $44.7 \text{ mgC m}^{-2} \text{ d}^{-1}$ over 40 d.

INTRODUCTION

During the last 15 yr, studies of the fate of large biogenic particles produced in the marine pelagic environment have revealed that large fast-sinking particles are responsible for the majority of the downward vertical mass flux in the sea. The downward flux of such particles (1) provides almost all the energetic needs of deep-sea fauna (e.g. Wiebe et al. 1979) and (2) controls the distribution and cycling of chemical elements (including radionuclides) in the water column by rapidly transporting these elements to great depths (e.g. Coale & Bruland 1985). In the open sea, most large particles are biogenic (fecal pellets, carcasses, crustacean molts, etc.) and their flux is therefore closely related to the characteristics and variations of the marine pelagic ecosystem.

Given the numerous origins of particles, modelling of the marine ecosystem is essential to appreciate the importance of each particle type in the global flux. Previous ecosystem models are based chiefly on trophic relations between phytoplankton and herbivorous zooplankton. Few models consider sedimentation, and, when they do, either only the sinking of phytoplankton is represented (e.g. Steele & Henderson 1976, Smith et al. 1983) or fecal pellet sedimentation is briefly

described (e.g. the zero-dimensional model of Moloney et al. 1986). To our knowledge, the only model including biological processes which describes the production of fecal pellets and the resulting flux is the analytical model of Hofmann et al. (1981), but this is restricted to a population of various sizes of copepods.

Therefore, our purpose is to present a pelagic ecosystem model that considers not only phytoplankton and its sedimentation, but also copepods, salps, and the faeces and carcasses derived from them. Salps and copepods are the 2 groups of abundant herbivores in the simulated ecosystem. This depth-dependent 1-dimensional model simulates the general characteristics of the 0 to 200 m layer pelagic ecosystem in the coastal waters of Villefranche-sur-Mer (Mediterranean Sea). Irradiance, temperature and eddy diffusivity drive this system. We assume that there is no nutrient input in this water column. Simulated vertical distributions of the different phyto- and zooplanktonic organisms and of the fecal pellets are presented. This model allows us to estimate the contribution of each particle type to the vertical biogenic matter flux and its qualitative and quantitative temporal variation, by assuming the deployment of a sediment trap at 200 m depth.

Salps play a very conspicuous role in our model. They are often present in dense swarms in the ecosys-

tem we are simulating. Their high filtration and defecation rates (Madin 1982, Andersen 1985), and the particularly high sinking rate of their fecal pellets (Bruland & Silver 1981, Madin 1982) confer them an essential role in supplying food to the deep-sea organisms (Wiebe et al. 1979, Iseki 1981, Matsueda et al. 1986). Salps also greatly influence cycling of chemical elements and radionuclides in the water column (Coale & Bruland 1985, Krishnaswami et al. 1985). They ingest organic and inorganic particles, even those of very small size (Harbison & McAlister 1979) and package them in fecal pellets that are rapidly transported to depth. It is also known that salp fecal pellets are enriched in many trace elements and radionuclides (Krishnaswami et al. 1985), and Coale & Bruland (1985) reported that the short residence time of particulate thorium observed at some periods on the California coast is governed by the abundance of salps.

MODEL DESCRIPTION

The model has been developed for spring (40 d; from 1 March to 9 April) during which maximum concentrations of phytoplankton and herbivores (copepods, salps) occur. Homogenous layers of 4 m thick are considered, down to 200 m, the chosen depth to set up a sediment trap.

The following state variables are taken into account (Fig. 1): (1) phytoplankton, (2) living copepods, (3) living salps, (4) dead phytoplankton, (5) fecal pellets of copepods, (6) carcasses of copepods, (7) fecal pellets of salps and (8) carcasses of salps. Two forcing variables drive the food-web: irradiance and temperature. The physical processes considered are the vertical eddy diffusivity and the sinking of the 5 types of non-living particles and of the living phytoplankton, each of these types being characterized by a different sinking rate. We assume here that phytoplankton consists almost exclusively of diatoms and that ciliates and microflagellates are of minor importance.

Model formulation

The temporal and spatial variation of each compartment is represented by a 2-order partial differential equation with 2 independent variables. This equation comprises one time-dependent rate of change of the compartment concentration in a given volume (biological process), one space-dependent rate of change due to eddy diffusivity (second-order physical process) and, for some compartments, one spatial rate of change due to sinking (first-order physical process).

Mathematical formulations representing the different biological processes (e.g. assimilation of dissolved

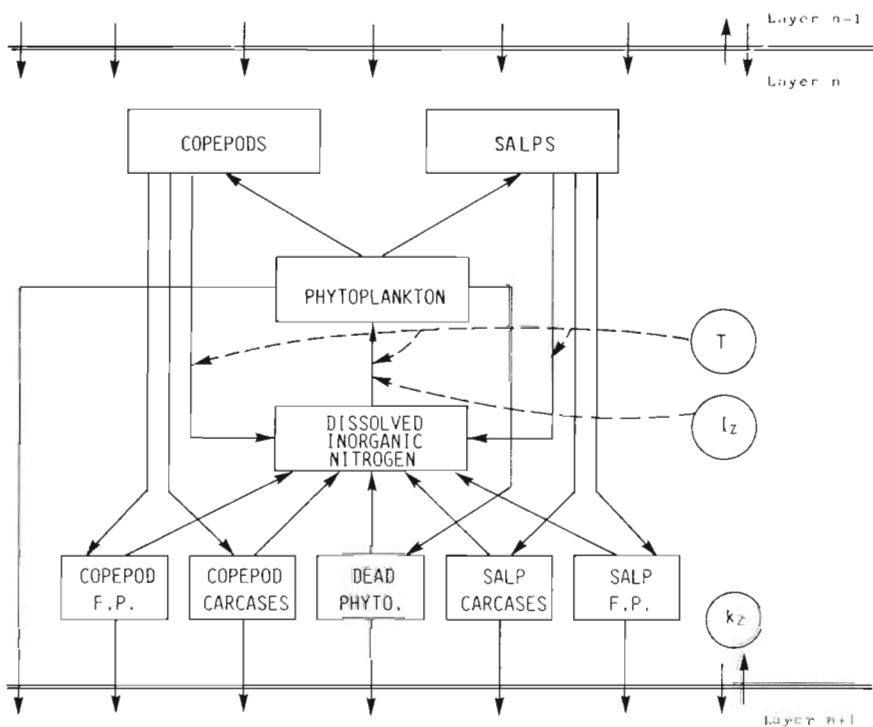


Fig. 1. Block-diagram of the model. F.P.: fecal pellets; I_z : irradiance; T : temperature; k_z : vertical eddy diffusivity

inorganic nitrogen by phytoplankton, mortality and feeding of zooplankton) are those usually used in similar ecosystem models. Their appropriateness and their underlying assumptions are discussed in Andersen et al. (1987) and Andersen & Nival (1988). The regeneration rate of the different particles is assumed to be constant in the water column. We assume that no decomposition takes place once particles entered the trap, as if the trap is filled with a fixing solution. The model parameters, the mathematical formulations of the biological processes and the differential equation system are listed in Tables 1, 2 and 3 respectively.

Our model is not intended to simulate the diel cycles of variables and therefore does not take into account zooplankton vertical migration and diel changes in irradiance. The time-courses of temperature and irradiance are taken from Andersen & Nival (1988) in which adjustment of the curves to field measurements were worked out. For each 24 h period and each 4 m layer the mean irradiance at depth z , I_z (ly d^{-1}), is calculated as follows:

$$I_z = \frac{1}{z_2 - z_1} I_0 \int_{z_1}^{z_2} e^{-\alpha z} dz \quad (1)$$

Table 1 Variables and parameters used in the model. Subscripts p , c and s mean respectively phytoplankton, copepods and salps. Subscripts 1, 2, 3, 4 and 5 mean respectively dead phytoplankton, dead copepods, dead salps, copepod fecal pellets and salp fecal pellets

Parameter	Definition	Unit
Variables		
N	Dissolved inorganic nitrogen	$\mu\text{g-at N l}^{-1}$
P	Phytoplankton	$\mu\text{g-at N l}^{-1}$
C	Copepods	$\mu\text{g-at N l}^{-1}$
S	Salps	$\mu\text{g-at N l}^{-1}$
M_1, M_2, M_3	Dead organisms	$\mu\text{g-at N l}^{-1}$
M_4, M_5	Fecal pellets	$\mu\text{g-at N l}^{-1}$
I_z	Irradiance at depth z	ly d^{-1}
T	Temperature	$^{\circ}\text{C}$
Phytoplankton parameters		
μ_m	Maximum growth rate	d^{-1}
k_N	Half-saturation constant for dissolved inorganic nitrogen	$\mu\text{g-at N l}^{-1}$
I_s	Optimal irradiance	ly d^{-1}
β_I	Shape factor for the photoinhibition curve	-
T_s	Optimal temperature	$^{\circ}\text{C}$
T_e	Lower lethal temperature	$^{\circ}\text{C}$
β_T	Shape factor for the thermoinhibition curve	-
Zooplankton parameters		
a_c, a_s	Assimilation coefficients	-
i_m	Maximum ingestion rate for copepods	d^{-1}
k	Ivlev's coefficient for copepods	$\text{l} (\mu\text{g-at N})^{-1}$
P_o	Threshold concentration for feeding of copepods	$\mu\text{g-at N l}^{-1}$
f	Filtration rate of salps	$\text{l} (\mu\text{g-at N})^{-1} \text{d}^{-1}$
b_c, b_s	Excretion rate at 0°C	d^{-1}
δ_c, δ_s	Shape factor for the excretion curve	-
Mortality and regeneration parameters		
m_{mp}, m_{mc}, m_{ms}	Maximum mortality rates	d^{-1}
m_{op}, m_{oc}, m_{os}	Minimum mortality rates	d^{-1}
N_p, P_c, P_s	Thresholds of the mortality curve	$\mu\text{g-at N l}^{-1}$
Φ_p, Φ_c, Φ_s	Shape factors for the mortality curve	$\mu\text{g-at N l}^{-1} \text{d}^{-1}$
r_1, r_2, r_3, r_4, r_5	Regeneration rates	d^{-1}
Vertical parameters		
k_z	Vertical eddy diffusivity at depth z	$\text{m}^2 \text{d}^{-1}$
w_p	Living phytoplankton sinking rate	m d^{-1}
w_1, w_2, w_3	Dead organism sinking rates	m d^{-1}
w_4, w_5	Fecal pellet sinking rates	m d^{-1}
α	Vertical attenuation exponent	m^{-1}

Table 2. Biological processes used in the model

Process	Model
Phytoplankton growth	
μ Growth rate of phytoplankton	$\mu = \mu_m I_N I_I I_T$
I_N Limitation of growth by dissolved inorganic nitrogen	$I_N = \frac{N}{k_N + N}$
I_I Limitation by irradiance	$I_I = 2(1 + \beta_I) \frac{x_I}{x_I^2 + 2\beta_I x_I + 1}$ where $x_I = I_z/I_s$
I_T Limitation by temperature	$I_T = 2(1 + \beta_T) \frac{x_T}{x_T^2 + 2\beta_T x_T + 1}$ where $x_T = \frac{T - T_e}{T_s - T_e}$
Zooplankton consumption	
i_c Ingestion rate of copepods	$i_c = i_m (1 - e^{-k(P-P_d)})$
i_s Ingestion rate of salps	$i_s = f P$
Zooplankton excretion	
e_c, e_s Excretion rate of copepods and salps	$e_c = b_c \delta_c^T$
Phyto- and zooplankton mortality	
m_p, m_c, m_s Mortality rate of phytoplankton, copepods and salps	if $N \leq N_p$ then $m_p = m_{mp}$ if $N > N_p$ then $m_p = \Phi_p/N + m_{op}$

Table 3. System of differential equations

$\frac{\partial P}{\partial t} = (\mu - m_p) P - i_c C - i_s S - w_p \frac{\partial P}{\partial z} + k_z \frac{\partial^2 P}{\partial z^2}$
$\frac{\partial C}{\partial t} = (a_c i_c - m_c - e_c) C + k_z \frac{\partial^2 C}{\partial z^2}$
$\frac{\partial S}{\partial t} = (a_s i_s - m_s - e_s) S + k_z \frac{\partial^2 S}{\partial z^2}$
$\frac{\partial N}{\partial t} = r_1 M_1 + r_2 M_2 + r_3 M_3 + r_4 M_4 + r_5 M_5 + e_c C + e_s S - \mu P + k_z \frac{\partial^2 N}{\partial z^2}$
$\frac{\partial M_1}{\partial t} = m_p P - r_1 M_1 - w_1 \frac{\partial M_1}{\partial z} + k_z \frac{\partial^2 M_1}{\partial z^2}$
$\frac{\partial M_2}{\partial t} = m_c C - r_2 M_2 - w_2 \frac{\partial M_2}{\partial z} + k_z \frac{\partial^2 M_2}{\partial z^2}$
$\frac{\partial M_3}{\partial t} = m_s S - r_3 M_3 - w_3 \frac{\partial M_3}{\partial z} + k_z \frac{\partial^2 M_3}{\partial z^2}$
$\frac{\partial M_4}{\partial t} = (1 - a_c) i_c C - r_4 M_4 - w_4 \frac{\partial M_4}{\partial z} + k_z \frac{\partial^2 M_4}{\partial z^2}$
$\frac{\partial M_5}{\partial t} = (1 - a_s) i_s S - r_5 M_5 - w_5 \frac{\partial M_5}{\partial z} + k_z \frac{\partial^2 M_5}{\partial z^2}$

where z_1 and z_2 = respectively the upper and the lower limits of the layer; I_0 = incident irradiance; α = vertical attenuation exponent, for which a value of 0.066 m^{-1} was adopted (Béthoux 1968).

Sinking rates of the particles are assumed to be independent of depth. According to the measurements

of σ_t of Braconnot et al. (1966), the eddy diffusivity coefficient is considered increasing with depth but independent of time during the period covered. From these data, the eddy diffusivity coefficient, k_z ($\text{m}^2 \text{ d}^{-1}$) was calculated using the empirical formulation given by Coste (1971):

$$k_z = \frac{0.096}{d\sigma_t/dz} \quad (2)$$

where $d\sigma_t/dz$ = density gradient (m^{-1}). The values of k_z used in the model are given in Table 4.

Table 4. Numerical values for model variables and parameters

Vertical eddy diffusivity					
k_z	4.8 (0–12 m)	5.3 (12–20 m)	8.7 (20–32 m)		
	32.0 (32–76 m)	73.8 (76–100 m)	68.6 (100–200 m)		
Initial concentrations of state variables					
P	0.35 (0–20 m)	0.02 (20–80 m)	0 (80–200 m)		
C	0.12 (0–80 m)	0 (80–200 m)			
S	0.06 (0–80 m)	0 (80–200 m)			
N	1 (0–16 m)	5 (16–36 m)	7 (36–200 m)		
M_1, M_2, M_3, M_4, M_5	0 (0–200)				
Parameters					
μ_m	2.16	a_c, a_s	0.70	0.55	
k_N	1	i_m	0.96		
I_s	200	k	0.33		
β_l	-0.6	P_o	0.05		
T_s	15.5	f	0.50		
T_e	11.0	b_c, b_s	0.067	0.074	
β_T	-0.8	δ_c, δ_s	1.025	1.050	
m_{mp}, m_{mc}, m_{ms}	0.067	0.045	0.103		
m_{op}, m_{oc}, m_{os}	0.03	0.03	0.04		
N_p, P_c, P_s	0.31	1.6	0.7		
Φ_p, Φ_c, Φ_s	0.012	0.024	0.045		
r_1, r_2, r_3, r_4, r_5	0.10	0.10	0.10	0.08	0.08
w_1, w_2, w_3, w_4, w_5	1.5	120	60	70	900
w_p	0.35				

Numerical integration and boundary conditions

The time rate of change of concentrations in a given volume is calculated by the Runge-Kutta fourth-order method with a constant time step. Depth-dependent rates are calculated by the finite difference method, largely described by Steele & Henderson (1976) for their model. The stability conditions for this scheme, $dt \leq dz/w$ and $dt \leq dz^2/4k_z$, where dt = the time step, dz = space step, w = the maximum sinking rate and k_z = the maximum eddy diffusivity coefficient, are conserved, given the values of the model parameters, with $dz = 4$ m and $dt = 2.5$ min.

The equations used here require 2 types of boundary conditions. First the vertical distribution of the state variables is given at an initial time, $t = 0$ (cf. Table 4). Boundary conditions at the surface and at the bottom must also be defined. There is no sinking or mixing across the upper boundary; at the bottom there is no mixing but material sinks into and accumulates in the sediment trap.

Estimation of model parameters

This model aims to reproduce the general characteristics of spring changes in major planktonic groups in the coastal waters of Villefranche. As reference data we used the mean values of organism concentrations found in this area. Copepods generally reach their maximum biomass between mid-March and the beginning of May, with values of 0.15 to 0.75 $\mu\text{g-at N l}^{-1}$ in the 0 to 75 m layer (years 1967 to 1971; Dallot pers. comm.). Measurements of salp biomass by trawling a net between 3 and 10 m depth in 1960 and 1963 to 1966 (Braconnot 1971) show that maximum salp abundance occurs between end of March and end of May with a biomass of 0.024 to 0.054 $\mu\text{g-at N l}^{-1}$. In the case of phytoplankton, Nival (1976) found in 1969 a concentration of 0.52 $\mu\text{g-at N l}^{-1}$ in the 0 to 75 m layer and during cruise 'Mediproduct I' the concentration varied between 0.13 and 1.32 $\mu\text{g-at N l}^{-1}$ in the 0 to 75 m layer (Jacques et al. 1973). Collection of these data and estimation of the conversion factors used to convert plankton concentrations into a single unit of nitrogen have been already discussed elsewhere (Andersen & Nival 1988). In the case of nutrients, nitrate measurements taken during the same period in the northwestern Mediterranean sea (Coste et al. 1972) were used as reference data.

The coefficient values used in the model's biological processes are in the ranges found in the literature, and are those which provide a satisfactory simulation of the mean organism concentration in this area at this period (Table 4). Since our principal concern is to estimate the flux of matter generated by this system, we shall discuss only the values of coefficients related to production and flux of biogenic particles. First, we point out the difference between copepods and salps in the assimilation rate of the food ingested. Copepods assimilate food with a mean efficiency of 70 % (Conover 1966, Corner et al. 1967, Pagano 1980), a value higher than the 55 % efficiency of salps (Andersen 1986).

Salp fecal pellets appear as rectangular flakes, sometimes attached end to end, while copepod fecal pellets are relatively cylindrical. Copepod fecal pellets are also relatively small, with volumes 10^3 to 10^4 less than those of salp fecal pellets. From literature measurements (Table 5), we assumed sinking speeds of 900 m d^{-1} and 70 m d^{-1} for salp and copepod faeces respectively. Sinking rates of zooplankton carcasses have been little studied. As euphausiid carcasses settle faster than fecal pellets produced by these crustaceans (Small & Fowler 1973), we chose a sinking speed of 120 m d^{-1} for copepod carcasses. Concerning salp carcasses, we assumed that this gelatinous material sinks at lower rate than copepod carcasses, and at a rate similar to that

Table 5. Sinking rates of different particle types. Average sinking rates are in brackets or designed by an asterisk

Particle types	Sinking rate (m d ⁻¹)	Source
Salp fecal pellets		
2 different species	450–1210 (836)	Bruland & Silver 1981
	600–2700 (1680)	
3 different species	320–1987 (1060)	Madin 1982
Copepod fecal pellets		
<i>Acartia tonsa</i>	80–150	Honjo & Roman 1978
<i>Calanus finmarchicus</i>	180–220	
Different species		Paffenhöfer & Knowles 1979
various ages	10–145	
adults	54–145	
Different species		Small et al. 1979
various ages	19.5–100.7	
adults	12–225	
<i>Calanus</i> sp.		Bienfang 1980a
on diatom diet	70–171 (123.3)	
on flagellate diet	51–152 (87.9)	
Larvacean houses		
<i>Oikopleura dioica</i>	64.9* at 5°C	Silver & Alldredge 1981
	57.0* at 16°C	
<i>Oikopleura dioica</i>	26–157 (4–25°C)	Gorsky et al. 1984
Diatom cells		
Different species	0.10–2.10*	Smayda & Boleyn 1965, 1966a, b
Freshwater diatoms		Titman & Kilham 1976
exponential phase	0.08–0.67*	
stationary phase	0.24–1.87*	
<i>Fragilaria crotonensis</i>	0.27*	Burns & Rosa 1980
Natural community		Bienfang 1980b
3–20 µm	0.34–0.83*	
20–102 µm	0.95–1.65*	
Natural community	0.32–1.69 (0.64)	Bienfang 1981
Natural community	0.21*	Smayda & Bienfang 1983

of larvacean houses (cf. Table 5). Sinking rates of diatoms are very low compared with those of faeces and carcasses (cf. Table 5). Increasing sedimentation rate with nutrient impoverishment of the milieu has been suggested by some authors (Titman & Kilham 1976, Harrison & Turpin 1982) but, as this phenomenon does not seem a general rule (Bienfang 1981), the sinking rate in the model was taken as constant.

Some laboratory studies have shown that at high temperatures, between 20 and 25 °C, fecal pellets are degraded in periods of several hours to several days (Honjo & Roman 1978, Paffenhöfer & Knowles 1979, Turner 1979). Pomeroy & Deibel (1980) suggest that residence time of doliolid pellets in the water column might be only 5 d, based on decomposition rates at 15 to 20 °C, although at 5 °C degradation is always weak and slow (Honjo & Roman 1978, Turner 1979). Decomposition of fecal pellets of a gastropod would require 78 d at 19 °C (Peduzzi & Herndl 1986), copepod fecal pellets at 18 °C would require 50 d (Jacobsen & Azam

1984). Sediment trap studies suggest that decomposition of large particles, due to bacteria and protozoa, is slow in the water column (Ducklow et al. 1985). Given the absence of consistent values in the literature, we chose therefore decomposition rates of 0.08 to 0.10 d⁻¹, similar to those used in other ecosystem models (0.5 d⁻¹ in O'Brien & Wroblewski 1973, 0.1 d⁻¹ in Vinogradov et al. 1973). Carcasses are degraded faster than the fecal pellets produced by the same organisms: over 60 h, the sinking speed of euphausiid carcasses decreases from 4000 to 2400 m d⁻¹, reflecting an important and rapid decomposition, while the sinking speed of the fecal pellets remains constant (Small & Fowler 1973). Harding (1973) reported that killed copepods decomposed within 11 d at 4 °C and within 3 d at 22 °C, periods which appear shorter than those reported for the decomposition of copepod fecal pellets. Because of these results, a slightly higher regeneration rate for carcasses (0.10 d⁻¹) than for fecal pellets (0.08 d⁻¹) has been assumed.

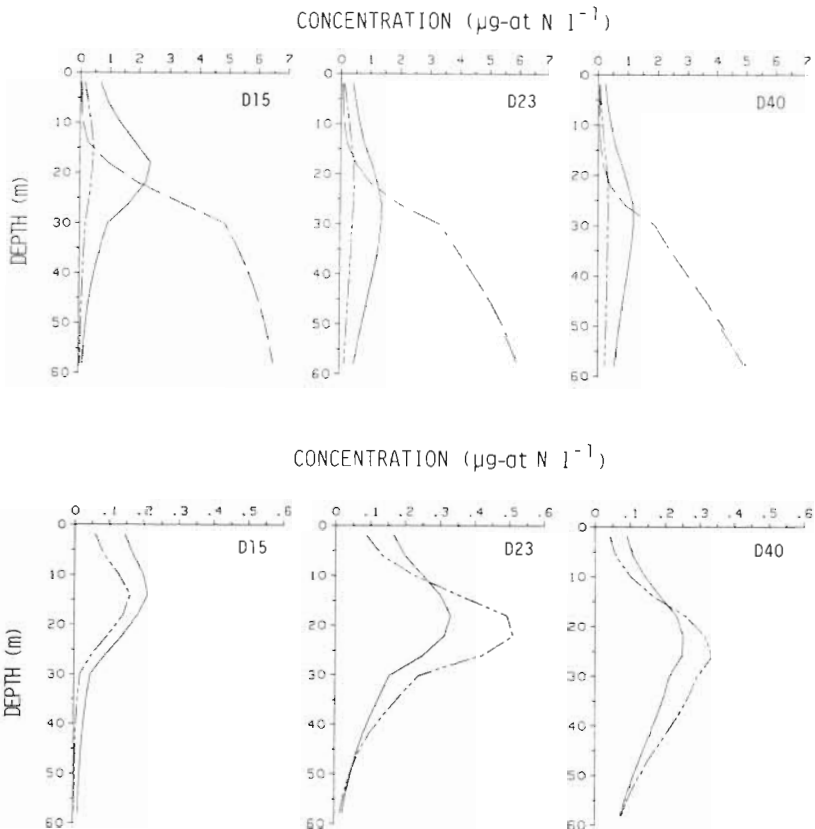


Fig. 2. Simulated vertical distribution on 3 dates (Days 15, 23 and 40). Above: (—) living phytoplankton; (---) dead phytoplankton; (-.-) dissolved inorganic nitrogen. Below: (—) copepods; (---) salps

RESULTS

Fig. 2 shows the simulated vertical distributions in the 0 to 60 m layer (concentrations being nearly constant below) of live and dead phytoplankton, dissolved inorganic nitrogen, and copepods and salps, for 3 selected dates in the simulation: Day 15, the phytoplankton maximum; Day 23, the herbivore maximum; and Day 40, the end of the simulation. The set of model parameters used and the model structure allow reproduction of the general temporal variation of the variables for the studied area. The phytoplankton bloom is at a maximum on Day 15 (15 March in the model) with a concentration of $2.37 \mu\text{g-at N l}^{-1}$ in the 16 to 20 m layer, and a mean concentration of $0.78 \mu\text{g-at N l}^{-1}$ in the 0 to 76 m layer, a value in the range of the reference data given above. The vertical profile of dead phytoplankton nearly follows that of living phytoplankton. Dissolved inorganic nitrogen distribution is typical: exhausted in surface waters, higher in deeper waters, with a clear nitricline; concentrations are similar to those measured offshore Villefranche by Coste et al. (1972). On Day 15 copepod biomass is slightly higher than salp biomass; thereafter, salps become clearly more abundant than copepods. For both kinds of zooplankton, maximum concentrations occur nearly simul-

taneously (Day 22 for copepods, Day 23 for salps). Thereafter, the difference in biomass between salps and copepods diminishes. In the 0 to 200 m layer salp biomass was $0.061 \mu\text{g-at N l}^{-1}$ on Day 23 ($0.068 \mu\text{g-at N l}^{-1}$ on Day 27). Maximal concentrations observed in situ varied from 0.024 to $0.054 \mu\text{g-at N l}^{-1}$. These values have been measured between 3 and 10 m depth; in our model salp concentrations at these depths are higher, but net tows taken in daytime certainly underestimate salp biomass. In fact, *Salpa fusiformis*, the predominant salp species in the plankton of Villefranche during spring, appears to undergo vertical migration, being rather at depth during day (Franqueville 1971, Harbison & Campenot 1979, Bruland & Silver 1981). Copepod concentration in the 0 to 76 m layer ($0.126 \mu\text{g-at N l}^{-1}$ on Day 22, $0.139 \mu\text{g-at N l}^{-1}$ on Day 29) appears a little low compared with reference data.

We shall now consider the vertical profiles themselves. During the simulation the phytoplankton maximum occurs between 16 and 20 m. This can be related to 2 factors: first, as phytoplankton growth is limited in the upper layers where nutrients are exhausted, phytoplankton develops at levels where nutrients are still abundant although irradiance is not optimal; and, second, sinking of phytoplankton transports it to deeper layers. The effects of sinking appear clearly on the

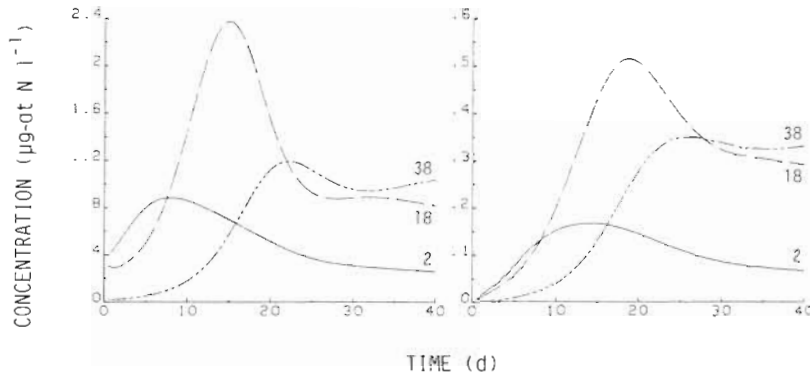


Fig. 3. Simulated temporal variation of living phytoplankton (*left*) and dead phytoplankton (*right*) at 3 depths (2, 18 and 38 m)

curves: on Day 15 the peak occurs in the 16 to 20 m layer, on Day 23 in the 24 to 28 m layer.

Maximum concentrations of copepods and salps develop where phytoplankton is most abundant: in the 16 to 20 m layer for copepods, in the 20 to 24 m layer for salps. Below 50 m herbivores are nearly absent, as a result of 2 assumptions made in the model: first copepods and salps are considered as strict herbivores and ingest neither dead phytoplankton nor faeces, and, second, the vertical migration which these organisms can undergo is not taken into account.

Effects of sinking of living and dead phytoplankton are clearly illustrated by comparing the temporal variation of these variables at different depths (Fig. 3). As depth increases, the temporal maximum is delayed for all variables under consideration: at depths 2, 18 and 38 m, the peak appears, for living phytoplankton, on Days 8, 15 and 22 respectively; for dead phytoplankton, on Days 14, 19 and 26 respectively.

The simulated vertical profiles of copepod and salp fecal pellets in the 0 to 200 m water column are presented in Fig. 4. As a consequence of high sinking rates of fecal pellets, these profiles are very different from

those of the organisms that produced the pellets: no very pronounced maximum can be observed, with fecal pellets reaching the bottom very rapidly as soon as they are produced. In surface layers, fecal pellets are sparse due to their sinking speed and to low concentrations of copepods and salps. The just-discernible maximum concentration in the water column becomes deeper with time. Below the maximum, concentration of copepod fecal pellets decreases linearly, while it remains constant for salp fecal pellets, showing a very fast enrichment of the deep layers. Moreover, nitrogen concentrations of salp fecal pellets in this water column are about 5 to 10 times lower than those of copepod fecal pellets although copepod and salp concentrations are of the same order of magnitude.

The importance of fecal pellets as a means of transporting energy to deep-sea organisms is clearly brought out by this model. While salps and copepods are nearly absent below 60 m in the model, fecal pellets are abundant there. Vertical distributions of copepods and salps carcasses (sinking rates of 120 and 60 m d⁻¹ respectively) look like those of copepod fecal pellets. The temporal peak of copepod fecal pellets is delayed with increasing depth (Fig. 5). At 18 m, where herbivore biomass is maximal, feces concentration is low, as a consequence of the few fecal pellets coming from the upper layers. For salp feces, no marked difference is observed between 58 and 178 m, due to their very high sinking rate.

Composition of the particulate organic matter which accumulated over the 40 d simulation in the sediment trap assumed to be set up at 200 m depth is presented in Fig. 6. The relative contribution of nitrogen by each particle type to the total particulate nitrogen in the trap is expressed as a percentage. We mention again that we have assumed that no decomposition took place once particles entered the trap. Phytoplankton cells are not included because they account for only 0.07 % of the total nitrogen mass (0.02 and 0.05 % for living and dead phytoplankton respectively). Salp fecal pellets constitute the major part of the material, although salp

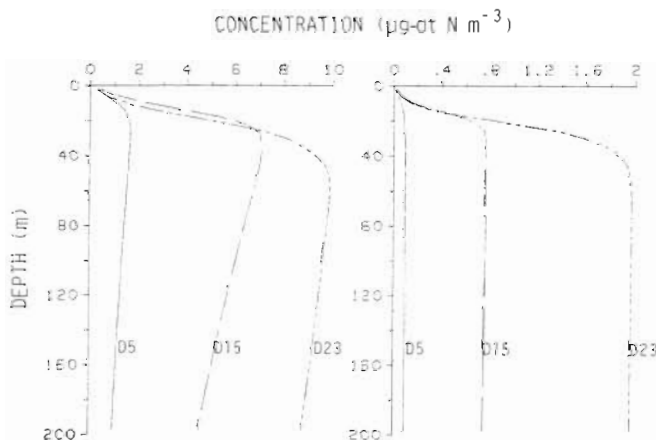


Fig. 4. Simulated vertical distribution of fecal pellets of copepods (*left*) and salps (*right*) on 3 dates (Days 5, 15 and 23)

Fig. 5. Simulated temporal variation of fecal pellets of copepods (left) and salps (right) at 4 depths: (—) 18 m; (— · —) 58 m; (---) 118 m; (----) 178 m

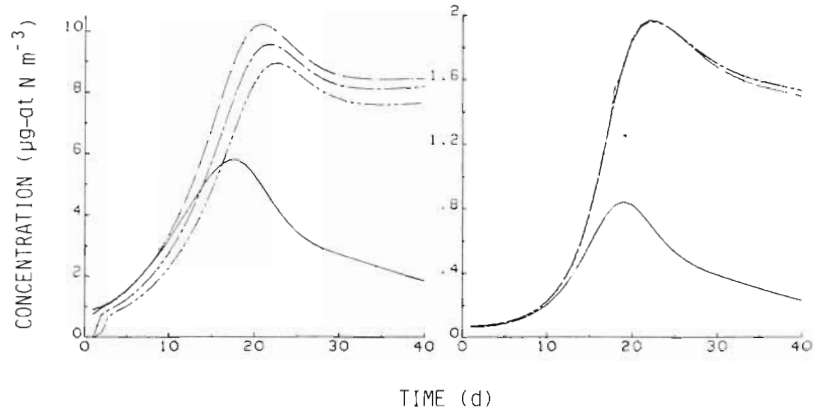


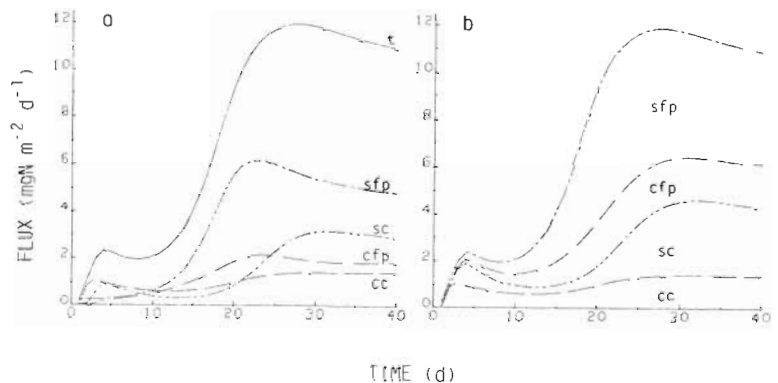
Fig. 6. Composition of particulate organic matter in the 200 m trap after 40 d of simulation. For each particle type, percentage of nitrogen mass of total nitrogen in the trap is calculated. f.p.: fecal pellets

and copepod biomasses are similar. This results chiefly from 2 factors: first, a very high sinking rate of salp fecal pellets; and, second, a lower assimilation rate of food ingested in salps than in copepods (cf. Table 4). The percentage of salp carcasses is higher than that of

copepod carcasses although the latter have a higher sinking rate than the former. This apparent contradiction is explained by the slightly higher biomass and death rate of salps in comparison to copepods (cf. Table 4). Of the total organic matter in the trap, 68.4 % originates from salps, so salps certainly play a predominant role in the transport of matter to the deepsea. Fecal pellets of both salps and copepods account for the major part of the matter in the trap (64.9 %).

The time-courses of the daily total matter flux and of the daily flux specific to each particle type are presented in Fig. 7. Again the important contribution of fecal pellets appears: the curve of the total flux follows, by shape and magnitude, the curve of the salp fecal pellet flux (Fig. 7a). Maximum flux occurs on Day 28 with a contribution of 72.1 % of salp feces and carcasses. Herbivore fecal pellet fluxes reach a maximum on Day 23, while fluxes via carcasses are at a maximum on Days 31 to 33. Changes with time in the composition of the flux can be clearly seen by this type of model (Fig. 7b). The contribution of fecal pellet to total flux is maximum on Day 19 (81.2 %) when phytoplankton is abundant, decreasing at the end of the simulation when phytoplankton concentration is lower and herbivore mortality higher.

Fig. 7. Variation of particle fluxes during the 40 d of simulation. (a) Flux. (b) Cumulative flux – a given flux is represented by the height between 2 adjacent curves. cc: copepod carcasses; cfp: copepod fecal pellets; sc: salp carcasses; sfp: salp fecal pellets; t: total



DISCUSSION

We saw in the model that herbivore fecal pellets accounted for 64.9 % of the accumulated matter in the sediment trap after the 40 d simulation period, and yet at one point in time (Days 18 and 19) they represented up to 81.2 % of the total flux. These results are similar to those observed in the field from sediment traps which showed that fecal pellets of zooplanktonic organisms, and particularly those of salps, contributed highly to the matter flux and often accounted for a large part of the matter in the trap. Iseki (1981) found a predominance of salp fecal pellets in a 200 m trap, as did Matsueda et al. (1986) in a 740 m trap; during the cruise 'CEROP I', salp fecal pellets accounted for 90 % of the matter collected in traps at 58 and 580 m (Coale & Bruland 1985). Contributions of fecal pellets to the flux, and producing organisms, vary according to the area and to the period. Fowler & Knauer (1986) report unpublished data of Knauer & Martin who observed in one of the VERTEX experiments that up to 40 % of the C flux could be accounted for by large pellets produced by the pelagic crab *Pleuoncodes planipes*. In the northwest Mediterranean Sea, in an area similar to that taken as reference in our model, about 70 % of the total dry weight in a 200 m trap was due to copepod fecal pellets early in May 1986 (Fowler et al. 1987); it should be noted that 1986 in this region was exceptional due to the lack of a salp bloom in spring. Numerous studies illustrating the importance of fecal pellets in the vertical matter flux are available and we shall mention only 2 more: Small et al. (1983) reported that 41 % of the total C flux into a 120 m trap could have been via fecal pellets from small and large zooplankton (including salps) and Bishop et al. (1977) showed that fecal material accounted for 99 % of the vertical flux through 388 m.

In our model, at the opposite extreme from fecal pellets and carcasses, living phytoplankton accounted for only 0.02 % of the total nitrogen in the trap after a 40 d simulation. Sinking of intact algae out of this 0 to 200 m water column therefore appears to be of minor importance. Lorenzen et al. (1983) reached similar conclusions for waters south of the Hawaiian Islands: at 100 and 400 m the daily flux of chlorophyll represented only 0.8 and 0.08 % of the integrated standing crop of chlorophyll above these depths.

Flux values from the literature and from our model are collected in Table 6. One must keep in mind some limitations when examining these values: the flux values have been determined in various areas and at different periods, and we used several conversion coefficients to obtain a given unit of flux. According to literature data, we assumed a C/N ratio (by atoms) of 7 for salp fecal pellets (Bruland & Silver 1981, Madin

1982, Small et al. 1983), of 6.5 for copepod fecal pellets (Small et al. 1983), and of 4.5 for copepod and salp carcasses (Boucher et al. 1976, Madin et al. 1981, Small et al. 1983, Ikeda & Bruce 1986). Carbon is taken as 28 % of dry weight in feces (Madin 1982, Small et al. 1983) and as 40 % in herbivore carcasses (e.g. Small et al. 1983). Flux values given by our model are comparable to those reported in the literature. Fluxes of salp fecal pellets (maximum $43.2 \text{ mgC m}^{-2} \text{ d}^{-1}$, mean $24.5 \text{ mgC m}^{-2} \text{ d}^{-1}$ over the 40 d simulation) are of the same order of magnitude as those observed by Iseki (1981) and Matsueda et al. (1986) (10.5 and $23 \text{ mgC m}^{-2} \text{ d}^{-1}$ respectively). Flux estimates of Wiebe et al. (1979) are not based on sediment trap results but on data on salp biomass in the 0 to 100 m layer and on defecation and death rates. This calculation allows a relatively complete comparison between the results of Wiebe et al. (1979) and those of the present model. In the 2 cases, salp biomass in the 0 to 100 m layer is much the same: $0.144 \text{ } \mu\text{g-at N l}^{-1}$ for *Salpa aspera* in Wiebe et al. and a maximum of $0.136 \text{ } \mu\text{g-at N l}^{-1}$ for *Salpa fusiformis* in the model. Moreover, values of the fluxes via carcasses and fecal pellets are of the same order of magnitude: $3.6 \text{ mgC m}^{-2} \text{ d}^{-1}$ for *S. aspera* carcasses (the only published estimate of salp carcass flux to our knowledge), and $14.4 \text{ mgC m}^{-2} \text{ d}^{-1}$ at the maximum for *S. fusiformis* carcasses; simulated fecal pellet flux reaches a maximum of $43.2 \text{ mgC m}^{-2} \text{ d}^{-1}$, within the range of the data of Wiebe et al. (8.5 to $137 \text{ mgC m}^{-2} \text{ d}^{-1}$). Simulated copepod fecal pellet flux is about 3 times lower than that of salp feces, and is comparable to the lower limit of the value range observed by Fowler et al. (1987) in an area similar to that taken as reference in the present study. The model does not simulate the higher flux observed by these authors and this could be related to 2 factors: the simulated copepod concentrations were lower than the in situ ones, and our simulated conditions included competition with salps which was absent during the Fowler et al. study. The fluxes calculated from the copepod population dynamics model of Hofmann et al. (1981) appear comparatively very low. The general agreement of total fecal pellet flux in our simulation with data of Bishop et al. (1977) as well as comparison of the total flux with data of Karl & Knauer (1984) and Knauer et al. (1984) emphasizes the agreement between fluxes calculated by the model and observed ones in the field.

This simple ecosystem model reflects the conspicuous role of salps in the vertical flux and cycling of matter, a role previously recognized in situ (Coale & Bruland 1985, Krishnaswami et al. 1985). Although the model generated satisfactory values of particulate flux, it is somewhat simplistic and includes some hypotheses which could perhaps be improved. The food web considered here is very simple and it would be probably

Table 6. Comparison of flux values cited in the literature and those found in the model

Depth of trap (m)	Flux (mgC m ⁻² d ⁻¹)	Composition of particulate matter	Source
100	3.6	Salp carcasses	Wiebe et al. 1979 ^a
	8.5 to 137	Salp fecal material	
200	10.5	Salp fecal pellets	Iseki 1981
740	23	Salp fecal pellets	Matsueda et al. 1986
35	0.5 to 1.0	Copepod fecal pellets	Hofmann et al. 1981 ^a
200	10.5 to 41.8	Copepod fecal pellets	Fowler et al. 1987 ^b
400	0.6	Fecal pellets	Bishop et al. 1977
	30.2	Fecal material	
100	45 to 70	Various	Karl & Knauer 1984 ^c
100	31.5 to 49.0	Various	Knauer et al. 1984 ^c
100	38.3 to 59.5		
125	27.9 to 43.4		
125	40.5 to 63.0		
150	22.5 to 35.0		
	Max. Mean		
200	43.2 24.5	Salp fecal pellets	Present model results ^d
	13.9 8.5	Copepod fecal pellets	
	57.2 33.0	Total fecal pellets	
	14.4 7.1	Salp carcasses	
	6.3 4.6	Copepod carcasses	
	72.3 44.7	Total flux	

^a Flux has not been calculated from a sediment trap (see text for details)

^b Copepod fecal pellets represented 70 % of the total dry weight in the trap during the 8–15 May period. We assume that this percentage is also true for other fluxes

^c First value is calculated by assuming C/N = 4.5, the second with C/N = 7

^d Max. is the maximum of the flux, mean has been calculated for the 40 d simulation period

necessary to take into account some other planktonic organism types which can be important (appendicularians for example). Even so, as a first step, some processes represented in the present structure of the model would have to be modified. The main process to consider would be, in our opinion, the ingestion of dead phytoplankton and feces by copepods and salps. Various studies reported that copepods feed not only on living organisms, but also on dead phytoplankton and on fecal pellets produced by the same copepod species, and this at about the same rates as for a live phytoplankton diet (Paffenhöfer & Strickland 1970, Paffenhöfer & Knowles 1979). To our knowledge, no such laboratory study has been done for salps, but there is no reason to exclude the possibility of the same phenomenon. In the model, salps and copepods are very sparse below 50 m; ingestion of non-living matter would contribute to reproducing their non-negligible concentrations observed in deeper waters in the field.

In the present work, sinking rate of non-living particles has been taken as independent of time and depth. However, Smayda & Boleyn (1965, 1966a, b) have observed increasing sinking rate with culture age in

several algal species, and Lännergren (1979) noticed higher settling rates in situ during the post-bloom period when cells are senescent. Bienfang (1980b) observed a variation of phytoplankton sinking rate with depth: it was significantly lower at 71 m than at 24 and 400 m. Various processes can also influence sedimentation of fecal pellets. For example, their degradation during descent or their adherence to gelatinous aggregates, such as salp carcasses or appendicularian houses (Silver & Alldredge 1981), slow their fall. On the other hand, vertical migration of zooplankton can accelerate the downward matter transport by production of fecal pellets at depth during the day. Because numerous copepods and several salp species undergo conspicuous diel vertical migrations, it would therefore be necessary to take this into account in further studies.

Flux of biogenic particles in the water column can be estimated by 3 methods: (1) from sediment traps or pumps, (2) from measurements of the zooplankton composition and abundance, particle production rates and sinking rates, (3) from a model of the pelagic ecosystem. The first method integrates flux over rather long periods and provides only little information on the

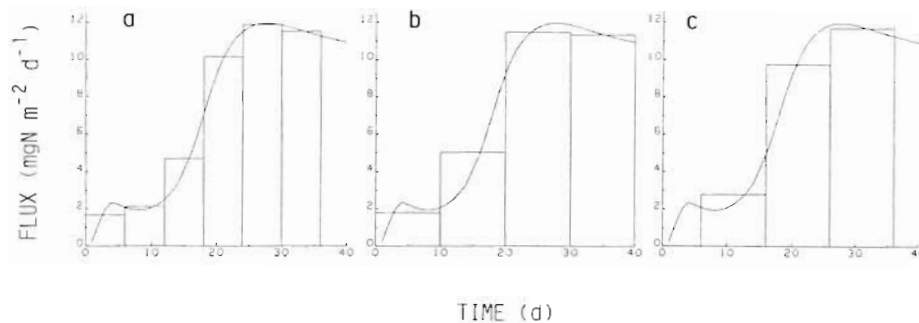


Fig. 8. Comparison of daily flux values with flux values calculated with different time-steps. (a) $dt = 6$ d; (b) $dt = 10$ d; (c) $dt = 10$ d, beginning on Day 6

flux changes as a function of the variation of the composition or abundance of the zooplankton populations. As an illustration we can compare the daily fluxes and the fluxes calculated from the matter in the trap after different time-steps (Fig. 8). When the time-step increases, daily fluxes and integrated fluxes become more different (under- or overestimation of 3.1 and 4.2 $\text{mgN m}^{-2} \text{d}^{-1}$ at a maximum with time-steps of 6 and 10 d respectively) and this discrepancy increases again when the trap is assumed to be set up after the fifth day of simulation (maximum difference of 4.8 $\text{mgN m}^{-2} \text{d}^{-1}$). The flux estimates from measurement of the in situ zooplankton biomasses are generally intermittent, due to the technical difficulties in making such measurements at frequent intervals over long periods. An adequate modelling of this flux based on a set of measured biomasses allows one to follow continuously the qualitative and quantitative variation of the flux. We think that these 3 methods are interdependent. The comparison of model results with trap measurements can help elucidate the workings of the trophic web and may permit the testing of hypotheses. Thus, modelling of the marine pelagic ecosystem complements studies in the field.

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